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VOLUME 17

*Edited by*

J. H. S. BLAXTER

*Dunstaffnage Marine Research Laboratory, Oban, Scotland*

SIR FREDERICK S. RUSSELL

*Plymouth, England*

*and*

SIR MAURICE YONGE

*Edinburgh, Scotland*

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# CONTRIBUTORS TO VOLUME 17

G. M. Branch, *Department of Zoology, University of Cape Town, Cape Town, South Africa.*

Llewellya Hillis-Colinvaux, *Department of Zoology, The Ohio State University, Columbus, Ohio, U.S.A.*

R. C. Newell, *Department of Zoology, University of Cape Town, Cape Town, South Africa.**

Leslie Stewart, *The Lodge, Claughton, Nr Lancaster, Lancashire, England.*

* Present address: Institute for Marine Environmental Research, Prospect Place, Plymouth, Devon, England.

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# ECOLOGY AND TAXONOMY OF *HALIMEDA*: PRIMARY PRODUCER OF CORAL REEFS

LLEWELLYA HILLIS-COLINVAUX

*Department of Zoology, The Ohio State University, Columbus, Ohio, U.S.A.*

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## I. Morphological Definition of *Halimeda*

*Opuntia marina*. The Sea Garland.

> This dainty plant groweth up from some Rockes or stones, in or neere the Sea, spreading sundry flat, thicke, short and round leaves, one set on the toppe of another, and some also growing from the sides, forming branches of leaves leaning downewards, each being as it were strung on a thred which yet is scarce to be discerned, like as a Country Garland of field and corne flowers, are used to be made to decke the Country houses, and their places of sport, so that the whole plant seemeth to be made of nothing but strung leaves, bearing a large yellow flower at the toppe saith *Bauhinus*, but I much doubt he taketh that supposition from the *Ficus Indica Americana*, the lower leaves are somewhat browne, the rest are whitish greene, and those that are new sprung are greene, and all of them smooth and shining, even kept betweene papers for a long time, and of a saltish taste, yet by long time growing rougher and full of wrinckles, but still tough and not brittle like Corall or Coralline, and growing soft againe steeped in water, yet still very salt.
>
> *Parkinson* (1640)

Over 300 years ago Parkinson provided this first English description of a *Halimeda*, calling it *Opuntia marina*, the sea garland. With prose and drawing (Fig. 1), he so clearly captured the essence of the only species then known, *H. tuna* of the Mediterranean, that his words seem an appropriate introduction to this entire genus of green, calcareous marine algae.

FIG. 1. *Halimeda tuna*, as *Opuntia marina* in Parkinson's "Theatrum Botanicum", 1640. (Photograph by the British Museum (Natural History).)

The discovery of other species, in the intervening years, has shown that the genus is not always dainty and the descriptive terminology has grown accordingly. Nevertheless, the overall appearance of the genus is characteristic, and whether one first encounters it while swimming in a coral reef, or examining an array of dried herbarium specimens, it can be identified almost at once, for it looks like some form of underwater cactus, with photosynthetic portions consisting of series of calcified *segments* or joints, the strung leaves of Parkinson, which may be arranged in some branching pattern. The plant body, or *thallus*, also possesses a holdfast which provides attachment to or in the substrate (Fig. 2).

All species of *Halimeda* deposit calcium carbonate in the form of aragonite. Hence, the green colour of the segments, which are the photosynthetic portions of the thallus, is muted. Calcification begins when the segment is about 36 hours old (Wilbur *et al.*, 1969); therefore, even those small young thalli that appear flatulent and green are calcified. The only uncalcified portions are nodes (to be described below), apical segments younger than about 36 hours old, and rhizoidal filaments.

FIG. 2. Basic parts of a *Halimeda*, and the three main types of holdfast. Thalli which sprawl over rock or sand usually have a number of places of attachment, provided by a few loose filaments from between segments or sometimes from the ends of segments. In rock-growers generally the branched filaments form a mat which holds to rock, whereas in sand-growing species the branched holdfast filaments adhere to fine particles of substrate, and the whole forms a sizeable "root". (Drawings by D. Dennis, The Ohio State University.)

## A. *The basic plan*

The constructional unit of the entire alga, both holdfast and segment, is the filament (Fig. 3), which has a diameter of approximately 0·05–0·1 mm. These filaments, with a resemblance to fungal hyphae, are matted and branched in such a way as to build plants which range in size from 5 cm or less in *H. lacrimosa*, to over 1 m in sprawling forms of *H. opuntia*.

The filament itself is unusual. Unlike those of most other plants it lacks cross walls which would divide it into a linear row of cells. The *Halimeda* organism, which is constructed out of a mass of these filaments, may therefore be considered one giant multinucleate cell. This filament without cross walls, or *coenocytic* filament, occurs also in a few other algae such as *Penicillus*, *Tydemania*, *Udotea* and *Caulerpa*, all of them green algae or members of the Chlorophyta, and in the Phycomycete fungi. These green algae, with their siphon-like filaments,

FIG. 3. The constructional unit of *Halimeda* is the coenocytic filament. In segments, in contrast to holdfasts, there is a definite pattern of organization which is least complex in *H. cryptica*, a species with a single main filament. This central medullary filament branches several times, producing lateral branches which also branch. In most species there are several to many medullary filaments. Scale bar is 1 mm. Material is stained with dilute Lugol's solution, and mounted in glycerine. (From Colinvaux and Graham, 1964.)

were formerly classified in the order Siphonales. Hence they often are described as *siphonaceous*.

Cross walls in the filaments have not been observed to form regularly at any stage in the life-history of *Halimeda*. In this way, and in its regular multinucleate condition, this genus differs from *Acetabularia*, another well-known calcareous green alga.

FIG. 4. *H. cylindracea*, from the lagoon of Enewetak Atoll. The specimen has been decalcified to show the extensiveness of the mass of holdfast filaments which are normally obscured by adhering particles of substrate.

1. *Holdfast*

The filaments of the holdfast are not organized into a regular shape such as a segment. They generally branch irregularly to form a mass of threads, which may remain loose, as in much of the *opuntia* material, may become tangled into a mat as in *H. tuna*, or may adhere to fine particles of loose substrate and with these particles produce an impressive bulbous structure to 13 cm or more in length (Figs 2, 4, 5). These large holdfasts sometimes grow in a reducing environment.

In at least some species the main rhizoidal filaments have much-thickened walls, whereas the walls of the finer branches are not noticeably thickened.

2. *Segment*

In contrast to the holdfasts, the filaments within segments show a definite pattern of organization. In most species several central, so-called *medullary* or axial, filaments run the length of the segment (Figs 3, 6) and the entire length of the branch, "stringing" the segments together. These filaments form the central axis, core or *medulla*. The exception, *cryptica*, has a core of but a single filament (Colinvaux and Graham, 1964), which is two or more times the diameter of such filaments in other species (personal observation).

The medullary filaments generally branch trichotomously, with the resultant branches becoming displaced laterally and rebranching one to three times. This lateral branch system is the cortex (Figs 3, 6). The branches themselves, called *utricles*, are relatively short, and become progressively shorter towards the periphery of the segment. They also may be swollen, except at their bases, where in most species they are usually constricted and the wall thickened. The outermost or peripheral branches are called *primary utricles*, the ones immediately to the inside are *secondary utricles*, and so on until cortex disappears into medulla (Figs 6, 7).

The primary utricles of most species touch at their peripheral edges and adhere in mature segments. In surface view, therefore, the peripheral utricles generally appear polygonal, like a section of honeycomb (Fig. 8). They give the impression of cells and in the older literature sometimes, erroneously, were called cells, although they are but the adhering tips of coenocytic filaments.

The cortex of the segment is not uniformly developed over the entire plant but varies with the relative age of the segment, and is

METRIC

FIG. 6. Longitudinal sections through part of a segment (*incrassata*) showing its basic filamentous construction. Note absence of cross walls throughout, which makes this plant a coenocyte. In the right-hand diagram the medullary filaments at the apex of the segment (right) have started to grow and branch to form a new segment. Such filaments show a distinct gradient in kinds and quantities of organelles. (Redrawn by D. Dennis, The Ohio State University, from Hillis (1959).)

FIG. 7. Schematic enlargement of a small portion of the cortex illustrated in Fig. 6 showing variable thickening of filament wall at bases of utricles, and the interfilamental spaces of the cortex. Those of the medulla are not included. It is in these interfilamental spaces that aragonite is deposited. (Drawing by D. Dennis, The Ohio State University.)

absent in the juncture between segments. Consequently, the intersegmental region or *node*, for a very short distance, is composed only of axial filaments. For most species this is where the filaments fuse in some characteristic pattern, a circumstance useful to taxonomy

FIG. 5. (Opposite.) *H. cylindracea*, a non-decalcified plant from Enewetak lagoon showing the usual appearance of the holdfast. The holdfast shown was one of the smaller ones of over 50 specimens examined from the lagoon.

(Section III). Only in the species *cuneata* is the uncorticated region more extensive, and this is described in the discussion of this species.

In the spaces of the cortex and medulla (Figs 6, 7), outside the filaments, the deposition of aragonite occurs (Askenasy, 1888; Wilbur *et al.*, 1969; Borowitkza and Larkum, 1976a, b). Calcification, therefore, takes place entirely outside the filament.

FIG. 8. *H. monile*, surface view of peripheral utricles of a segment about 48 hours old. The ends of the filament, or peripheral utricles (large circles or polygons) adhere to form a continuous outer surface. The corners are less rounded in older segments. Scale bar is 10 μm.

## B. *Wall structure in a cellulose-free plant*

The walls of the filaments, at least those comprising the segments, are microfibrillar (Preston, 1974; Borowitzka and Larkum, 1977), the microfibrils containing chains of β-1,3-xylan (Miwa *et al.*, 1961). The chains within the crystalline xylan fibril are coiled in double helices (Preston, 1968). A β-1,3-linked glucan is also present, in the ratio of one glucan molecule to four of xylan, and may form the cortex of the microfibril surrounding a xylan crystallite (Preston, 1974). These investigations elucidate, as well as extend, early critical wall studies

carried out by Mirande (1913) who, through differential staining techniques, deduced the walls to be composed mainly of what he called callose, which is a polymer of β-1,3-linked glucose residues (Aspinall and Kessler, 1957). Cellulose, until recently thought to be present in the walls of all plants except fungi, has not been found in *Halimeda*, although it has been demonstrated in some of its siphonaceous relatives (Feldman, 1946; Huitzing and Rietema, 1975).

FIG. 9. The wall of a young filament from *H. monile*, showing the outer layer of fine fibrils (top), the osmiophilic covering lamella (appears dark) and main part of wall. Calcification has not yet started in this segment, but the first aragonite crystals form in the vicinity of the fine fibrils, and therefore outside the filament. The plasma membrane has separated from part of the wall. Scale bar is 0·1 μm.

The outermost region of the filament wall contains one or more osmiophilic layers (Fig. 9) which sometimes separate from the rest of the wall. Their precise chemical nature as yet is unknown. Although this region may be equivalent to the "cuticle" of Hanic and Craigie (1969), a word they employed with reservation, it seems more appropriate to use the earlier terminology of Brand (1901) and call it a "covering lamella" (Decklamella). This lacks the chemical connotation of cuticle, and clearly indicates the region of the filament wall involved. Numerous fine fibrils, approximately 5–10 nm in diameter and 200 nm long (Wilbur *et al.*, 1969; Borowitzka and Larkum, 1977), often with knob-like ends, project from this covering lamella into the lumen of the segment. This fibrillar or pilose layer, which contains polysaccharide

(Borowitzka and Larkum, 1977), is most readily observed in young segments and often is obscured by calcium carbonate crystals.

### C. *Inside the filament*

The filament wall bounds the cytoplasm. The organelles are not uniformly distributed throughout the cytoplasm although the construction

FIG. 10. *H. manile.* Section of a filament from a segment less than 48 hours old showing wall with fine fibrils on outer surface, two nuclei (n), chloroplasts (c), plastid with concentric lamellae and starch grain (upper right-hand corner), chloroplast with small starch grain (below the nuclei), mitochondria (m) and electron-dense bodies (e). Calcification has begun in the spaces outside the filaments. The white spaces near the filament wall represent the location of crystals that were lost in the sectioning process. Stained with lead tartrate. Scale bar is 1 μm.

is coenocytic (Fig. 10). In mature, metabolically active segments the cytoplasm of inner filaments is a thin peripheral layer with relatively few chloroplasts, whereas in outer filaments, that is, in the utricles, it occupies much of the volume, the vacuole thereby being less extensive. The small, disc-shaped chloroplasts may be very numerous in the peripheral portions of the organism, but are reported to move internally at night (Stark *et al.*, 1969). A gradient in the kinds and quantities of organelles occurs in young growing filaments such as those forming a new segment (Fig. 6), and across a segment from periphery to medulla (Wilbur *et al.*, 1969; Borowitzka and Larkum, 1977). The arrangement at times suggests cytoplasmic streaming.

### 1. *Plastids*

Feldmann (1946), building on the earlier microscopic observations of Askenasy (1888), Czurda (1928) and Chadefaud (1941), delimited two basic types of plastids in a number of siphonaceous algae including *Halimeda*. They were plastids with very large starch grains which he called amyloplasts (Figs 55, 59), and those with no starch grains, the chloroplasts (Figs 10, 59). He called this two-plastid system *heteroplasty*. The plastic condition, however, is not so clear cut since starch is also present in chloroplasts (Section III; Figs 10, 59; Wilbur *et al.*, 1969; Colombo and Orsenigo, 1977).

Amyloplasts are the only plastids in the rhizoidal filaments (personal observation), whereas chloroplasts predominate within photosynthesizing mature, but not aged, segments, at least in the daytime (Wilbur *et al.*, 1969; Borowitzka and Larkum, 1974b; Colombo and Orsenigo, 1977). In the non-peripheral utricles of the segment both kinds of plastids may occur (personal observation). The pigments contained by the chloroplasts are chlorophylls *a* and *b*, in a ratio usually of about 2 : 1 (Jeffrey, 1968), together with the principal carotenoids known for other green algae, as well as two additional carotenoids siphonoxanthin and siphonein (Kleinig, 1969).

The chloroplasts of *Halimeda* are bounded by a double membrane, although the outer one is not always intact. They are disc-shaped, and when mature are approximately 2–5 μm long, 1–3 μm broad (Wilbur *et al.*, 1969; Palandri, 1972b; Borowitzka and Larkum, 1974b). Large amyloplasts have ruptured and lost much of their outer membranes and are about twice the size or larger (Wilbur *et al.*, 1969). The membranes, before they break with age, may be as resistant to breaking as are those of the related, but non-calcified *Caulerpa*, which Giles and Sarafis (1974) were unable to rupture by blending, grinding, freezing,

thawing, sonication or a variety of chemical treatments. Such rigescent membranes may explain the resistance of siphonaceous chloroplasts to digestion by opisthobranchiate mollusc grazers, and the survival of the chloroplasts within the animals for a month or more.

Thylakoids, or photosynthetic lamellae, are present in chloroplasts, and in amyloplasts in which the starch grain does not completely fill the boundary membrane (Borowitzka and Larkum, 1974b; personal observation). They traverse the length of the plastid, and in so doing may encircle a central starch grain if present. The lamellae appear to be constructed of linearly arranged vesicles (Borowitzka and Larkum, 1974b) and are appressed into groups (Fig. 10). In chloroplasts, their number, within limits, increases with age, whereas in amyloplasts the starch grain may become so large that the development of thylakoids is restricted, and the lamellae are displaced outwards until the plastid membrane eventually ruptures.

Synthesis and organization of the thylakoids involve a system of concentric lamellae at one end of the plastid (Fig. 10), variously called "concentric lamellae" (Descomps, 1965), "concentric lamellar system" (Hori and Ueda, 1967; Hori, 1974), "thylakoid organizing body" or "TOB" (Borowitzka and Larkum, 1974a, b), and "dome-shaped body" (Turner and Friedmann, 1974). These concentric lamellae persist throughout much or all of the life of the plastid, and are also present in other siphonaceous heteroplastic algae such as *Avrainvillea*, *Caulerpa*, *Chlorodesmis* and *Penicillus* (Hori and Ueda, 1967; Turner and Friedmann, 1974). They also occur in amyloplasts in which starch does not fill the entire space (Palandri, 1972b).

Osmiophilic globules may be prominent in chloroplasts (Wilbur *et al.*, 1969) and DNA fibrils are present (Palandri, 1972b; Borowitzka and Larkum, 1974b). Pyrenoids or starch-storing bodies have not been observed, but have been reported for some species of *Caulerpa* (Hori and Ueda, 1967; Calvert *et al.*, 1976), a genus which is also heteroplastic.

### 2. *Nuclei and other components*

Our knowledge of most other microcomponents of the filament system of *Halimeda* is more restricted. The many small nuclei, each containing several small electron-dense masses but usually only a single nucleolus, are bounded by a double membrane possessing pores (Palandri, 1972b). This author has also reported an association between nuclear envelope and smooth endoplasmic reticulum. Data on nuclear division are scant, and studies of the chromosomes of *Halimeda* do not appear to have been published (Puiseux-Dao, 1966; Lewin, 1976).

Other components of the cytoplasm include both smooth and rough endoplasmic reticulum, free ribosomes, Golgi bodies, microtubules, lipid globules and mitochondria (Fabbri and Palandri, 1969; Wilbur *et al.*, 1969; Palandri, 1972b; Borowitzka and Larkum, 1977). Palandri (1972a) describes some unusual forms of mitochondria, and Borowitza and Larkum (1977) report DNA-like fibrils in the matrix of giant mitochondria occurring in the tips of young growing filaments. Palandri (1972b) reported DNA in older mitochondria.

3. *Central vacuole*

The central vacuole in filaments of mature segments generally occupies much of the filament system of the medulla and inner cortex and contains a granular to somewhat fibrillar ground substance with a variety of inclusions. Prominent among these are two distinctive types of unidentified bodies (Wilbur *et al.*, 1969). One is rounded or angu ar, usually of high electron density (Figs 10, 55, 65, 66); the other is spherical (Figs 56, 59, 66). Subsequently the spherical body has been reported by other workers (Palandri, 1972b; Borowitzka and Larkum, 1977; Colombo and Orsenigo, 1977). Both unidentified structures may also be associated with the cytoplasm.

The spherical unidentified bodies are the larger, measuring 0·5–3 μm in diameter (Wilbur *et al.*, 1969). They may consist mostly or entirely of polysaccharide (Borowitzka and Larkum, 1977), and some may have a hollow core. Texture is of non-oriented fibrillar substance throughout, or of one or more zones of radially oriented material which at times shows some resemblance to the ground substance of the central vacuole. Sometimes the outer margin is barely distinguishable from surrounding material, and in places fibrils extend from the spherical body to the surrounding region. At other times tiny vesicles of varying sizes, together with the electron-dense unidentified bodies, are closely associated with the outer boundary (personal observation).

Similar spherical bodies and the considerably smaller electron-dense unknowns have both been found in *Penicillus* (Turner and Friedmann, 1974). Borowitzka and Larkum (1977) also report spherical bodies for *Udotea* and the non-calcareous, siphonaceous genus *Avrainvillea*. These workers (1977) did not find them in *Caulerpa*, nor were they observed in another siphonalean non-calcareous genus *Bryopsis*, for which Burr and West (1970, 1971a, b) report a "schizogenous body". This unknown also seems to have some association with the fibrillar–reticulum systems of the alga, but superficially is different from the spherical body, and schizogenous bodies are proteinaceous.

The calcium oxalate monohydrate crystals observed in *Penicillus* (see Friedmann *et al.*, 1972; Turner and Friedmann, 1974) have not been reported for *Halimeda*.

### D. *Microstructure of rhizoidal filaments*

The rhizoidal filaments of the holdfasts have been little studied. Hillis (1959) provided a very basic account of gross microscopic structure. A preliminary examination of the fine structure of *incrassata* (personal observation) indicates that chloroplasts, as expected, are absent, but amyloplasts, together with starch grains without apparent plastid boundary membranes are common, at least in certain regions. Vesicles of various sizes are present, particularly along the peripheral edge of the cytoplasm, and both kinds of unidentified structures mentioned above were prominent in much of the material examined.

The walls of at least some of the rhizoidal filaments are layered, and up to several times thicker than the filament walls of the mature segments described above. No aragonite crystals were found associated with them, but fine fibrils somewhat similar in appearance to those associated with the walls of the filaments in segments (as described above) were observed along the peripheral edge of the electron-dense outer wall layer of young filaments.

### E. *Summary: facets of the unusual structure and chemistry of* Halimeda

*Halimeda* is one of the largest and most complex of the green algae. It is a filamentous alga which has been elaborated from a simple plan of rows of tube-like filaments and is without cells.

The resultant plant, which may sometimes reach 0·25 m in height if erect, or sprawl to over 1 m in length, is composed of a photosynthetic portion of many segments, the "strung leaves" of Parkinson, and a holdfast system which ranges from a few short loose filaments to a truly massive production which may extend to 13 cm or more. The holdfast may exist in an anoxic environment.

Such a plant is derived by the extensive growth, with limited and controlled branching, of one or a few closely associated filaments. Aided by their wall chemistry, the branch tips of the filaments, with growth completed, stick together forming a closed or nearly closed internal environment in which the precipitation of aragonitic calcium carbonate occurs.

The algal walls are made without cellulose and the component filaments lack cross walls. The resultant "siphon", which contains the

nuclei equivalent to many cells but not the compartments, is a coenocytic filament.

Much of the filamentous system contains a large central vacuole pushing against a thin cytoplasmic layer which is pressed to the filament wall. Many of the usual microcomponents are present within the filament: nuclei, plastids, smooth and rough endoplasmic reticulum, free ribosomes, Golgi bodies, mitochondria, microtubules and lipid globules. Some plastids, the amyloplasts, contain mostly starch. Chloroplasts, with their well-developed system of photosynthetic lamellae, may contain some starch as well or this may be absent. No pyrenoids have been observed. The pigments present in the chloroplasts are chlorophylls *a* and *b*, in a ratio usually of about 2 : 1, and the principal carotenoids known for the other green algae. Two other carotenoids, siphonoxanthin and siphonein, are also present.

The chloroplasts, which are discoidal, are relatively small compared to those of many green algae, and the nuclei are also small. Little is known about the chromosomes, DNA or RNA of this alga, although DNA has been reported to be present in chloroplasts and mitochondria.

Other microcomponents of the filament include two characteristic unknown bodies, one that is electron dense, the other which is spherical and reticular.

## II. A Brief History of *Halimeda* Studies

The first taxonomic description of a *Halimeda* appeared in 1599, in a book of Mediterranean natural history by the naturalist Imperato (Fig. 11). Using the name *Sertolara* he both drew and wrote about a Mediterranean sea plant, which in subsequent binomial nomenclature eventually was called *Halimeda tuna*. This *Halimeda* species remained the only member of this taxon for more than a century, even though there was considerable botanical activity at the time. Its loneness, however, is not surprising, for it is the only recognized *Halimeda* species of this essentially tropical genus that grows in the Mediterranean. Authentic additions to the *Halimeda* species list had to await the work of naturalists and collectors in areas remote from European centres of learning.

All references to Halimedae in the seventeenth century, therefore, are to this one species, *H. tuna*, but it is heard of with many different names. Clusius (1601) called it *Lichen marinus*. Parkinson (1640) named it *Opuntia marina*. And in their catalogue of 1651 Bauhin and Cherler listed both these names, as well as introducing two more, *Fucus folio rotunda* and *Scutellaria sive Opuntia marina*. But all are the same plant.

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Sertolara. La Sertolara è nell'ordine de fogli marini, nell'effigie ſimile alquanto ad Aſpleno, de fogli ſemicircoli, de quali l'vno con picciolulimo piccino attaccando alla ſommità dell altro, fanno continuata filza de frondi ſenza tronchi, e ſenza coſtole, ilche communemente nelli fogli marini ſi è detto. l'iſteſſa maniera ſegue nel ramificare, attaccandoſi ad vno iſteſſo foglio due fogli copi di filze diuerſe: allunganſi circa due terzi di ſpanna. li fogli ſono da ambe le bande di conſiſtenza ſimile à vello ammaſſato. il ſuo colore è verdaccio.

*Sertolara fa apparenza di fogli infilzati.*

S E R T O L A R A.

FIG. 11. The earliest description and scientific illustration of a *Halimeda* was by Imperato (1599). The species is *H. tuna* from the Mediterranean. (From Imperato (1599); photograph by the British Museum (Natural History).)

Further details of these epithets are listed in the species description for *tuna* by Barton (1901).

The first and possibly only published recipe for *Halimeda* as food is another seventeenth-century contribution. Bauhin and Cherler (1651) report that it makes a good dish when treated with vinegar, salt and oil.

The earliest non-Mediterranean collections of *Halimeda* came from the West Indies, notably those obtained in about 1687 by the physician Hans Sloane, later Sir Hans Sloane, who stopped at Jamaica in the suite of the Duke of Albemarle. Sloane's visit was curtailed by the

death of the Duke, but nonetheless he collected some 800 new plant and animal species during the 15 months of his stay (Sloane, 1707). Among these was the second species of *Halimeda* to be discovered. In his volume dealing with the natural history of Jamaica, Sloane (1707) called this species *Corallina opuntia*. It is what is now known as *Halimeda opuntia*, the straggly cushion-shaped clusters of which are a prominent feature of shallow parts of Caribbean reefs. Sloane's specimen is contained in the Sloane Herbarium of the British Museum (Natural History).

### A. *Ellis: microscopy and the plant or animal question*

The most significant contributor to early *Halimeda* history, however, was John Ellis, one of the outstanding naturalists of Great Britain of the last half of the eighteenth century. Indulging his interest in plants and animals of land and sea, he developed a network of correspondents in various parts of the world, especially America and the West Indies, receiving from them numerous materials for study. His eventual appointments as King's Agent for the province of West Florida (1764) and the Island of Dominica (1770) provided him with sufficient income to follow his inclinations more freely (Smith, 1819; Savage, 1948).

Of especial interest to Ellis were the "Corallines", a group of calcareous and horny sea organisms which he successfully established as an animal group in his classic "Essay Towards a Natural History of the Corallines" of 1755, although Peyssonnel had somewhat earlier recognized an animal nature in at least some of them (Savage, 1948). This coralline group was diverse, and although the principal representatives were various cnidarians, the complex also included calcareous sea organisms such as the green alga *Halimeda* and the red alga *Corallina*. Because of this, two *Halimeda* species, subsequently known as *incrassata* and *opuntia*, were included in the 1755 publication as "Articulated Corallines of Jamaica".

Eventually Ellis separated five species of *Halimeda*: *incrassata*, *tridens*, *monile*, *opuntia* and *tuna*, but the genus had not been established as yet, and they were assigned to *Corallina*. As such they appear in his treatise with Solander (Ellis and Solander, 1786), published after the death of both Ellis and Solander under the direction of Ellis' daughter, Martha Watts. The use of binomial nomenclature in this work and in an earlier publication (Ellis, 1767) probably grew out of his extensive correspondence with Linnaeus and work with Solander, a favourite student of Linnaeus. Four of the species with their epithets are still accepted; the remaining one, *tridens*, has been placed in synonymy

under *incrassata* (Section IV). The species *incrassata* (*tridens*) and *monile* were new with Ellis, whereas *opuntia* had been described by Linnaeus in his "Systema Naturae" (1758), using the binomial *Corallina opuntia*. Others before this had assigned other names to it, generally polynomials.

Ellis' examination of *Halimeda* material included microscopical study of both surface and internal features (Fig. 12) in what seems to

20. The Corallina incraſſata, from the Weſt-Indies.
21. One of the joints of its natural ſize.
22. The ſame magnified a little, to ſhew its pores in its calcareous ſurface.
23. Part of the inſide tubes of the joint, of their natural ſize.
24. The ſame magnified, to ſhew the openings of the cells on the ſurface, conneſted together.
25. A perpendicular ſection of half of one of theſe joints.
26. The ſame magnified, to ſhew the figure of the veſſels leading to the ſuckers in the calcareous ſurface.
27. A piece of the calcareous ſurface highly magnified, to ſhew ſome of the pores open, and others covered with their convex opercula; letter *a* ſhews the figure of one of the trumpet-ſhaped ſuckers highly magnified.

FIG. 12. *Halimeda* (*Corallina*) *incrassata*. These illustrations with analysis, by Ellis (1767), provide the type description of the species *incrassata*. Ellis' work also represents the earliest known microscopical study of the genus. The habit (No. 20) illustrates the caulescent effect obtained when basal segments remain unbranched. In older plants a number of basal segments may become consolidated into a relatively massive structure. (From Ellis (1767); photograph composition by The Ohio State University Department of Photography.)

be the earliest comparatively detailed examination of internal structure in *Halimeda*. More intensive microscopic examination was not undertaken until over a century later, first by Askenasy (1888) and then by Barton (1901). Ellis particularly noticed the pits and facets given to the surface of *Halimeda* segments by the peripheral utricles, and compared them with the surface patterns of cnidarian corals:

> We see in the greatest number of Corallines their surface full of holes; we saw the same in Escharas and Milleporas thirty years ago; since that time magnifying glasses have been improved, so as to shew us, that they are all orifices, for polype-like suckers; why should not we now admit that glasses may be still more improved, so as even to make us able to see what may be the intention and use of these minute orifices, which according to all rules of reasoning, we must suppose to approach in nature to them they are most alike.

This provided part of the basis for considering *Halimeda* as an animal.

Ellis' conclusions had force because of his skill and reputation as a microscopist. Linnaeus wrote to him, "I beg of you to lend me your lynx-like eyes" (Library of the Linnean Society of London; Savage, 1948). Furthermore, Ellis worked with some of the best laboratory hardware of the day including an "aquatic microscope" (Fig. 13) made by a London optician and "improved" by Ellis specifically for examining living corallines. I used Ellis' aquatic microscope at the Science Museum (London) and found the resolution to be surprisingly good. Figure 14 shows a photomicrograph of the surface of *Halimeda incrassata* made with it. The more obvious surface features of the plant can be conceived almost as certainly as with a modern microscope. The smallness of the field, and its curvature, are the main problems of these simple instruments. Chromatic aberration led to some vexing difficulties, but not as much as in the compound microscopes of the time.

Ellis provided additional contemporary insights on microscopes and viewing in a letter to Dr David Skene in 1770 (Library of the Linnean Society of London; Savage, 1948).

> I find Wilsons or the Single microscope much the best; there need not be any plano convex glass screwd in at bottom if you have a good illuminating concave speculum to throw up the light, and at the same time to take instead of the plano convex on the bottom to screw on the bottom a brass circular plate with a hole in the centre in proportion to the size of your magnifier; the largest magnifier as No. 1 requires the smallest hole, by this means in a clear day youll easily see the minutest animal distinctly. Mr. Dollond has at my request fitted up a pocket microscope that pleases most people; it consists of my aquatic & Wilsons combind together so as to be very little larger than the aquatic alone

FIG. 13. Ellis Aquatic Microscope, Inventory 1911–294, in the Science Museum, London. The Museum description states: "This type of microscope may be regarded as the precursor of the most complete and perfect of our simple dissection microscopes, and it was made with slight modifications by all the leading opticians until the early years of the 19th century. . . . The round hollow pillar screws into a socket in the lid of the fish-skin case. The mirror mounted in gimbals is fitted to the pillar by a spring-pin and socket. The inner sliding rod which carries the objective arm can be fixed at the desired height by a clamping screw. The stage is removable for portability, and a Wilson screw barrel microscope with three additional powers is added, which can be adapted to the stand". (Photograph British Crown Copyright. Science Museum, London.)

FIG. 14. Surface utricles of *H. incrassata*, as observed with an Ellis Aquatic Microscope (Fig. 13) from the collection of the Science Museum, London, using the No. 1 objective. Most of the numerous faint dots or small circles in the utricles are chloroplasts; the darker spots and curves are associated with subsurface structure. Both may have encouraged Ellis to think of polyps (cf. Fig. 12). The average diameter of the surface utricles is 45–85 μm. (Photograph British Crown Copyright. Science Museum, London.)

> which he sells at 3 Guineas & half; the Wilsons at the same time is fitted for the Solar apparatus so that by having a small box with the Solar apparatus which cost[s] 2 & ½ Guineas more you have a compleat Microscope for any object. I never could see the smallest animalcules in the Double or Compound microscope. This does very well for the larger objects and is pleasing to many on acct of the largness of the Field.

Ellis' consideration of corallines as animals was further strengthened by his deductions about their chemistry such as he demonstrated to the Society of Arts, Commerce and others. He showed that corallines, when burned, produced not the "smell of burnt vegetables", but "an offensive smell like that of burnt bones, or hair". Indeed, the door of the room where the Society was meeting "was obliged to be opened, to dissipate the disagreeable scent, and let in fresh air" (Ellis, 1767).

Such arguments for the animal nature of *Halimeda* were part of the fascinating and well-reasoned letter Ellis wrote to Linnaeus in 1767. This letter, a portion of which is also a paper in the *Philosophical Transactions*, was one of two of Ellis' works chosen for citation in the

presentation speech for the Royal Society's Copley Medal award to Ellis the following year (Smith, 1819).

Linnaeus accepted much of Ellis' position on the animal nature of corallines, and in his own last edition of "Systema Naturae" (1766–1767) wrote of calcareousness indicating animal origin: "Corallinas ad regnum animale pertinere ex substantia earum calcarea constat, cum omnem calcem animalium esse productum verissimum sit." That Linnaeus had reservations, however, is shown by his keeping the corallines in his rather ambiguous group "Zoophyta", which he defined as compound animals bearing flowers, their vegetating stem passing by metamorphoses into a flowering animal. Included under Zoophyta in the tenth edition (1758), as well as in the last (1767), was *Halimeda opuntia* (as *Corallina opuntia*), the only *Halimeda* species Linnaeus apparently knew.

Other contemporary workers such as Baxter (1761) and Pallas (1766) objected to this animal classification of the genus *Corallina* since the actual polyps had not been observed, but Ellis' arguments were sufficiently convincing that for the remainder of the century the genus generally was placed among the animals. The practice was continued into the nineteenth century with the work of naturalists such as Lamarck (1813) and Lamouroux (1812, 1816), but the term "zoophyte" was replaced with the preferred "polypier". More significantly, Lamouroux subdivided the coralline group into a number of genera. One of these was *Halimedea* (1812) or *Halimeda* (1816), to which he transferred the five species delimited by Ellis. The generic name we now use had been born. Another name, *Sertolaria*, with Imperato's *Sertolara* as type specimen, actually had been proposed earlier by Boehmer (see Ludwig, 1760), but the epithet *Halimeda* is the one that became established and in 1956 this familiar name was conserved (Lanjouw *et al.*, 1956). That these organisms really were plants, however, still had to be worked out.

The first person in the nineteenth century recorded as definitely placing *Halimeda* in the plant kingdom, but under the name *Hormisus*, appears to have been Targioni-Tozzetti, whose unpublished manuscript was cited by Bertolini (1819). Link (1834), Chauvin (1842) and Decaisne (1842) also placed this genus in the plant kingdom, and by 1842 it was generally accepted that *Halimeda* was a plant.

### B. Halimeda *discoveries: the beginnings of critical taxonomy*

Voyages of exploration as well as travels of individuals interested in living organisms in the eighteenth century yielded additional new species which were described by Decaisne (1841, 1842), Krauss (1846),

Zanardini (1851, 1858), Kützing (1857–1858), Piccone (1879), Hauck (1886), Agardh (1887) and Askenasy (1888), changing the species total from 5 to 27 in about 50 years. Not all of these species proved satisfactory, however. Until 1888, the taxonomy was based almost entirely on external characteristics, with emphasis on what is now recognized as an exceedingly variable character, "segment shape". The microscope was not used critically for identification and Kützing's statement (1857), that internal organization was uniform among the species of *Halimeda*, provides some insight into the "state of the science" at that time. With such heavy reliance on segment shape, it is not surprising that certain taxa such as *opuntia*, and to a lesser extent *incrassata*, both of which commonly show a large variety of segment types, were at one time each described as more than one species. Segment shape, along with habit, also formed the basis of Agardh's (1887) sections within the genus which subsequently have been ignored (Hillis, 1959), at least partly because of their unsatisfactory definition.

The cornerstone of critical modern taxonomy and microscopy for the genus was laid by Askenasy (1888) who used microscopic characters to distinguish the few *Halimeda* species collected during an expedition of the S.M.S. *Gazelle*, as well as to delimit the new species *macrophysa*. Of special significance was the fusion he described of medullary filaments at the node in the species *incrassata* (Table III, Type 1). A brief reference to altered medullary filaments at the node, made by Agardh (1887) and by Ellis as early as 1755, provided some microscopic observations, but Askenasy's work represents the first detailed account of a major microscopic characteristic.

Askenasy not only emphasized nodal patterns of medullary filaments but also discovered that the sizes and shapes of peripheral utricles ("Rindenschläuche") differed significantly among taxa. He also provided a very clear description of the calcium carbonate deposits within *Halimeda*, pointing out that the crystals develop in the spaces outside the filaments, but within the confines of the segment, that is, that calcification is not external to the segment. The perceptive account shows his skills as an able contemporary microscopist and investigator. Little was added to this description until the 1960s (Lewin, 1962), when the tools of electron microscopy and radioisotopes became available.

### C. *The discovery at Funafuti: the reef-building capabilities of* Halimeda

At the close of the nineteenth century the Royal Society and the Government of New South Wales sponsored an expedition to Funafuti

Atoll in the Ellice Islands of the south Pacific for the purpose of boring a deep hole to test Darwin's hypothesis on the origin of atolls. The first hole had to be abandoned after about 25 m of drilling, but two long cores were successfully taken, the deepest penetrating to 339 m.

For the history of *Halimeda* this expedition and its results were especially significant for three reasons. An analysis of the cores showed not only that *Halimeda* segments were prominent, and hence that this alga participated in reef building, but also that in these particular cores this calcareous green alga, by the volume of sediment contributed, appeared to be more important than corals (Finckh, 1904). This activity will be discussed in Section IX.

A collection of intact specimens of *Halimeda* from various sites in the atoll was also made during the expedition, and was given to Miss Ethel Sarel Barton, later Mrs Gepp, of the British Museum (Natural History) to identify. This led to a paper on the *Halimeda* of Funafuti (Barton, 1900), but of much greater significance was her realization of the vast inconsistencies in the existing taxonomy of the genus and the need for its serious revision. Askenasy's skilful work pointed the way, and the opportunity soon arose. In 1900, Madame Weber-van Bosse asked Barton to work on the large collection of *Halimeda* made during the Siboga expedition led by her husband to the Dutch Indies in 1899 and 1900. Barton began an intensive study of the genus as then available to her, which led to the important monograph of 1901.

### D. *The taxonomy of Barton*

Barton's investigation was a careful one. She dissected specimens and measured various characters. But, most importantly, she saw and examined as much of the type material of the species then recognized as she could obtain. Consequently, she was able to compare specimens with authority. She examined a number of characteristics in the many plants available, mostly East Indian, and concluded that the pattern of medullary filament fusion at the node was the most consistent character and the only one of significant taxonomic value.

Barton established three patterns of nodal medullary filaments (Table III, Types 1, 2, 3, respectively) as follows:

> all medullary filaments come together into a single unit, often with conspicuous pits or pores between adjacent filaments, and then separate;
>
> the filaments fuse, in pairs, for a short distance and then separate;

filaments fuse completely in groups of twos or threes and do not separate thereafter, although the filaments eventually branch in the segment above that particular node.

The first type was originally described by Askenasy (1888) and is represented by the species *incrassata*. The second type, represented by *opuntia*, and the third by *tuna* and *gracilis* were first delimited by Barton.

The usefulness of Barton's monograph at that particular time was strengthened further by her rigid application of this nodal character. Her taxonomy was supplemented with one other microscopical character, the extent of adhesion of the peripheral utricles and by judicial use of segment shape. As a result, specimens with similar nodal anatomy, such as *incrassata* and *tridens*, were assigned the same epithet instead of different ones which had happened when the taxonomy was based on segment morphology. Ellis and Solander (1786), and subsequently others, including Agardh (1887), had considered them distinct species on the basis of the predominant segment shape being plano-convex in *incrassata* and tridentate in *tridens*.

A prime result of Barton's treatment was the retention of but 7 species of *Halimeda* (Table I) out of the more than 25 that had been recognized hitherto. A second result was that order within the genus was established.

A few specimens, however, were obviously troublesome to Barton, for they did not fit her scheme. Of these, a few are best interpreted as being poorly developed individuals. A very few were aberrant in that the medullary filaments did not fuse at the node in any of the designated ways, but remained entirely separate. Barton did not interpret this pattern as representing a separate category of nodal filament structure, however, because she felt she had plants with "all gradations of the character from filaments with well-developed pits to those which were entirely free and shewed even no trace of thin places on their unusually thick walls". Consequently those that she did not consider to be stunted or small specimens of the typical *incrassata*, she designated as a distinct form of *incrassata*, f. *ovata*. The form epithet was chosen because these plants resembled, at least externally, Agardh's *incrassata* v. *ovata*, the type of which she was unable to examine microscopically.

Although Barton was apparently satisfied with this decision, and her conservatism was reasonable considering the small number of such specimens available to her, the true nature of the material is more interesting. I have examined all Barton's material at the British Museum (Natural History) as well as the Siboga collection in the

TABLE I. *Halimeda* SPECIES AND THEIR RELATIONSHIPS IN THREE PAPERS[a]

| *Barton* (*1901*) | *Hillis* (*1959*) | *Hillis-Colinvaux* (*this paper*) |
|---|---|---|
| *incrassata* | *incrassata* | *incrassata* |
| | *simulans* | *simulans* |
| f. *monilis* | *monile* | *monile* |
| | *cylindracea* | *cylindracea* |
| | | *borneensis* |
| | *favulosa* | *favulosa* |
| | *stuposa* | *stuposa* |
| f. *ovata p.p.* | *micronesica* (including *orientalis*) | *micronesica* |
| | *fragilis* | *fragilis* |
| | | *melanesica* |
| | | *cryptica* |
| *macroloba* | *macroloba* | *macroloba* |
| *opuntia* | *opuntia* | *opuntia* |
| | | *minima* |
| f. *renschii* | | *renschii* (incl. *batanensis*) |
| | | *goreauii* |
| | | *velasquezii* |
| f. *hederacea* | v. *hederacea* | *copiosa* (incl. *hederacea*) |
| | | *distorta* |
| *tuna* | *tuna* | *tuna* |
| | *scabra* | *scabra* |
| | *lacunalis* (incl. *gracilis* f. *lata*) | *lacunalis* |
| | *gigas* | *gigas* |
| | *discoidea* | *discoidea* |
| | *taenicola* | *taenicola* |
| *cuneata* | *cuneata* | *cuneata* |
| *gracilis* | *gracilis* | *gracilis* |
| | *lacrimosa* | *lacrimosa* |
| | *bikinensis* | *bikinensis* |
| *macrophysa* | *macrophysa* | *macrophysa* |

[a] Arrows link entities that are the same.

Rijksherbarium of Leiden, the herbaria where most, if not all, of the f. *ovata* material is deposited.

The f. *ovata* specimens are relatively few, occasionally poorly developed, and sometimes too scant to be adequately examined. However, most of those on which it has been feasible to work are *micronesica*, a species described in 1941 which will be discussed later on p. 32, and which is of especial interest because of the pattern of its nodal medullary filaments. A few are *opuntia* or *simulans*, the latter a taxon in which the pores of the fused nodal filaments are sometimes small and not readily noticeable (Hillis, 1959). It, therefore, presents some of the gradations Barton indicated for this character in the above quotation. These identifications of the anomalous f. *ovata* material have clarified and to a certain extent strengthened the major portions of Barton's work.

In retrospect, Barton's taxonomy was conservative, which was an approach much needed at the time. Its strengths lay in the discovery of essentially one microscopic characteristic of major taxonomic significance, in the fairly rigid application of it in identification, in the emphasis on examination of type specimens, and in the inclusion of material from other than the Siboga collection, which, although severely limited, did extend the work to all the tropical oceans. After the monograph was published, Barton continued identifying algae, published one paper on reproductive structures in *Halimeda* (Gepp, 1904), and more on Siboga algae in the important joint publication, with her husband, about the Codiaceae (Gepp and Gepp, 1911). The work after 1911 was not extensive, however; there appeared to be little further study of *Halimeda*, and one suspects that marriage in 1904 to Anthony Gepp, Curator of Botany at the British Museum (Natural History), and the contemporary attitude towards women and careers had their impact. For a brief time, however, the genus *Halimeda* was tidy.

### E. *Howe, Børgesen, Taylor and Hillis: the modern taxonomy*

No taxonomic scheme of living organisms is fixed, however, and in a very short time after the publication of Barton's monograph many new collections became available to test the workability and validity of her system. Initially specimens came mostly from the Caribbean, a tropical region scantily represented in Barton's work, and for the first time the material was studied by workers who had some responsibility for collecting it. They were Marshall A. Howe of the New York Botanical Garden and Frederick Børgesen of the Botanical Museum, Copenhagen,

Denmark, who worked in the Danish West Indies and published extensively on the algae of the Canary Islands and Mauritius. Both adopted Barton's fused filament characteristic for separating species, and Howe added other characters which subsequently proved as useful. While examining a certain abundant and distinctive West Indian plant, he noticed, for example, that its secondary utricles were more than twice as broad as those of most other specimens (Fig. 20, No. 11). Furthermore, the character was consistent. It could be used, therefore, to distinguish species, and Howe reasoned that specimens with this character should have separate status and not be considered synonymous with *H. tuna* as Barton had done. Howe (1907), therefore, re-established the species *discoidea*, which brought the total of accepted *Halimeda* species to eight.

TABLE II. USE OF THE MICROSCOPIC CHARACTER OF AVERAGE DIAMETER OF PERIPHERAL UTRICLES (SURFACE VIEW) BY HOWE (1907) TO SEPARATE *Halimeda* SPECIES WITH THE SAME TYPE OF NODAL FILAMENT PATTERN

| *Peripheral utricles, average diameter < 80 μm* | | | *Peripheral utricles, average diameter > 80 μm* |
|---|---|---|---|
| Peripheral utricles, average diameter 49–77 μm | Peripheral utricles, average diameter 30–44 μm | | |
| | Predominant segment shape | | |
| | Subterete | Discoid | |
| *tridens* ( = *incrassata*) | *monile* | *simulans* | *favulosa* |

Among the microscopic characteristics investigated by Barton were those of appearance and size of the peripheral utricles in surface view. She did not find them particularly helpful, however, which in retrospect is reasonable because her species concept was exceedingly broad. Howe observed, though, that average diameters of the peripheral utricles in surface view could be used to separate entities with the same basic type of filament fusion at the nodes. Using the characters of average diameter of peripheral utricles (surface view) and predominant shape of segments (Table II), he re-established the species *monile*, which had been placed in synonymy under *incrassata* by Barton, and recognized a new species, *simulans*, which possessed the same type of nodal character as the other two species (Howe, 1907).

This use of additional microscopic characters represents an important refinement of taxonomic criteria for the genus and an early application of field experience with this taxon, which Barton and most of the preceding workers on *Halimeda* did not have. Howe appears to have been provoked into looking for reliable differences in microscopic structure because he had observed *incrassata* (his *tridens*), and *monile* growing in close proximity in Bermuda, Puerto Rico and the Bahamas, yet remaining distinct. Where *simulans* was observed growing near *incrassata* he also reported no intergrading forms (Howe, 1907). This character remains one of the most useful microscopic criteria for separating species of *Halimeda*.

Howe (1907) also suggested changes in nomenclature to take account of apparent priority of species authorship. He renamed *incrassata* with the epithet *tridens*, which he believed had priority. Barton had chosen the epithet *incrassata* when merging older species, but Collins (1901), whose "Algae of Jamaica" preceded Barton's monograph by a few months, had chosen *tridens* for a similar merger. Howe's decision depended on Collins having correctly identified the type description of *incrassata* and *tridens* as being that referred to in a single publication by Ellis and Solander (1786). The first author to merge species erected in a single earlier paper has priority of choice for the name to be used (International Rules of Nomenclature). Collins chose *tridens*; Barton chose *incrassata*; Collins chose first.

Børgesen (1911, 1913) put the merged species back to *incrassata* where Barton put it. This argument over naming the species has had the heritage that American and European workers gave the same species different names for much of this century. Americans followed Howe in using *tridens* and Europeans followed Børgesen and Barton in using *incrassata*. This confusion was only resolved with the monograph of Hillis (1959). In this it was demonstrated that *incrassata* is the appropriate name because Ellis, in his 1767 publication, included excellent illustrations, with analyses, of a "coralline" to which he applied the specific epithet "*incrassata*" (Fig. 12). This meets the requirements for valid publication as stated in the Paris Code (Lanjouw *et al.*, 1956, Article 43). The original merger proposed by both Collins and Barton is still accepted, and the name of the species is *Halimeda incrassata* and not *H. tridens*.

Børgesen's (1911, 1913) interpretation of Caribbean material tended to parallel Howe's, yet reflected his own thinking. He considered that *monile* and *simulans* differed sufficiently from *incrassata* to be treated as separate taxa, but that they were only varieties of *incrassata*. These subspecies were considered of specific rank by Hillis (1959), as originally

suggested by Howe. In this way Hillis' monograph resolved both differences of usage between America and Europe: the correct name for Barton's *H. incrassata*, and the specific status of *H. monile* and *H. simulans*.

The preceding brief account of the history of *Halimeda* shows that the major collections which had been examined critically by the 1930s had come, first from the Mediterranean, then the Dutch East Indies, followed by the West Indies. Not until the 1940s were concentrated studies made of *Halimeda* in Pacific atolls. The Japanese phycologist Yamada (1941) described a new species *micronesica* from the Caroline Islands. This taxon is particularly noteworthy because it possesses a fourth pattern of nodal medullary filaments (see discussion of f. *ovata* earlier on p. 29). The medullary filaments of this species do not fuse at the node, but pass unchanged, except for branching, from one segment to the next (Table III, Type 4).

In 1946, William Randolph Taylor of the University of Michigan participated in "Operation Crossroads", the detailed scientific study of the Marshall Islands before and after atom bomb trials. Prominent in his collection of the vegetation of four of the atolls was a large and exciting series of *Halimeda* plants which were included in his book "Plants of Bikini" (Taylor, 1950). Some were new species, and one of them, *fragilis*, was a second species with unfused medullary filaments.

By 1950, then, the species total of *Halimeda*, counting *monile* and *simulans* as species rather than varieties, was about three times that accepted by Barton. A quiet outburst of *Halimeda* data had occurred, and, as a result, Barton's monograph could no longer be used exclusively to study the Halimedae of any one region. It remained a useful introduction to the critical taxonomy of *Halimeda*, but was not the definitive work on the genus.

In the mid-1950s Hillis, later publishing as Colinvaux and Hillis-Colinvaux, began working on *Halimeda*. Studying at the University of Michigan she had available the university's herbarium containing extensive collections from several Caribbean Islands as well as from the Marshall Islands. Curators of the New York Botanical Garden and the British Museum (Natural History) lent considerable portions of their large *Halimeda* holdings, the former collection containing much of Howe's and some of Børgesen's material, the latter including important specimens examined by Barton, although the bulk of Siboga expedition material, housed in the Rijksherbarium, was examined several years later in Leiden. A loan from the University of California provided additional plants from Pacific reefs. The collections, supplemented with other important although smaller loans and some live material,

provided about as extensive a world coverage as then existed, and formed a good basis for the investigation which led to a revision of *Halimeda* taxonomy (Hillis, 1959), with the recognition of 21 species (Table I).

A weakness of the Hillis monograph is that important regions of the world, particularly the Indian Ocean, are poorly represented. This is because little collecting had been done in these regions up to the 1950s. Where phycologists had collected, their specimens provided little ecological information, so that the treatment of the data had to be without detail. In addition some type specimens and important collections could not be examined.

In the years since 1957 it has been possible to extend the work considerably in both traditional and new ways. The International Indian Ocean Expedition yielded good collections obtained by phycologists from new as well as familiar sites, and the new tool of scuba provided the opportunity of exploring and collecting in sites that grapple and dredge could not probe or penetrate. This led to the discovery of new species, including the first species of *Halimeda* with but a single medullary filament passing through the node (Fig. 15; Colinvaux and Graham, 1964), which represents a fifth nodal medullary filament pattern (Table III).

Scuba diving, supplemented with skin diving and submersibles, actually enable us, at last, to see these organisms in their communities down to the limits of their depth range of approximately 100 m, and also to investigate and eventually to understand their role in the complex reef system. There have now been studies on the productivity of *Halimeda* in culture and on the reef, on the processes of calcification, on reef building, on ultrastructure and on ecology. This modern work is reviewed here and is added to with many unpublished data.

### F. *Summary: the evolution of* Halimeda *studies*

*Halimeda* was first known from the single species *H. tuna* that lives in the Mediterranean Sea, and this species continued to be the only one known for more than a century. The second, the familiar *H. opuntia*, was found by Sloane (1707) in Jamaica. Only 8 of the species now accepted were known by the turn of this century, and most of the 30 species now accepted are discoveries of the last three decades. *Halimeda*, like so many other genera, was too easily split into many species on the basis of superficial surface features during the nineteenth century. The taxonomist who brought order to the genus was Barton (1901), and

FIG. 15. A single medullary filament occurs in the node of *H. cryptica*, and the wall is much thicker in this region than elsewhere. The collar of smallish utricles from the upper segment which would surround much of the exposed filament has been dissected away. Scale bar is 100 μm. (From Colinvaux and Graham, 1964.)

the genus received its second monographic treatment by Hillis (1959). A number of new species has been found since then.

Studies on the structural and functional biology of the genus were begun by the early microscopist Ellis, and for long had the result of producing arguments over whether Halimedae were plants or animals.

By 1842 this doubt was resolved, but little more structural work was undertaken until Barton's studies at the turn of this century. Functional and ecological studies had to await the demonstration that *Halimeda* would grow in culture (Colinvaux *et al.*, 1965) and the availability of modern diving techniques. This article is the first review of these functional and ecological studies.

## III. Basis of the Taxonomy

The principal theme of this section is the *Halimeda* species. In it I am concerned with the more obvious ways in which the species vary and how they may be distinguished, rather than with precise details of how one species differs from another. Details of species description, species synonymies and keys to species are therefore reserved for Section IV. Both types of data, however, are brought together in Table X, which summarizes important characters for each of the currently recognized 30 species. The taxonomic information available up to the early 1960s also has been quantified and incorporated into a system of numerical taxonomy developed by Rogers and Fleming (1964) who were then working at the New York Botanical Garden.

So that the genus may be considered in the framework of the green algae (Chlorophyta) and the plant kingdom, I include a discussion of taxonomic categories above the genus level.

### A. *The species*

Barton, as a pioneer in the microscopic taxonomy of this genus, relied principally on one anatomical characteristic, the organization of filaments in a mature node, to distinguish the seven species of *Halimeda* she recognized (1901). However, with the splitting of some of these species, and the discovery and description of others, such heavy reliance on a single microscopic character is not possible. And if the many new species have validity—there are now over four times the number Barton recognized (Table I)—it follows that reliable characters exist to separate them. For *Halimeda* many of these are known and tested, and as with most algae they are principally microscopic. However, I have found a few macroscopic characteristics to be reasonably dependable, and when they are combined with distributional data reliable field identification of some species is possible. These non-microscopic characters can, of course, also be used for laboratory determinations.

I describe macroscopic and microscopic characters in the subsections that follow, but reserve distributional and ecological data for Sections VIII and X respectively. All may be useful in delimiting groups of species, or individual ones. Specialized reproductive structures or gametangia are described in Section VII. They are not present on most of the material collected and so far have not contributed significantly to taxonomy.

1. *Macroscopic characters*

Three characters are commonly used:

appearance of segment;
appearance of holdfast;
appearance of thallus.

The first of these, segment appearance, is the original character used to separate and establish the early species of *Halimeda* (Section II). The other two were developed as key characters by Hillis (1959), so that some specimens could be identified in the field. All three, together with data on geographic and ecological distribution, are essentially the only characters available for the field determinations essential to any critical ecological study involving the genus.

(a) *Segment pattern.* The usefulness of the appearance of segments to species identification may rightly be questioned when one recalls the early taxonomic confusion created by relying on this characteristic. From direct observation of extensive collections of dried material one is well aware that the segments, even of a single thallus, may be highly variable in shape and size, and species such as *incrassata* and *opuntia* are good examples.

Such doubts are further strengthened by evidence that some variability is environmentally induced. Techet (1908), for example, attributed the changed shape of the segments of Mediterranean *tuna*, when kept in laboratory tanks, to reduced salinity. In some of their culture studies, Colinvaux *et al.* (1965) observed a marked change in the segments of *discoidea* which may be a response to reduced light intensity. I have also noted a considerable reduction in the size, as well as change in shape of the segments of *gigas* growing in aquaria (Fig. 16). My field observations have also indicated changes of shape in response to environmental factors. The dwarf *opuntia* growing shallowly in a fast-flowing inter-island channel of Enewetak Atoll in the Marshall Islands is a good example.

FIG. 16. Some of the variability which may occur in segment size and shape shown for *H. gigas*. Portions of the typical segments, which are reniform to discoidal and very large (Fig. 39), appear in the bottom of the picture, particularly the right-hand corner. The remainder of the segments, which are predominantly cuneate, were produced in culture at light intensities of approximately 125 ft-c. The tips of several of the segments have the whitish cone-like extensions of medullary filaments, indicating that new segments are forming. Scale bar is 10 mm.

Variations, therefore, do occur. The important point is that the variations do fall fairly well within the range recognizable for each species. I have found that size, shape, texture (and occasionally colour) of segments may, with care, be used in species identification. One can easily see, for example, that the segments of *macroloba* and *lacrimosa* are very different from those of *incrassata* or *opuntia* (Figs 28, 45, 22, 19, respectively), and other examples can be found in a study of the species illustrations of Section IV. By contrast, the segments of *incrassata* and *simulans* or even of *monile* and *cylindracea* may be so similar that identification by segment appearance alone is not reliable.

The shape of segments may be spherical, to cylindrical, to flattened, with the upper margin of broad flattened segments entire, undulating or lobed, and the lower margin cuneate to auriculate. In size, the range extenss from the small (2–5 mm), tear-shaped segments of *lacrimosa* to

FIG. 17. Appearance of the surface of a portion of a *Halimeda* segment, showing some of the range in size and pattern among the different species. Each polygon or circle represents the surface of a peripheral (primary) utricle, and is the tip of the cortical branch system. Some of the variations which occur with age are shown in Nos. 14, 18, 20 and 23. Taxonomic characters shown include size; whether the utricles adhere laterally, or separate as in Nos. 10, 13, 16 and 19, or remain somewhat attached but separate easily as in Nos. 14, 17, 24 and 25; the presence of spines, No. 5; and the presence of thickening as in Nos. 2, 23 and 25. (1) *H. cuneata*, regular segment; (2) *H. cuneata*, from a cushion segment showing the thickened walls which are fairly common in these small segments; (3) *H. opuntia*; (4) *H. copiosa*; (5) *H. scabra* showing the spines as small circles in the polygons; (6) *H. lacunalis*; (7) *H. gracilis*; (8) *H. lacrimosa*; (9) *H. tuna*; (10) *H. fragilis*; (11) *H. discoidea*; (12) *H. taenicola*; (13) *H. micronesica* from a mature segment; (14) *H. micronesica* from a very young segment, showing slight adhesion of peripheral utricles; exact age unknown, but

FIG. 18. *H. cuneata*, longitudinal section, showing parts of two regular segments, a "cushion" segment and a "stalk" region. At the left is the upper portion of a regular segment with part of the cortex included. To the right of it are parts of the small "cushion" segment which is corticated, and the uncorticated stalk region. One or both may be present, and commonly neither occurs. The pattern of medullary filaments at the node, shown at the juncture of regular and cushion segments, is that of fusion in twos and threes, with the participating filaments remaining fused. The entangled condition of the filaments just below the region of fusion adds to the difficulty of nodal dissection. The base of a regular segment, without cortical detail, is shown at the right. (From Hillis, 1959.)

the broad flat ones of *gigas*, which may measure to about 31 mm in length and 42 mm in breadth.

Thickness of segments varies with the number and height of the inner cortical layers, and often decreases from base to apex within a plant. This gradient reflects the relative ages of segments, with older segments towards the base, youngest at the branch tips. Some segments are ribbed, others plane, and the surface of *macrophysa* and *favulosa* often appears pitted or stippled because of the large diameters and separateness of their peripheral utricles (Fig. 17, Nos. 16, 24). The species *cuneata* is unusual in that a small "cushion" segment or an uncorticated "stalk" region, or both, may be interposed between a node and the next regular segment above (Figs 18, 61).

Colour is influenced by the amount of calcification, proceeding from green to white or yellowish-brown as calcium carbonate increases with age. Young apical segments, therefore, may be a more prominent green than well-developed basal segments (Hillis, 1959). Colour, as a diagnostic

after the onset of calcification; (15) *H. gigas*; (16) *H. macrophysa*; (17) *H. bikinensis*, a mature segment; (18) *H. bikinensis*, a very young segment (green) showing adhesion of utricles at this stage of growth; (19) *H. macroloba*, mature segment; (20) *H. macroloba*, young segment; (21) *H. incrassata*; (22) *H. cylindracea*, mature segment; (23) *H. cylindracea*, showing somewhat thickened walls of a basal (old) segment; (24) *H. favulosa*; (25) *H. stuposa*; (26) *H. monile*; (27) *H. simulans*. (From Hillis, 1959.)

character, is rarely useful except in living specimens of *scabra* and *micronesica*, which may both have a pronounced bluish cast.

In some species the degree of calcification appears noticeably different between deep and shallow forms (Hillis, 1959; Goreau, 1963; Böhm, 1973a; Section IX), and species such as *fragilis*, *gracilis*, *lacrimosa* and *bikinensis* usually seem considerably more calcified than *cuneata* or *lacunalis*. Finally, the shape of basal segments may be noticeably different from the shape predominating in upper portions of the thallus. This is most marked in *micronesica* where the lowermost segment is usually several times larger than the other segments and very irregular in outline (Fig. 46). In members of the *incrassata* group several of the lowermost segments may remain unbranched, producing a caulescent effect, or adjacent basal segments may consolidate laterally forming a rather massive fan-shaped structure (Fig. 12).

(b) *Holdfast style*. Appearance of the holdfast is a character which is more useful in delimiting groups of species than in identifying individual ones, and is correlated, to some extent at least, with type of substrate.

Holdfasts of one group of species (Fig. 2) are conspicuous and bulbous. They consist of a mass of loose filaments to which particles of substrate freely adhere, so that the structure looks like cemented conglomerate of sand. These holdfasts range in length from about 1 cm to over 13 cm. Halimedae with these holdfasts belong to the Rhipsalis section of the genus (Section IV), a group which contains all the species growing on unconsolidated substrates. Thalli with such holdfasts represent less than one-quarter of the described species, but as a group are the most readily separated. It is possible to find Rhipsalian Halimedae attached to rocks or cobbles, usually where there is a thin layer of sand over the stone. The holdfast is then likely to be at the small end of the size range, but is still definite and is usually clearly separable from Halimedae with holdfasts of the remaining types.

Most Halimedae are attached to a firm, generally stable substrate such as coral rock. The holdfast is usually less than 1 cm long, is frequently inconspicuous, and may be missing from the specimen unless the thallus has been carefully collected. Holdfasts are commonly lacking in dredged material, for example. These smaller holdfasts often appear as orangey-brown, rather tightly compressed mats (e.g. *tuna*). The mats can be peeled off the rock substrate, though the operation is delicate. In some of these holdfasts the filaments remain loose so that the plant appears to be attached to the rock by a random web of fine string.

(i) *Multi-holdfast species*. In a few species there is a complex system of attachments in place of a single holdfast. There are two

multi-holdfast systems: the "rope-like extensions" of *micronesica*, and a system of adventitious attachment found in spreading and cushion life-forms.

FIG. 19. *H. opuntia*, festooning *Acropora* sp. on the reefs of the Similan Islands, eastern Indian Ocean. The spreading thallus is anchored at several places, and the older parts of the thallus (shown near the centre) die away and become separated from the younger portions, producing a clone of several younger thalli. The multi-holdfast system is a useful growth strategy for a clone that may be grazed. Long dimension of the clump in right-centre is approximately 7 cm.

"Rope-like extensions" were described by Hillis (1959) for *micronesica*. Fine rhizoidal-type filaments extend from several apical segments and become intertwined into ropes which attach to the substrate. *Halimeda micronesica* plants may be held down by an orange–brown mat of these ropes which may be up to 6 cm or more in length.

In several species the basal point of attachment is poorly developed and may be difficult to locate, particularly in dried material. Instead, where some of the branches touch the substrate fine rhizoidal filaments may develop, giving attachment. This pattern may occur together with a spreading type of growth where thallus branches along crevices, or over and around coral heads. Adventitious holdfasts occur in some plants of *opuntia* (Fig. 19), *distorta*, *gracilis* and *copiosa*.

(c) *Habit and growth form.* The habit of the various species may be erect, pendant, prostrate or spreading, and may be distinctive for certain species such as the flaccid straggling thalli of the typical *gracilis*, the pendant form of a number of species of the Halimeda section (Section IV), or the generally erect pattern of members of the Rhipsalis. The axis of new growth is predominantly vertical for thalli with erect or pendant habits, horizontal for those that are prostrate or spreading. Some members of the section Opuntia, with their sprawling habit, may exhibit both horizontal and vertical axes of strong growth.

2. *Microscopic characters*

Three main sets of microscopic characters are useful in the taxonomy of *Halimeda*. They are:

pattern of medullary filaments at the node (Table III; Figs 3, 15);
size and appearance of primary, secondary and tertiary utricles (Figs 17, 20);
pattern of cortex, and extent of its development (Fig. 20).

The use of these characters almost always requires the magnification of low and high powers (× 10 and × 40) of a compound microscope, preceded by selection and preparation of the material.

(a) *Choice of segments for examination.* In using these characters to identify Halimedae, it is important to select only mature segments from the plant. In so doing much of the variation which is the product of growth rather than of the individual species is avoided. The ideal segment for examination is free of epiphytes and usually is about the middle of the thallus. Material from such a location is nearly always old enough to be reasonably calcified, but has not developed various features of aged or senescent segments which could mislead. The variations I describe herein and the range of measurements given in this section and in Section IV are from such "mature" segments. Some

of the changes associated with yet older segments are also included in the account if they can be used in species identification.

(b) *Preparation of material*

(i) *For nodal structure.* Generally all the required information can be obtained by removing from the nodal region a thin rectangular strip approximately 6 mm long, 1·5 mm broad and the thickness of the segments included. The long axis of the rectangular strip should be along an imaginary line connecting nodes of sequential segments. The sample should include a small portion of the segments adjoining the node. If material is scarce, as it generally is with herbarium specimens, one can generally manage with only part of a node. By such parsimonious tactics, adjoining segments remain attached and the continuity of the thallus is maintained. If material is ample, as generous a strip can be cut as is desired. This rectangular strip may be sectioned or dissected.

For routine taxonomic examination the information on nodal structure often can be obtained from sections, and I prefer this approach because one frequently can obtain data on other microscopic characteristics from the same preparation.

A satisfactory technique is to section the strip lengthwise on a smooth card with a razor blade, using the short edge of a microscope slide as a guiding edge.

With a slightly moistened needle transfer the sections to a drop of water on a slide, decalcify with about 20% hydrochloric acid, remove excess acid with a tissue, and resuspend the sections in water. This sometimes is sufficient preparation, particularly if the material is living, and all that is needed before examining with a compound microscope is to add a coverslip. The slides subsequently may be made semi-permanent by infiltrating with glycerine or another medium if desired.

With some types of nodal structure, and with dried thin specimens, some teasing or dissecting apart of deflated filaments in the sections, with fine needles or fine pins such as insect mounting pins, is required before examining.

Entire nodes also may be decalcified and dissected for the required information. This technique is the obvious one for a species such as *cryptica* with only one nodal filament. For some species, however, the resultant numbers of filaments make elucidating the structure more difficult than working from sections.

(ii) *For surface of peripheral utricles.* The diameters of the peripheral (primary) utricles and surface detail are obtained from a

thin slice of a bit of surface from about the centre of a segment. Place it in a drop of water on a slide making certain the outer surface is outermost, decalcify with 20% hydrochloric acid, drain excess acid with a tissue and refloat in water. The preparation is ready for examining with a compound microscope.

(iii) *For inner utricles and development of cortex.* Much of this information can be obtained from the same sections prepared for nodal examination if the rectangular strip removed extends sufficiently deeply in the segment below the node sampled. However, if a nodal sample was not made, cut a similarly shaped piece, oriented along the same axis, from slightly above the centre of the selected segment. Section and prepare according to the instructions for nodal preparation.

(c) *Pattern of medullary filaments at the node.* The character of medullary filament pattern at the node was referred to at some length in Section II because it is essentially the only character used by Barton (1901) in her taxonomy. The discussion herein involves their interpretation and use in modern *Halimeda* taxonomy.

The three patterns Barton recognized are:

> the filaments all fuse together in a single unit for a short distance (about 1–1·5 times the diameter of the filament) and then separate; openings, pits or pores develop in the walls between adjacent filaments;
>
> filaments fuse for a short distance in pairs and then separate;
>
> filaments fuse completely in twos or threes and do not separate therafter (although the filaments continue their branching pattern).

With Yamada's (1941) new species a fourth category was needed:

> filaments remain separate throughout the node.

A fifth type (Colinvaux and Graham, 1964) has been added:

> node composed of a single filament.

Until the discovery of *cryptica* all known species of *Halimeda* were multiaxial, that is they possessed a core of medullary filaments. Species with this fifth pattern of nodal filaments are uniaxial.

The study of nodal anatomy can be as tedious and difficult as Taylor (1950) understandingly writes, and it should not be surprising that the structure one is seeking to unravel is not always clear cut. Since Barton's publication in 1901, many hundreds of Halimedae have been examined, and many new species recognized. The effect has been not only to add new categories of nodal pattern, but also to extend or modify the definition of patterns already recognized.

The most difficult categories are the second and third which involve fusion of filaments in small groups, and they have sometimes been considered subunits of but one category (Taylor, 1950; Hillis, 1959). However, with the many additional species now placed in these categories this treatment no longer seems appropriate. In spite of apparent overlap, the two categories are distinct and should be considered of equal importance to the others. It has been necessary, however, to modify their definition. These new, or extended definitions have been used in Table III which is an illustrated listing of the five patterns, together with the species in which they are found. Modifications and variations are discussed below.

(i) *Further definition of second and third patterns of nodal filaments, and their variations.* In both categories fusion may be for a very short distance (approximately 1·5 times the filament diameter) or may be complete, with the participating filaments continuing as one filament which subsequently branches. These sometimes are referred to as "short" and "complete" fusion respectively.

In both categories the fusion may involve units of up to six filaments, and possibly more (Colinvaux, 1968a, and unpublished).

In both categories the occasional filament may remain separate. Such anomalous behaviour is perhaps most likely in filaments with a peripheral position (Colinvaux, 1968a, and unpublished).

Also, in certain species of both categories the fused units may adhere laterally, giving the impression of fusion into large bundles. Such adhesion may be demonstrated by teasing apart the units. This can be done with care, and the filament walls remain intact (Hillis, 1959; Colinvaux, 1968a).

However, in species of the second category, which is delimited (Table III) as "filaments mostly fuse in pairs for a short distance", this is the predominant type of nodal filament pattern. In addition, the participating filaments generally are not intricately intertwined before fusion. Therefore, the pattern "definite short fusion in pairs by most or all of the filaments, with participating filaments very little entangled" is diagnostic, whenever observed, for the species listed, that is, for the entire section Opuntia (Section IV).

Category three now is delimited as "filaments fusing in small groups, commonly twos or threes, for a short distance (approximately 1·5 times the filament diameter) or completely; filaments are frequently much intermeshed before fusing" (Table III). This category contains the greatest number of species, is the most variable, and its species are often the most tedious to dissect. The nodes may contain a more or less equal mixture of "short" and "complete" fusion units, or completely

TABLE III. PATTERNS OF NODAL MEDULLARY FILAMENTS

| *Type of pattern* | | *Section and species* |
|---|---|---|
| 1. Filaments come together essentially in a single unit, and intercommunicate by pores, then separate. In some species or specimens pores may be small, or connections between filaments weak. | | Rhipsalis<br>*incrassata*<br>*simulans*<br>*monile*<br>*cylindracea*<br>*macroloba*<br>*favulosa*<br>*stuposa*<br>*borneensis* |
| 2. Filaments mostly fuse in pairs for a short distance. The left-hand type is the most usual. (Arrows indicate position of node.) | | Opuntia<br>*opuntia*<br>*goreauii*<br>*velasquezii*<br>*minima*<br>*renschii*<br>*copiosa*<br>*distorta* |

3. Filaments fuse in small groups, commonly twos or threes, for 1·5 to several times the filament diameter, or "short" and "complete" fusion respectively, and may be mixed in the same node. Filaments immediately below node frequently interlaced.

Halimeda
*tuna*
*discoidea*
*scabra*
*macrophysa*
*cuneata*
*gracilis*
*lacrimosa*
*bikinensis*
*gigas*
*lacunalis*
*taenicola*

4. Filaments unfused.

Micronesicae
*micronesica*
*fragilis*
*melanesica*

5. Node composed of a single filament.

see Figs 3, 15

Crypticae
*cryptica*

fused units may definitely predominate. The participating filaments may be so interlaced that the structure is very difficult to sort out, and the whole may be further complicated by the fused units firmly adhering for a length approximately equal to the diameter of a filament (Hillis, 1959), so that initially one feels that all the filaments are fused together as in pattern one.

(ii) *Variations in the other three categories of nodal filaments.* For most species of the first group (filaments fusing into a single unit) nodal structure is unequivocable. The pores associated with this pattern of filaments generally show up well if good longitudinal sections are made. The pores are lined up in adjacent filaments, and all the filaments appear to be involved in the fusion. Diagnosis for such material is straightforward. Occasionally, however, particularly in material of *simulans*, the pores may be small and relatively inconspicuous (Hillis, 1959). And in some specimens the connections between some of the filaments may be delicate and easily broken, giving the impression that the nodal structure is that of two or three large groups. Hillis (1959) reported this for *monile*. Occasionally, in *monile* two or three separate bundles of fused filaments occur.

The fourth group (separate filaments) is essentially uncomplicated, except that the filaments may adhere, usually only slightly, and then have to be gently teased apart without tearing, to establish the absence of fusion. In *melanesica* a very few filaments may join briefly in pairs.

The fifth category (a single filament) is straightforward.

(d) *Pattern of peripheral or primary utricles.* Useful characters are:

diameter in surface view;
surface appearance;
presence of spines (in *scabra*);
type and extent of lateral adhesion of adjacent utricles;
number borne by a single secondary utricle.

Length of these utricles, although usually given in species descriptions, has not proved useful taxonomically.

For the first two of the characters surface sections are required; for the remainder, longitudinal sections are used. In three species surface characteristics are so outstanding that these microscopic characters may be checked in the field without magnification, or with a $\times 10$ handlens, and the identification subsequently verified in the laboratory. These species are *scabra*, *macrophysa* and *favulosa*.

(i) *Identification without a microscope.* In *scabra* the surface of each peripheral utricle is prolonged into a spine (Fig. 20, No. 4), a feature which occurs in no other *Halimeda*. Consequently, thalli of this species without a surface growth of epiphytes feel slightly rough. This character may be used, with extreme caution, to distinguish *scabra* from *tuna* in the field. *Halimeda scabra* may be often bypassed in Caribbean reefs where it grows because it is considered to be *tuna*. Field identification should be checked with a handlens or (preferably) a microscope to verify the presence of spines. A lateral view (as in a longitudinal section) is preferred.

*Halimeda macrophysa* can be tentatively identified in the field by the very finely stippled appearance of the segment surface (Fig. 40). This pattern results from exceedingly large surface utricles which are round rather than hexagonal in appearance (Fig. 17, No. 16) and are separated by calcium carbonate partitions. However, if a first-time field identification for a given site is made this way, it should be verified microscopically.

*Halimeda favulosa* may give somewhat the same impression as *macrophysa*. The diameters of its surface utricles are larger, but the calcium carbonate partitions are not as complete. The two species cannot be confused because they look different macroscopically, and there is no overlap of distribution.

An awareness of this characteristic for *favulosa* may ease its being mistaken, and therefore bypassed in the reef, for *incrassata* which is considerably commoner.

(ii) *Surface diameter of peripheral utricles.* The surface diameters of the peripheral (primary) utricles together with their surface appearance are, perhaps, the most useful characters for separating *Halimeda* species at the microscopic level, and surface preparations are the most easily made. With × 100 magnification these utricles generally appear as a "sheet of polygons" or like a honeycomb. Sometimes the units are roundish, and then may be disconnected rather than united into a "sheet". High-power magnification (× 400) is usually required for accurate measurement.

The range in diameters is shown in Fig. 17. The smallest occur in species of section Opuntia; the largest are in the species *favulosa*.

(iii) *Surface appearance of peripheral utricles.* The predominant surface pattern of the peripheral utricles is hexagonal (Fig. 17), a result of the pressing together of the many branch tips of the cortical filament system. In some species such as *macrophysa*, the separateness of the utricles is maintained by relatively thick deposits of calcium carbonate between utricles, and the utricles retain their roundness. Intermediate

FIG. 20. Sagittal sections through an outer portion of about the middle of a *Halimeda* segment to show different characteristics of the cortical utricles, and of the extent of development of the cortex. A portion of the medulla is included in each. Important characters for the primary utricles are the extent of their lateral attachment, which ranges from about half their length in Nos. 10 and 11 to a thin platform-like edge in Nos. 9 and 12, to none at all in Nos. 1, 8 and sometimes 20; and the number of peripheral utricles supported by each secondary utricle, which ranges from 1, 2 or 4 in No. 20 to 14 in No. 11 and 18 in No. 12, but the usual number for most species is 2 or 4. (All the utricles supported cannot be shown in a two-dimensional drawing, but the range is apparent.)

Useful taxonomic characters of the secondary and tertiary (inner) utricles include shape, diameter and length. In diameter, the largest secondary utricles are the bullate ones of *discoidea* (No. 11). Numbers 12, 9 and 3 are swollen at their peripheral ends. The tertiary utricles of No. 14 are diagnostic, except for some regional specimens of *discoidea* which have a swollen tertiary layer (see text).

There are two general patterns of development of the cortex. Most species have

conditions occur in other species where the calcium carbonate deposits do not extend as completely to the surface and some of the utricles are slightly attached to each other.

An illusion of roundness seems to be produced by preparations from a few species, especially *gracilis* and *lacrimosa*. However, by focusing up and down with the microscope, very faint hexagonal lines can generally be observed (Hillis, 1959). The appearance seems to result both from the slightly convex outer surface of the peripheral utricles and by adjacent utricles touching only very slightly.

There are other variations. The walls appear somewhat thicker in *stuposa* and *cylindracea* for example (Hillis, 1959), and in *velasquezii* and *cylindracea* the "covering lamella" (Section I) of the outer surface of the peripheral utricles (Taylor, 1962, for *velasquezii*; Borowitzka and Larkum, 1977, for *cylindracea*; both using the term "cuticle") appears to be more prominent than in some other species. This may also vary with condition of the material.

Yet another variation occurs in *cuneata*, *discoidea*, *gigas*, *taenicola*, *tuna* and sometimes other species, in the occasional lateral fusion of adjacent utricles in twos, threes and rarely fours (Fig. 17, Nos. 11, 12; Fig. 20, Nos. 5, 11). This fusion is distinct from adhesion, the usual pattern, where the utricles retain their individual walls.

(iv) *Lateral adhesion of adjacent peripheral utricles.* Longitudinal sections (Subsection 2.b.iii) are required to observe this character.

Adjacent peripheral utricles usually adhere where they touch. In *cylindracea*, and very possibly all of the species, this appears to be brought about by the fusion of the covering lamellae of the participating utricles (Borowitzka and Larkum, 1977). The remainder of the filament walls in the region of contact generally retain their distinctiveness, although there are exceptions as noted in Subsection (iii).

The extent, or length, of the adhesion ranges from none (*macrophysa*, *fragilis* and often *favulosa*) to about half their length (*cuneata* and *discoidea*; Fig. 20). In *lacrimosa* and *gracilis* it is restricted to a thin

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distinct utricles (are utriculiform); but in species of section Opuntia and a few other species the utricles, formed by dichotomous branching, are not swollen or specialized, and hence appear like regular branches. This type of cortical development is shown in Nos. 1, 2 and 6.

(1) *H. fragilis*; (2) *H. micronesica*; (3) *H. bikinensis*; (4) *H. scabra*; (5) *H. gigas*; (6) *H. opuntia*; (7) *H. tuna*; (8) *H. macrophysa*; (9) *H. gracilis*; (10) *H. cuneata*; (11) *H. discoidea*; (12) *H. lacrimosa*; (13) *H. lacunalis*; (14) *H. taenicola*; (15) *H. simulans*; (16) *H. monile*; (17) *H. macroloba*; (18) *H. stuposa*; (19) *H. cylindracea*; (20) *H. favulosa*; (21) *H. incrassata*. The long scale applies to No. 6; the short scale to the others. (Adapted from Hillis, 1959.)

platform-like edge of the utricle (Hillis, 1959), so that these utricles may separate readily after decalcification if the coverslip over the preparation is pressed gently.

The degree of adhesion also varies somewhat with the age of the segment. In some species at least, the utricles, while adhering in young and mature segments, may separate readily in old yellowish or whitish basal segments (Hillis, 1959), and sometimes in mature segments as well (Fig. 17).

(v) *Number of peripheral utricles supported by a secondary utricle.* Longitudinal sections (Subsection 2.b.iii) are required to observe this character, and some of the range is illustrated in Fig. 20.

Usually 2 or 4 peripheral utricles are supported by each secondary utricle. In *favulosa*, however, sometimes only one is borne on a secondary utricle, in *bikinensis* and *gracilis* up to 8 frequently may be so supported, with as many as 14 in *discoidea* and 18 in *lacrimosa*. Numbers between 2 and 8 occasionally occur in species in which 2 or 4 are usual (Hillis, 1959).

(e) *Shape, diameter and length of inner utricles.* Inner utricles show up in longitudinal sections like those described in Subsection 2.b.iii. They are best seen at $\times 100$ magnification when they appear rather like expanded sacs, or sometimes as continuations of filaments, between the outermost (primary) utricles and the longitudinally oriented medullary filaments. Striking differences in shape and diameter are apparent in different species, and length may also be a useful parameter. High-power magnification ($\times 400$) should be used in measuring the diameters of the inner utricles at the small end of the size range. Utricle diameter is measured at what is usually the broadest part, just below the insertion of the primary utricles.

The most dramatic secondary utricles are the greatly swollen "bullate" utricles of the Atlantic *discoidea* (Fig. 20, No. 11), and in these plants usually only two layers of utricles, the peripheral and secondary, are present. In Pacific–Mexican and Hawaiian *discoidea*, a third or tertiary layer of utricles is commonly present and then the secondary utricles are less conspicuous and at the lower end of the size range (Howe, 1911; Hillis, 1959).

Other distinctive secondary utricles are those of *lacrimosa*, and to a lesser extent *gracilis* (Fig. 20, Nos. 12 and 9, respectively). Those of *lacrimosa* are frequently very long and are much swollen at their peripheral end. Those of *gracilis* are of a similar style, long and swollen, but the amount of distension at the peripheral end is considerably less and sometimes almost imperceptible (Hillis, 1959, and Section IV).

It is the tertiary utricles of *taenicola* that are swollen and distinctive (Fig. 20, No. 14), rather like the secondary utricles of *discoidea* (Taylor, 1950; Hillis, 1959).

Length of the inner utricles in some species varies considerably with the age of the material or the number of layers of utricles. It is therefore generally not a helpful character.

(f) *Pattern and extent of inner cortex.* For many species the distinctiveness of the inner cortex lies as much in the pattern formed by the inner utricles (inner cortex) as a whole, as in the initial distinctiveness of secondary or tertiary utricles. The pattern may be observed in sagittal sections (Fig. 20).

There are two general patterns of development of the cortex (Hillis, 1959, and Fig. 20).

The branching and rebranching of the lateral filaments may be accompanied by generally pronounced constrictions and wall thickening at the sites of branching, and swelling of the intervening regions. These swollen regions form the distinctive utricles. Branching to form the inner utricles is generally tri- or tetrachotomous.

The branching and rebranching of the lateral filaments is dichotomous, and is not accompanied by pronounced constrictions at sites of branching, or by swelling of the intervening regions. The utricles appear like continuations of the branches.

The second of these patterns occurs in the Opuntia group of species (nodal filaments mostly fusing in pairs for a short distance) (Hillis, 1959; Colinvaux, 1968a), as well as in the sections Micronesicae (except for *melanesica*) and Crypticae (see Table III for species included and later (overleaf) for a discussion of sections). Somewhat modified, it also appears in *gracilis*, *lacrimosa* and *bikinensis*.

The first pattern occurs in members of section Rhipsalis and many members of section Halimeda. In members of the Rhipsalis except for *favulosa*, the diameters of the utricles become progressively larger proceeding towards the medulla.

(i) *Extent of inner cortex.* The number of layers of utricles in the cortex may be a helpful taxonomic character for some determinations, although this character is more variable than many of the others.

The number of layers ranges from two to five, rarely six, with two usual in *discoidea*, *gigas* and *macrophysa*, and five in *opuntia* and some of the species belonging to section Rhipsalis. Exceptions include the presence of a third layer in some material of *discoidea* (Subsection (e) above), and sometimes only two layers in *lacunalis*, where usually there are three.

Extent of the cortex also varies with other factors including age and location in the segment. The number of layers is generally fewer in young segments, and greater in old basal segments which are often greatly thickened. Their number frequently is reduced or they may be absent in the vicinity of the node (Fig. 6), with peripheral utricles then being supported directly by short, unmodified branches of the medullary filaments. And, in *cryptica*, a Caribbean species found often in heavily shaded crevices at depths of about 25 m or greater (Colinvaux and Graham, 1964), and which grows more openly in the reef to 100 m (Moore *et al.*, 1976), the cortex of the under (umbral) surface is frequently somewhat atrophied. Asymmetry in cortical development between the two surfaces of a segment is not conspicuous in typical thalli of the other known *Halimeda* species.

### B. *The genus and its sections*

Although the pattern of nodal filaments can no longer be relied on almost exclusively for separating the species of *Halimeda* as Barton chose to do, it is helpful and reliable for recognizing groups of species. I became increasingly aware of the significance of this feature, as a kind of "master character", while working on my 1959 revision (Hillis, 1959), and in it referred to *tuna* and *incrassata* complexes. From continued herbarium studies, combined with more extensive field work, I have found that separation along these lines not only seems valid on the basis of phylogenetic implications, but also that each of these patterns of nodal filaments is frequently accompanied by other similarities. This seems especially true of a number of habit characters, and is well illustrated by species with the *incrassata* type of fusion (Table III, filaments fuse into a single unit), all of which possess a large bulbous holdfast and grow erect, or essentially so, in an unconsolidated substrate. These groups appear to represent natural units within *Halimeda* which should be recognized formally.

A meagre framework for sections within the genus exists in the extensive publication on algal systematics by Agardh (1887), in which four subcategories, Tunae, Pseudo-Opuntia, Opuntiae and Rhipsales, are indicated (Table IV). De Toni (1889) called them sections and applied Agardh's descriptions to them. Since appearance of the segments is the major character used, it perhaps is not surprising that the categories, as delimited, do not seem meaningful or useful. They were not even mentioned a few years later by Barton (1901). Indeed, they disappeared from use with De Toni (1889). Agardh's framework can be developed, however, into a modern system of categories delimiting various species groups.

TABLE IV. THE CATEGORIES OF *Halimeda* SPECIES DELIMITED BY J. AGARDH (1887), RECOGNIZED AS SECTIONS BY DE TONI (1889)

"Species, aegre characteribus circumscribendas, sequenti mode disponere conatus sum:

I. *Tunae* virescentes, parum incrustatae, adscendentes aut erectiusculae, articulis planis enervibus, simplicibus discoideis, ramos generantibus saepe subreniformibus, margine plerumque integerrimis."
*H. tuna, H. papyracea, H. macroloba,* (*H. macrophysa*[a])

II. "*Pseudo-opuntiae* albescentes et evidentius incrustatae, diffusae aut stipitatae articulis superioribus orbiculatis aut subreniformibus planis, saepius enervibus et margine integerrimis, plerumque in longos ramos simpliciusculos concatenatis."
*H. gracilis, H. nervata, H. brevicaulis*

III. "*Opuntiae* albescentes et evidentius incrustatae, conglobatae aut diffusae, nunc stipitatae, decomposito-ramoisissimae, articulis superioribus planis reniformibus, diametro transversali longitudinalem superante, enervibus aut plus minus conspicue nervosis, nervis ad lobos marginis superioris, saepe ramos plures generantes, excurrentibus."
*H. cordata, H. opuntia* (f. *opuntia,* f. *tribola*), *H. incrassata* (f. *ovata,* f. *Lamourouxii,* f. *tridentata*)

IV. "*Rhipsales* ex veridi aut cinereo albescentes et evidentius incrustatae, erectiusculae et saepius stipitatae, articulis aut teretiusculis, aut complanatis et a basi cuneata dilatatis, diametre longitudinali transversalem aequante aut superante."
*H. obovata, H. versatalis, H. tridens, H. cylindracea, H. monile, H. polydactylis,* (*H. renschii*[a])

"Species mihi ignota
*H. discoidea.*"

[a] Species added by De Toni.

The obvious character around which sections of the genus *Halimeda* should evolve is that of medullary filament pattern at the nodes. This character is the most important one in the taxonomy of the genus, and so may be expected to reflect fundamental phyletic divergence. The five groupings given in Table III, based on pattern of medullary filaments, provide a logical framework for sections of the genus. Consequently, I propose they be designated as sections, and called Rhipsalis, Opuntia, Halimeda, Micronesicae and Crypticae. The nodal structure on which they are based, and the species each contains, are shown in Table V. Formal descriptions are given in Section IV.

TABLE V. TAXONOMIC SECTIONS OF *Halimeda*, WITH THEIR SPECIES, AND THE MEDULLARY FILAMENT PATTERN OF THE NODE WHICH DEFINES THEM, TOGETHER WITH OTHER CHARACTERISTICS FOUND IN THE SPECIES GROUPS

| *Section and species* | *Nodal type* | *Other features commonly present* | | *Usual substrate* |
|---|---|---|---|---|
| | | *Macroscopic* | *Microscopic* | |
| Rhipsalis | | | | |
| *incrassata, borneensis, cylindracea, favulosa, macroloba, monile, simulans, stuposa* | Filaments fuse in a single unit | Holdfast bulbous, $\geqslant 1$ cm long; habit generally erect, occasionally lax | Inner utricles generally globular to subglobular | Generally soft such as sand, silt, gravel |
| Opuntia | | | | |
| *opuntia, goreauii, minima, renschii, velasquezii, copiosa, distorta* | Filaments fuse mostly in pairs for a short distance | Holdfast $< 1$ cm long, commonly obscure and often $> 1$; thalli often sprawling and extensive | Inner utricles not particularly expanded and of fairly uniform diameter throughout, and from series to series | Hard; many of the species often grow around and over it; sometimes on sand |
| Halimeda | | | | |
| *tuna, bikinensis, cuneata, discoidea, gigas, gracilis, lacrimosa, lacunalis, macrophysa, scabra, taenicola* | Filaments fuse in small groups for 1·5 to several times filament diameter | Holdfast usually $< 1$ cm long, often more conspicuous than in section Opuntia; segments generally reniform, subreniform, discoidal, cuneate or globular | Inner utricles expanded in various ways | Hard |

| | | | | |
|---|---|---|---|---|
| Micronesicae | | | | |
| *micronesica, fragilis, melanesica* | Filaments remain entirely separate (although there may be some adhesion) | Holdfast < 1 cm long; habit may be spreading and with > 1 holdfast, but thallus form discrete, not sprawling | Inner utricles generally as for Opuntia | Hard |
| Crypticae | | | | |
| *cryptica* | Node of but a single filament | Holdfast < 1 cm long; two surfaces of segment of distinctly different colour, upper greenish, lower whitish; node appears delicate and somewhat stalked; habit pendant or prostrate | Inner utricles generally as for Opuntia, those of lower surface may be somewhat atrophied | Hard |

The first two section names are taken from Agardh with spelling altered to the proper endings. The change from Tunae to Halimeda is required by the International Rules of Botanical Nomenclature, since this section includes the type genus *tuna*. Agardh's fourth section, Pseudo-Opuntiae, to which he assigned *gracilis* and two species of uncertain identity, is redundant in this nodal filament system since *gracilis* has been included in section Halimeda. This name, therefore, is not used. Each of these three sections retains some of the species originally placed in it by Agardh.

The two new categories, Micronesicae and Crypticae, have each been given the epithet (with appropriate ending) of the first species described with the pattern of nodal filaments characteristic of that particular section.

Section Crypticae (at present with only one species) could, with its single medullary filament, be considered an extreme form of section Micronesicae. Such treatment, however, with its phylogenetic implications, does not seem justified by our present knowledge of the species involved, which includes a distribution of Caribbean for section Crypticae and Indo-Pacific for Micronesicae. I consider them two separate groups.

For all five sections the only character truly diagnostic is the pattern of the filaments at the nodes. However, a few other characters, some of them macroscopic, seem to be associated, fairly reliably, with the nodal groups. These also are given in Table V.

Finally, the original circumscription of the genus by Lamouroux (1812) described its construction as multiaxial ("axe fibreux"). This excludes the uniaxial species *cryptica*. Therefore, in Section IV, the genus description is extended to include uniaxial as well as multiaxial species.

### C. *The genus* Halimeda *in higher taxonomy*

For the first few decades of the twentieth century *Halimeda* seemed securely placed in the order Siphonales. But just as taxonomy within the genus is changing to reflect new knowledge and concepts, so too is that above the genus level. New tools such as the electron microscope enable us to probe the structure of these algae more precisely, while improved culture and chemical techniques provide additional data on life-histories and chemical organization, and lead to new insights and evaluations of the position of *Halimeda* and its close relatives within the plant kingdom. A survey of some of the taxonomic changes is provided

in Table VI. Other aspects of a history which impinge on *Halimeda* are presented by Chapman (1964), Ducker (1967), Egerod (1952), Parker (1970) and Round (1963, 1971).

### 1. *Classification of* Halimeda *in the early twentieth century*

When Barton wrote her monograph on *Halimeda* she considered the genus belonged to the "order Siphoneae in the group Chlorophyceae". The descriptive term for this designated order was first introduced into the algal literature by Greville (1830), to delimit those green algae with "frond either composed of membranous, filiformis, single or branched tubes, or formed of a combination of similar tubes". It included the genera *Codium*, *Bryopsis*, *Botrydium* and *Vaucheria*. Blackman and Tansley (1902) formally established the order Siphonales for this group of plants which by then included *Halimeda*. They subdivided their new order Siphonales into two suborders, the Siphonocladeae for septate thalli, and the Siphoneae for those that were non-septate, that is, coenocytic. Soon afterwards Oltmanns (1905) elevated the first group to order status (Table VI), leaving only true coenocytes in the Siphonales.

### 2. *Subdivision of the Siphonales: Setchell and Feldmann*

Setchell (1929), in a discussion of the taxonomic position of *Microdictyon*, referred to the incorrectness of Siphonales as an ordinal name (since it was not based on the name of a genus), and mentioned, without discussion, that this order would be better separated into Codiales and Caulerpales.

Feldmann (1946) treated the subject considerably more substantially. Building on the microscopical observations of Ernst (1904), Czurda (1928) and Chadefaud (1941), he pointed out that in some members of the Siphonales only one kind of plastid occurred, the chloroplast. Such genera he called homoplastic. In other genera of the Siphonales two kinds of plastid were present, the chloroplast and the starch-storing leucoplast or amyloplast. These genera were heteroplastic. The heteroplastic genera included *Udotea*, *Pseudochlorodesmis* and *Halimeda*, for which "les chloroplastes sont entièrement depourvus d'amidon, l'amylogenèse étant assurée uniquement par les leucoplastes".

Feldmann also noted a complete correlation between wall chemistry as worked out by Mirande (1913) and the nature of the plastids in the siphonaceous taxa that he had studied.

TABLE VI. A HISTORY OF THE CLASSIFICATION OF *Halimeda*[a]

| *Blackman and Tansley, 1902* | *Oltmanns, 1905* | *Gepp and Gepp, 1911* | *Smith (1938), 1955* | *Fritsch (1934), 1948* | *Feldmann, 1946* | *Feldmann, 1954* |
|---|---|---|---|---|---|---|
| SIPHONALES | SIPHONO- | | SIPHONO- | Included in | Distinct from orders below and | |
| S.O. Siphonocladeae | CLADALES | | CLADALES | Siphonales | history not pursued further | |
| S.O. Siphoneae | SIPHONALES[b] | | SIPHONALES[b] | SIPHONALES[b] | EUSIPHONALES[b] (homoplastic) | DERBESIALES |
| | | | Halicystidaceae incl. | Protosiphonaceae incl. | Halicystidaceae | |
| | | | *Halicystis* | *Halicystis* | | *Halicystis* |
| | | | | Derbesiaceae | | |
| | | | *Derbesia* | *Derbesia* | | *Derbesia* |
| | | Bryopsidaceae | | | Bryopsidaceae | Bryopsidaceae |
| | | *Bryopsis* | | | *Bryopsis* | *Bryopsis* |
| | | Codiaceae | Codiaceae | Codiaceae | Codiaceae | Codiaceae |
| | | Codieae | | | | |
| | | *Codium* | *Codium* | *Codium* | *Codium* | *Codium* |
| | | *Pseudocodium* | | | CAULERPALES (heteroplastic) | CAULERPALES |
| | | Udoteae | | | Udoteaceae | Udoteaceae |
| | | *Halimeda* | | *Halimeda* | *Halimeda* | *Halimeda* |
| | | *Udotea* | | *Udotea* | *Udotea* | (*Udotea*) |
| | | *Penicillus* | | *Penicillus* | *Penicillus* | |
| | | *Rhipocephalus* | | *Rhipocephalus* | *Rhipocephalus* | |
| | | *Tydemania* | | | | |
| | | Flabellaricae | | | | |
| | | *Avrainvillea* | | *Avrainvillea* | *Avrainvillea* | |
| | | *Boodleopsis* | | *Boodleopsis* | | |
| | | *Callipeygma* | | | | |
| | | *Chlorodesmis* | | | | |
| | | *Cladocephalus* | | | *Cladocephalus* | |
| | | *Flabellaria* | | | | |
| | | | | | *Pseudochlorodesmis* | |
| | | | | *Pseudocodium* | *Pseudocodium* | |
| | | *Rhipidodesmis* | | *Rhipidodesmis* | | |
| | | *Rhipilia* | | *Rhipilia* | | |
| | | *Rhipiliopsis* | | | | |
| | | | Caulerpaceae | Caulerpaceae | Caulerpaceae | Caulerpaceae |
| | | | *Caulerpa* | *Caulerpa* | *Caulerpa* | *Caulerpa* |
| | | | | *Bryopsis* | | |
| | | | Dichotomosiphonaceae (in Vaucheriaceae in 1933) | | Dichotomosiphonaceae | DICHOTOMOSIPHONALES |
| | | | *Dichotomosiphon tuberosus* | | *D. tuberosus* | |
| | | | | | *D. pusillus* | |
| | | | | Phyllosiphonaceae | | |
| | | | | *Phytophysa* | | |
| | | | | *Ostreobium* | | |
| | | | | Chaetosiphonaceae | | |
| | | | | *Chaetosiphon* | | |
| | | | | *Blastophysa* | | |
| | | | | Vaucheriaceae | | |
| | | | | | Position uncertain | |
| | | | | | Derbesiaceae | |

[a] Some lists may not include all the genera recognized by the authors since some of the papers deal with specific groups.
[b] Not tenable under the rules of botanical nomenclature.

| *Egerod, 1952* | *Chadefaud, 1960* | *Miwa et al., 1961* | *Round (1963, 1971), 1973* | *Christensen, 1966* | *Neumann, 1974* | *Rietema, 1975* | *Bold and Wynne, 1978* |
|---|---|---|---|---|---|---|---|
| SIPHONALES[b] | DERBESIALES | | DERBESIALES | CAULERPALES | CAULERPALES | DERBESIALES | CAULERPALES |
| Bryopsidaceae | | Mannan as main wall constituent | | Bryopsidaceae | | Derbesiaceae | Derbesiaceae |
| | | | *Halicystis* | *Halicystis* | *Derbesia* (*Halicystis*) | *Derbesia p.p.* (= *Halicystis p.p.* | *Halicystis* |
| | | *Derbesia* | *Derbesia* | *Derbesia* | | | *Derbesia* |
| | CODIALES | *Codium* | CODIALES | | | | Bryopsidaceae |
| | | $\beta-1,3$ *xylan* | | | | | |
| *Bryopsis* *Pseudo-bryopsis* | | *Bryopsis* | *Bryopsis* *Pseudobryopsis* *Avrainvillea* | *Bryopsis* | *Bryopsis* *Pseudobryopsis* | *Bryopsidella* (= *Bryopsis halymenia* + *Derbesia neglecta*) | *Bryopsis* *Pseudobryopsis* |
| Codiaceae | | | | Codiaceae | | | Codiaceae |
| *Codium* | | | *Codium* | *Codium* only | | | *Codium* |
| | CAULERPALES | | CAULERPALES | | | | |
| | | | | Udoteaceae incl. | | | Udoteaceae |
| *Halimeda* *Udotea* | | *Halimeda* *Udotea* | *Halimeda* *Udotea* *Penicillus* | *Halimeda* *Udotea* | *Halimeda* *Udotea* | | *Halimeda* *Udotea* *Penicillus* |
| *Chlorodesmis* | | *Chlorodes-mis* | | | | | *Chlorodesmis* |
| Caulerpaceae *Caulerpa* | | *Caulerpa* | *Caulerpa* | Caulerpaceae *Caulerpa* | | | Caulerpaceae *Caulerpa* |
| | DICHOTOMOSI PHONALES | | DICHOTOMOSI-PHONALES (1971) | | | | Dichotomosi-phonaceae |
| | | | *Dichotomo-siphon* *Pseudodichoto-siphon* | | | | *Dichotomo-siphon* |
| | | | PHYLLOSI-PHONALES (1971) | | | | Phyllosiphonaceae *Phyllosiphon* *Ostreobium* |

TABLE VII. FELDMANN'S (1946) SUBDIVISION OF THE SIPHONALES

| *SIPHONALES* | |
|---|---|
| *Homoplastic (chloroplast only)*<br>*Filament wall with cellulose* | *Heteroplastic (chloroplast and amyloplast)*<br>*Filament wall without cellulose* |
| ORDER Eusiphonales<br>Halicystidaceae<br>Bryopsidaceae<br>*Bryopsis*<br>Codiaceae<br>*Codium* | ORDER Caulerpales<br>Udoteaceae<br>*Halimeda, Udotea, Avrainvillea, Penicillus, Cladocephalus, Rhipocephalus, Pseudochlorodesmis, Pseudocodium*<br>Caulerpaceae<br>Dichotomosiphonaceae<br>*D. tuberosus, D. pusillus* |

TABLE VIII. FELDMANN'S (1954) EXTENDED SUBDIVISION OF THE SIPHONALES

| *SIPHONALES*, sensu lato | | | |
|---|---|---|---|
| *Homoplastic* | | *Heteroplastic* | |
| *CODIALES* | *DERBESIALES* | *CAULERPALES* | *DICHOTOMO-SIPHONALES* |
| Life cycle mono-phasic and diplontic | Cycle hetero-morphic | Gametes slightly anisogamous | Oogamous |
| (Not holocarpic) | Zoospores with crown of flagellae | Entire thallus involved in sexual repro-duction, and dies thereafter (holocarpy) | |
| Gametes strongly anisogamous | Anisogamous gametes | | |
| Individual gametangia present | Individual gametangia absent | Individual gametangia absent | |
| *Codium*<br>*Bryopsis* | *Derbesia*<br>*Halicystis* | *Halimeda*<br>*Caulerpa* | *Dichotomosiphon* |

To reflect these differences he proposed a division of the Siphonales into two new orders, the Eusiphonales (a name which was also untenable) and the Caulerpales. Taxa of the Eusiphonales were homoplastic and had a wall containing cellulose; those of the Caulerpales were heteroplastic, and lacked cellulose in their walls. The division into families, and the genera assigned to them are included in Table VII which shows this subdivision of Siphonales.

Feldmann (1954) developed this yet further when, on the basis of available life-history data, he divided his two orders of 1946 (Eusiphonales and Caulerpales) each into two more orders (Table VIII). In doing so he abandoned the epithet Eusiphonales, thereby removing one nomenclatural problem.

From the Eusiphonales he separated the orders Derbesiales and Codiales. The Derbesiales were established as possessing a heteromorphic life-cycle, or a life-cycle in which the alternating gametophytic and sporophytic phases looked very different, and as a consequence may have been given different names. The culture studies of Kornmann (1938) provided some of the basic data, for Kornmann had observed the zoospores of *Derbesia marina* (Lyngbye) Sol., a small, branched filamentous alga, develop into plants identifiable as the sac-like *Halicystis ovalis* (Lyngbye) Aresch. And Feldmann (1950), in the years subsequent to his 1946 paper on siphonalean taxonomy, had linked *Derbesia tenuissima* (De Not.) Crn. with *Halicystis parvula* Schmitz.

In contrast, members of the Codiales were known for a life-cycle in which there was only one free-living phase (haplobiontic) which was diploid in these algae. As another difference between the two new orders special gametangia developed on the filaments of members of the Codiales, whereas specialized structures did not occur in the Derbesiales, the entire thallus of the gamete-bearing phase, *Derbesia*, functioning as a gametangium.

The other two orders of Feldmann's (1954) paper were derived by separating the oogamous *Dichotomosiphon tuberosus* (A. Br.) Ernst, a freshwater filamentous alga, from the Caulerpales, and placing it in its own order because of this distinctive reproductive feature which is unknown in the rest of the Siphonales. In contrast, the Caulerpales, from the data then available on the life-histories of *Caulerpa* and *Halimeda*, produced gametes that were only slightly different (anisogamous). In addition, the entire contents of the thalli of these two genera were transformed into gametes when gametogenesis occurred, so that death of the plant followed sexual reproduction (holocarpy).

In both of the Feldmann (1946, 1954) schemes the classification of *Halimeda* is in the family Udoteaceae of the order Caulerpales.

3. *Caulerpales: its classification among the Chlorophyta, or Chlorophycophyta* (*Papenfuss*, 1946)

(a) *Round's scheme of classification.* Relatively recently Round (1963, 1971) considered the classification of the Chlorophycophyta as a group, and his 1971 scheme is shown in Fig. 21. Only that part which impinges on *Halimeda* will be discussed.

The old order Siphonales is replaced by five orders, four of which are those of Feldmann (1954). In the fifth, Phyllosiphonales, Round places the single genus *Phyllosiphon*, which, as he suggests, may belong to the Xanthophyceae. *Ostreobium*, which is commonly allied with *Phyllosiphon* and which would seem reasonable to include here, is mentioned with the Chlorochytriales. Families within these orders are not discussed in these papers.

Round (1963, 1971) places the siphonaceous orders in the separate class Bryopsidophyceae, and within the class recognizes the three groups or "cohorts" as he calls them, and which appropriately could be considered subclasses, of Hemisiphoniidae, Cystosiphoniidae and Eusiphoniidae, which were set up by Chadefaud (1960) as Hémisiphonées, Eusiphonées cystosiphonées and Eusiphonées typiques. The orders within each are shown in Fig. 21. The Hemisiphoniidae, with walls dividing the thallus into multinucleate units, is the simplest of the three groups. Members of the Cystosiphoniidae produce cysts and may or may not have segregative division. Taxa belonging to Eusiphoniidae possess the additional carotenoid pigments siphonein and siphonoxanthin, have polysaccharides other than cellulose in their cell walls, and do not have the special characteristics of the other two groups.

(i) *Advantages of Round's scheme.* For siphonaceous algae the system of cohorts (subclasses) brings together three series of green algae with the multinucleate condition. The designation of a separate class (Bryopsidophyceae) for this group of three recognizes some of their distinctive differences from the other green algae, and seems particularly reasonable in a system which recognizes a number of classes of green algae (Zygemaphyceae, Oedogoniophyceae and Chlorophyceae). There are, as Round (1971) summarizes, a number of important features in the Bryopsidophyceae such as pigments, wall chemistry and plastid structure which separate them from the class Chlorophyceae, but none of these embraces the class as a whole.

(b) *Classification scheme of Bold and Wynne* (1978). In their massive and splendidly comprehensive introductory text on the algae these two authors recognize 15 orders within the division Chlorophycophyta (Table VI). One of these, the Caulerpales, replaces the former

FIG. 21. A classification scheme of the "green algae", by Round (1971). The "Siphonales" are placed in the five orders listed under the "Eusiphoniidae".

"Siphonales" in such a scheme. Within it 7 families are recognized: Derbesiaceae, Codiaceae, Bryopsidaceae, Udoteaceae, Caulerpaceae, Dichotomosiphonaceae and Phyllosiphonaceae.

(i) *Advantages of the Bold–Wynne scheme.* The recent discoveries such as chloroplast organization and wall chemistry are clearly and well described in the text dealing with the Caulerpales, and the authors have avoided premature taxonomic changes by treating the order as a broad assemblage of a number of families.

(c) *Validity of life-history, plastid and filament-wall data.* There is the urge, as well as the goal in classification schemes, to present the interrelationships of the various categories and the evolutionary trends. The three criteria used by Feldmann (1946, 1954), plastid structure, wall-chemistry and life-history data, appeared to provide such an approach for the truly siphonaceous algae.

In the intervening years, however, difficulties have developed with the use of each of these criteria. There also has been some support.

(i) *Life-history data.* Culture studies by Hustede (1964), subsequently confirmed by Rietema (1975), have indicated that *Bryopsis halymediae* Berth. and *Derbesia neglecta* Berth., taxa placed in different orders by Feldmann (1954), are alternate phases in the life-cycle of a single taxon. And Rietema (1969, 1970, 1975), working with several populations of *Bryopsis plumosa* (Hudson) C. Ag. in culture, has obtained a second life-cycle phase, a microthallus which, depending on the population, produces the familiar *Bryopsis* thalli directly, or produces zoospores which give rise to the *Bryopsis* thallus.

The linking of *Bryopsis* sp. and *Derbesia* sp. in a single life-cycle, the presence of heteromorphic life-cycles in some members of the Codiales, and other life-history data do not support the recognition of two separate orders Codiales and Derbesiales using the life-history criteria of Feldmann (1954). This conclusion was also reached by Rietema (1975), and Bold and Wynne (1978) suggest that the separation into two orders was premature. Hoek *et al.* (1972) earlier indicated problems with the division.

In contrast, the life-history character Feldmann (1954) applied to the Caulerpales, holocarpy or the complete involvement of the thallus in the production of gametes and its death thereafter, has received some additional support. Feldmann could cite only two examples, *Halimeda* and *Caulerpa*, where such a pattern had been observed. Holocarpy has now been reported for *Chlorodesmis* (Ducker, 1965), *Penicillus* (Hillis-Colinvaux, 1973; Meinesz, 1975) and *Udotea* (Nizamuddin, 1963). The one apparent modification is that holocarpy may involve only a portion

of the thallus. In my laboratory aquaria I have occasionally observed *Halimeda* to produce the conspicuous grape-like clusters of gametangia on only one to two branches of the thallus, or a relatively small portion of the entire plant. Subsequently, it was only this part of the plant that died.

Although the entire thallus (or branch) is involved in this production of gametes, specialized gametangia are formed in the process. Feldmann (1951) had described them on a Mediterranean *Halimeda*. Hence his key character "holocarpie sans gamétocystes individualisés" is surprising, and is misleading for *Halimeda*, although appropriate for *Caulerpa* as currently known. For the Codiales he indicates "gamètes . . . se formant dans des gamétocystes individualisés". The difference between the Codiales and Caulerpales, based on the available sexual thalli, is more appropriately described as the presence of a cross wall at the base of the gametangium in the Codiales, its absence in the Caulerpales.

(ii) *Wall chemistry.* Parker (1970) provided a very useful review of wall chemistry which included this group of algae and presented the problems of using this character for taxonomy. Data available on Caulerpalean algae have shown β-1,3-xylan to be a component of *Caulerpa, Chlorodesmis, Halimeda* and *Udotea* (Miwa *et al.*, 1961; Parker, 1970). It also occurs in *Penicillus*, and in *Dichotomosiphon*, the only member of the Dichotomosiphonales of Feldmann's classification (Frei and Preston, 1964), as well as in algae that would not be assigned to either the Caulerpales or Dichotomosiphonales, such as *Bryopsis* sp. (Miwa *et al.*, 1961; Frei and Preston, 1964; Maeda *et al.*, 1966). The complexity of wall chemistry and the difficulties of applying it broadly in the siphonaceous algae have recently been illustrated by the identification of different wall polysaccharides as predominating in alternating stages of the life-cycle of some taxa (Huizing and Rietema, 1975). Their evidence showed a mannan (probably β-1,4-mannan) as the principal filament-wall polysaccharide of the sporophytic stages of *Bryopsis plumosa* (Huds.) C. Ag. and *Derbesia tenuissima* (De Not. in Mor. et De Not.) Crouan frat. (Banyuls material), and a xylan (probably β-1,3-xylan) and cellulose as predominant wall polysaccharides of the gametophytic stages of both genera.

The work of Huizing and Rietema (1975), as they point out, does not support the division of the siphonaceous green algae into a "xylan group" (including *Bryopsis*) and a "mannan group" (including *Derbesia* and *Codium*) as proposed by Miwa *et al.* (1961) and adopted by Maeda and Nisizawa (1972). However, the evidence so far available on wall chemistry in Caulerpalean genera (*sensu* Feldmann, 1954) indicates that

the β-1,3-xylan of their walls may be a consistent characteristic. Round (1971) has accepted it as such. There is a need, however, to examine the walls of many more of the genera within the group, as well as of different species, particularly of *Caulerpa* where there is a range of chloroplast structure. The walls of holdfast filaments of different species of *Halimeda* should also be examined, as well as those of the filament developing from zygotes (Section VII).

(iii) *Plastid structure.* The presence of only one kind of plastid (the chloroplast) or of two kinds (chloroplast and amyloplast) with distinct photosynthetic and storage roles was the basis of Feldmann's separation (1946) of Caulerpalean and non-Caulerpalean orders of siphonaceous algae.

Amyloplasts or starch-storing plastids have been demonstrated in species of *Avrainvillea*, *Caulerpa*, *Chlorodesmis*, *Halimeda* and *Udotea* (Hori and Ueda, 1967, 1975), and in *Penicillus* (Turner and Friedman, 1974). Hori and Ueda (1967, 1975) report their absence in species of *Codium*, *Derbesia*, *Bryopsis* and *Pseudodichotomosiphon*. Concentric lamellar systems (Section I) have also been demonstrated in the amyloplasts of the above genera and in the chloroplasts of all but *Avrainvillea* (Hori and Ueda, 1967, 1975), and may be a Caulerpalean characteristic. Workers who have made similar observations on one or more of the above taxa include Descomps (1965) on *Caulerpa*, *Halimeda* and *Udotea*; Dawes and Rhamstine (1967) on *Caulerpa*; Sabnis (1969) on *Caulerpa*; Wilbur *et al.* (1969 and unpublished) on *Halimeda*; Borowitzka and Larkum (1974a, b) on *Halimeda*; Hori (1974) on *Caulerpa*; and Calvert *et al.* (1976) on *Caulerpa*.

In general, the presence of the so-called "heteroplastid" system seems reasonably substantiated for the *Caulerpa–Halimeda–Udotea* series of algae, as does its absence in the *Codium–Derbesia* algae. However, as mentioned in Section I, there is some modification of Feldmann's original account.

Feldmann (1946) indicated that some heteroplastic algae, *Avrainvillea* and *Cladocephalus*, have a starch-depositing pyrenoid in their chloroplasts, and that in *Penicillus* and *Rhipocephalus* the chloroplasts secrete several small grains of starch. However, in *Udotea*, *Pseudochlorodesmis* and *Halimeda* the chloroplasts "sont entièrement dépourvus d'amidon, l'amylogenèse étant assurée uniquement par les leucoplastes".

At least for *Halimeda* this is not so, as has been indicated by Wilbur *et al.* (1969), Borowitza and Larkum (1974b) and Colombo and Orsenigo (1977). Starch, with and without pyrenoids, also is present in the chloroplasts of *Caulerpa* sp. (Feldmann, 1955; Hori and Ueda, 1967;

Hori, 1974; Calvert *et al.*, 1976), a genus not discussed by Feldmann (1946). It seems likely that at least small grains of starch in chloroplasts may be fairly commonplace throughout the heteroplastic green algae, that their number or size may vary with the time of day, although not invariably (see Calvert *et al.* (1976) for behaviour in *Caulerpa* sp.), and that the real point of emphasis, as well as of interest, should be in the presence or absence of a separate starch-storing body (the amyloplast). The *Caulerpa–Halimeda–Udotea* algal series, then, has evolved a separate starch-storing plastid, whereas the *Codium–Derbesia* series does not use this starch storage plan, at least to any great extent.

(d) *Proposed scheme for classification of* Halimeda. Although filament-wall chemistry and life-history data do not satisfactorily delimit orders among the *Codium–Derbesia* group of algae at this time, there is more support for a separation of the *Caulerpa–Halimeda–Udotea* group from the *Codium–Derbesia* group. The data are limited to examination of the commoner genera and species, but the members of the *Caulerpa–Halimeda–Udotea* group examined have:

a separate starch-storing body (amyloplast);

xylan in their filament walls, at least those of the photosynthetic portions of the plant (although not detected in walls of cultured *Caulerpa ambigua* Okamura ( = *C. vickersiae* Børgesen) which was also morphologically unusual in lacking pinnae (Huizing *et al.*, 1979));

a life-history that involves the death of the alga (or the part of it involved) after sexual reproduction.

A fourth characteristic is valid for many of the taxa:

the presence of chloroplast lamellar systems.

To reflect these differences I suggest the recognition, or retention, of a system of either four or two orders (depending on the classification used):

Derbesiales (containing *Codium*, *Bryopsis* and *Derbesia* as well as related genera), and

Caulerpales (the *Caulerpa–Halimeda–Udotea* series), with the continued use or acceptance, for the other genera as required, of the orders

Dichotomosiphonales

Phyllosiphonales (or Ostreobiales if *Phyllosiphon* is transferred to Xanthophyta).

This scheme could fit into either the Bold–Wynne or Round systems, but is shown in Table IX as part of the Round scheme of classification. The effect of my proposal is to unite the Codiales–Derbesiales group of Feldmann (1954), which was also done by Rietema (1975), with the name Derbesiales. The proposed scheme also recognizes the distinctiveness of the *Caulerpa–Halimeda–Udotea* series.

TABLE IX. MODIFIED SCHEME OF ORDERS FOR THE EUSIPHONIIDAE

| | | | | |
|---|---|---|---|---|
| Class | Bryopsidophyceae | | | |
| Subclass | Eusiphoniidae | | | |
| Orders | DERBESIALES | CAULERPALES | DICHOTOMO-SIPHONALES | PHYLLO-SIPHONALES |
| | | Caulerpaceae | | |
| | | *Caulerpa* | | |
| | | Udoteaceae[a] | | |
| | | *Halimeda, Penicillus, Rhipocephalus, Tydemania, Udotea, Avrainvillea, Boodleopsis, Callipsygma, Chlorodesmis, Cladocephalus, Geppella, Pseudochlorodesmis, Pseudocodium, Rhipidodesmis,* ( = *Chlorodesmis,* at least *p.p.*), *Rhipilia, Rhipiliopsis* | | |

[a] Many of the genera are tentatively placed herein and require cytological and life-history studies.

Within the Caulerpales, I have followed, for the present, the traditional separation into two families, Caulerpaceae (which is monogeneric) and Udoteaceae, since we know very little about a number of genera in the Udoteaceae. One of the characters used to separate these two groups (Bold and Wynne, 1978), the presence of trabeculae or wall ingrowths in the filaments of *Caulerpa*, has been observed in the walls of the filaments of the segments of *Halimeda tuna* (Borowitzka and Larkum, 1977).

I have not accepted within the Caulerpales, either as delimited above or in the sense of Bold and Wynne (1978), the separation, by Gepp and Gepp (1911), of Udotean genera into calcareous (Udoteae) and non-calcareous (Flabellarieae and Codieae) categories, with *Codium* and *Pseudocodium* belonging to the Codieae, *Halimeda, Penicillus,*

*Rhipocephalus*, *Tydemania* and *Udotea* to the Udoteae, and *Avrainvillea*, *Boodleopsis*, *Callipsygma*, *Chlorodesmis*, *Cladocephalus*, *Flabellaria*, *Rhipidodesmis*, *Rhipilia* and *Rhipiliopsis* to the Flabellarieae.

The Gepps considered the calcified and uncalcified groups to have developed from calcified and uncalcified ancestors, and that they were "fundamentally and physiologically distinct", with their separation occurring far back in their developmental history.

This interpretation of evolution within the group has, as one of its weaknesses, the re-establishment of the two species of the type genus *Flabellaria* in the genus *Udotea* from whence the Gepps had removed them. In addition, MacRaild and Womersley (1974) have demonstrated the alternation of a calcified (aragonitic) with an uncalcified phase in the life-cycle of a single alga, the former *Derbesia clavaeformis* (J. Ag.) De Toni, which they transferred to the new genus *Pedobesia* MacRaild and Womersley of the order Derbesiales. Such an alternation of calcified and uncalcified phases, which may prove to be more widespread, indicates that the Gepps' scheme is neither as useful nor as basic as the proposed separation along cytological and reproductive lines of the two orders Caulerpales and Derbesiales.

### D. *Summary: the identification and classification of* Halimeda

Many of the characters which separate the different species of *Halimeda* require the use of a compound microscope (magnification usually ×100 and ×400), and some prior sectioning, followed by decalcification of the material. Nonetheless, a few macroscopic characters are separated which, within limits, are helpful in field determinations of groups or taxonomic sections of species, and occasionally of species themselves. These are: the appearance of the plant as a whole, of the holdfast system, and the of majority of the segments. Finer determination of species, or of species groups, in the field is helped by a knowledge of their geographic range.

Microscopic taxonomic characters which are most used are: pattern of medullary filaments at the node (Table III), size and appearance of the different series of utricles (Figs 17, 20), and pattern and extent of cortex (Fig. 20). All these characters vary somewhat with age and the position of the segment on the thallus. The specialized reproductive structures, the grape-like clusters of gametangia, do not occur on most material, and have not proved particularly useful in taxonomic work.

The different patterns of nodal filaments found in different groups of *Halimeda* species are useful in delimiting groups of species and are considered to reflect fundamental phyletic divergence. Five taxonomic

sections of the genus are established using this character. They are Rhipsalis, Opuntia, Halimeda, Micronesicae and Crypticae.

The presence of a special starch-storing body (amyloplast), xylan in the filament walls and a life-history that involves the death of the alga after sexual reproduction in the *Caulerpa–Halimeda–Udotea* group of algae, or at least in the genera examined, is the basis of a recommendation that this group of algae be placed (or retained, depending on the system of classification) in an order Caulerpales which would be separate from an order Derbesiales containing *Codium*, *Bryopsis*, *Derbesia* and related genera.

## IV. Taxonomy of the Genus *Halimeda* Lamouroux

### A. *Introduction*

In this section descriptions are provided for 30 species of *Halimeda*, as well as for the genus. Two keys are given, one to all the species, the other to the Atlantic taxa together with a list of Atlantic species. A list of Indo-Pacific species is provided but not a separate key because over two-thirds of the species are present in that region.

In choosing key characters I have avoided as much as possible those which involve extensive preparation of material. Microscopic characters can be checked when the identification has been made. This approach precludes the necessity of detailed microscopy for a single species identification. Within the limits of reliability macroscopic characters are the first pair of choices, and at times it has seemed sufficient that such characters provide the sole choice. At other times they are supplemented with microscopic characters.

The characters used in the species descriptions and in the keys were described in Section III. Some of the figures and tables presented therein will be useful here as well, particularly Fig. 17, showing peripheral utricles in surface view; Fig. 20, longitudinal sections of cortex; and Table III, nodal filament patterns. Table X, in this section, presents a synopsis of important taxonomic characters for the species, together with geographic ranges.

Section III, A.2.b on preparation of *Halimeda* for microscopic study should also be useful.

#### 1. *Materials studied*

The specimens examined for the *Halimeda* revision (Hillis, 1959) provided the nucleus consisting of the 451 "representative specimens"

cited and many not cited because of limited space. All the uncited material represented overlaps in geographic range. Institutes providing these specimens were the herbaria of the University of Michigan, Ann Arbor, and the University of California, Berkeley; the New York Botanical Garden; and the British Museum (Natural History), London. Dr W. E. Isaac, then of the University of Cape Town, South Africa, provided liquid-preserved material of *H. cuneata.*

Subsequently, *Halimeda* specimens and collections have been examined from the British Museum (Natural History); Royal Botanic Gardens, Kew (algal collections now housed in the former); the herbarium of the Linnean Society, London; Rijksherbarium, Leiden; Botanical Museum, Lund; Botanical Museum, Copenhagen; National Museum of Natural History, Paris; Botanic Garden, Brussels; Museum of Western Australia; Institute of Jamaica, Kingston, Jamaica; United States National Museum; New York Botanical Garden; Duke University; Farlow Herbarium, Harvard; University of California, Berkeley; University of Hawaii; University of Michigan; Yale University; and the personal herbaria of Drs R. Tsuda and G. Valet. Professor Y. Yamada kindly loaned the type collections he had made of *gracilis* f. *elegans*, *incrassata* f. *distorta* and *opuntia* f. *intermedia*, the second of which is now the holotype specimen for the species *distorta*. Professor W. R. Taylor and Dr G. Valet provided authentic material of *goreauii* and *melanesica* respectively.

In addition, many workers have sent specimens from special sites and expeditions. To these I have added my own field collections, principally from the eastern Indian Ocean, Jamaica and Enewetak Atoll in the Marshall Islands, and the especially valuable experience of having made them myself, which has provided understanding of populations of the various species in the reef, including their variation.

## 2. *Measurement of characters*

The various dimensions recorded, both macroscopic and microscopic, have been obtained mostly from dried specimens, some from preserved material, a few from living plants. The measurements on the dried and on some preserved material are smaller than would be obtained using living plants, but for microscopic characters the effect of shrinkage on the measurements for taxonomic purposes is probably generally relatively little.

For the macroscopic character of segment dimensions, however, the change on drying may be considerable for large segments. In the species

*gigas*, which has the largest segments in the genus, length and width data on two segments from living plants, measured a few hours after they were collected from the lagoon of Enewetak Atoll, were 31 × 36 mm and 20 × 36 mm. After drying, these segments measured 21 × 32 mm and 17 × 30 mm, respectively. Thickness may also be affected, and some segments, particularly those of many *discoidea*, *macroloba* and *taenicola* thalli, become conspicuously concave with drying. The change in all three dimensions is less dramatic with smaller, thinner segments.

Drying may occasionally collapse the filaments, particularly if segments are lightly calcified. For such specimens, it is very difficult to obtain good measurements from sagittal sections.

In the species descriptions of this section the principal measurements given are for the diameters of the peripheral utricles in *surface* view (from surface sections), the lengths of the peripheral utricles, the diameters of the secondary utricles and the diameters of the tertiary utricles (from longitudinal sections). For each specimen examined a minimum of ten measurements for each of these characters has been made, and very often more than twice that number, and at times two to several sets of preparations were made for each specimen. The precise number of measurements depends on the species, the reasons for examining it and the quality of the preparations. A good preparation of the surface of the peripheral utricles is usually relatively easy to make, and may have 100 or more utricles, depending on their size and how lavish one is with the specimen. With such a large sample the diameters of utricles were measured randomly, then the field specifically searched for the smallest and largest ones (fusions excepted).

In sagittal sections, the sample size per section is much more limited because there are many fewer utricles from which to choose initially, and of these some may not be fully expanded or may be damaged. As much as possible, the approach in measuring was the same as for the peripheral utricles.

For all but a few species the minimum number of measurements obtained for each of the microscopic characters is 100. The average for all species is well over 400, and for some species it is in the thousands.

The minimum number of nodes dissected for most species is 10, and for many species it is many times this.

These data provide a spread of measurements which are given in the species descriptions and synopsis (Table X) as the range of measurements for the various characters. Figures in parentheses usually represent a few extreme measurements which are included to provide a concept of the range that may be encountered. The narrower range is the one considered representative of the species.

TABLE X. SYNOPSIS OF *Halimeda* SPECIES

| | *Peripheral utricles Surface diameter (μm)*[a] | *Other comment*[a] | *Predominant segment shape, and max. L × W* (mm), excluding basal or suprabasal segments[a] | *Distribution*[b] I w | P e w | A e w | M e | *Other*[a] |
|---|---|---|---|---|---|---|---|---|
| I. UNIAXIAL | Plants with a single axial or central filament; holdfast generally less than 1 cm long. Section CRYPTICAE. | | | | | | | |
| *cryptica* | (36–)*56–76*(–103) | May separate slightly, yet retain hexagonal shape | Ovate and elliptic; 11 × 15 | | | N | 0 | Two surfaces of segment distinctly different in colour, upper greenish, lower whitish; from depths of *c.* 25–100 m |
| II. MULTIAXIAL | A. Holdfast usually ≥ 1 cm long; thalli fairly erect, nearly always growing in sand or mud, frequently associated with sea grasses; all nodal filaments generally briefly *fused into a single unit*, although in *monile* the single unit sometimes separates fairly readily into groups and thus can be mistaken for fusion in small groups; cortex usually of three to five layers with utricles becomes progressively larger towards medulla, least extensive in *favulosa* where often there are only two layers. Section RHIPSALIS | | | | | | | |
| *incrassata* | (34–)*45–85*(–105) | Laterally attached for *c.* 12 μm | Variable; 10 × 14 | √ | √ | N S | N S | 0 |
| *favulosa* | (110–)*125–220*(–260) | Rounded, tend to separate | Variable; *surface* appears *stippled* and is friable 9 × 13 | | | | N | 0 May be passed over as *monile* but pitted surface of segments is distinctive |

TABLE X (*cont.*)

| | *Peripheral utricles* *Surface diameter* (μm)[a] | *Other comment*[a] | *Predominant segment shape, and max.* $L \times W$ (mm), excluding basal or suprabasal segments[a] | *Distribution*[b] I w | I e | P w | P e | A w | A e | M | *Other*[a] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *monile* | (23–)*30–60*(–74) | Laterally attached for *c.* 6 μm | *Cylindrical* segments where no branching; 8 × 3 | | | | | N | | 0 | |
| *cylindracea* | *17–45*(–55) | *Tend to separate*; walls may be thickened | Cylindrical; 7 × 4 | √ | | N S | | | | 0 | |
| *stuposa* | *21–48*(–55) | *Tend to separate* and appear somewhat rounded; walls usually thickened | Cylindrical, flattened-cylindrical; 7 × 11 | | √ | N | | | | 0 | Generally *thickset* and compact |
| *simulans* | (21–)*31–60* | Laterally attached for *c.* 7 μm | Subcuneate to reniform; basal segments may have *imbricated* branching pattern; 11 × 15 | | | N | | N S | | 0 | |
| *borneensis* | *22–69* | Laterally attached for ≤ 2 μm | Ovate to reniform; imbricated branching pattern as in *simulans* may be present; 12 × 17 | | | S | | | | | *Basal or suprabasal segment* may be *fan-shaped* and much enlarged to *c.* 12 mm long, 20 mm broad and bearing several good-sized segments. |
| *macroloba* | *23–49* | May separate and then appear rounded, otherwise hexagonal | *Subcuneate, discoidal, subreniform*; 29 × 40 | √ R | √ | N S | | | | 0 | Superficially may be considered tunoid but grown in sand among sea grasses. |

B. Holdfast generally < 1 cm long, thalli frequently growing attached to coral rock.

1. Filaments completely separate at node except occasionally in *melanesica* where some filaments may be joined briefly; utricles generally not much expanded in *fragilis* or *micronesica*, more so in *melanesica*. Section MICRONESICAE

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *fragilis* | *21–52* | *Separate, rounded*; may be thickened | Subreniform to reniform; 9 × 16 | √ | N | | 0 | |
| *micronesica* | *28–48*(–55) | *Usually separate, rounded*; may be a *steel-blue* colour on drying | Subcuneate to discoidal; 7 × 9 | √ √ | N S | | 0 | Holdfast may have long fibrous extensions which are not conspicuously interlaced with substrate; *basal segment unusually shaped*, to 12 mm × 18 mm ($L \times W$) and bearing numerous small segments, other segments occasionally with rope-like holdfast extensions |
| *melanesica* | (20–)*40–72* | Remain attached | Trilobed | | S | | 0 | Basal segments larger, producing stalked appearance; basal segments also becoming matted to form a relatively extensive holdfast region |

TABLE X (*cont.*)

| | *Peripheral utricles* *Surface diameter* (μm)[a] | *Other comment*[a] | *Predominant segment shape, and max.* $L \times W$ (mm), excluding basal or suprabasal segments[a] | *Distribution*[b] I w | P e w | A e w | M e | *Other*[a] |
|---|---|---|---|---|---|---|---|---|
| | 2. *Most* or all of the filaments of a node *fusing briefly in pairs*, although sometimes they may fuse in other units or remain single; inner utricles usually not utriculiform, of three or more layers; holdfast region of *opuntia*, *distorta* and possibly the other species not restricted to one basal area; growth often horizontal and spreading. Section OPUNTIA | | | | | | | |
| *opuntia* | *12–41* | Utricles adhere slightly or up to 6 μm | Variable; 7 × 11 | √ R | √ | N S | N | N S | 0 |
| *goreauii* | (12–)*16–37* | Remain attached for *c.* 2–5 μm | Deltoid to trilobed; 4 × 5 | | | | | N | 0 |
| *minima* | *14–30*(–39) | Generally adhere slightly; may occasionally be rounded | Trilobed to flattened: cylindrical; 5 × 4·5 and 4 × 3 | | | N | | | 0 |
| *renschii* | (11–)*15–28*(–38) | Lightly joined, may separate into hexagons | Obtriangular to transversely oval; 4 × 5 | √ | | N S | S | | 0 |
| *velasquezii* | *9–22* | Adhere slightly, may separate into hexagons | Transversely oval to reniform; 6 × 11 | √ | | N S | | | 0 |
| *copiosa* | (22–)*28–46*(–64) | Adhere firmly for 1–5 μm | Transversely oval and flattened, obovate; 13 × 21 | √ | | N S | | N | 0 |
| *distorta* | (34–)*36–60* | Attached slightly or may separate in patches; remain hexagonal | Broadly oval to discoidal *contorted*, sometimes keeled (i.e. not flat); 16 × 19 | | | N S | | | 0 |

3. Filaments of a node fused most commonly in units of *both* twos and threes, but fusion units may occasionally be larger or filaments may remain separate; fusion short (incomplete) or complete depending on the species; segments generally some pattern of reniform, subreniform, discoidal, cuneate or globular. Section HALIMEDA

(i) Cortex of distinct expanded utricles with three or more series common in all but *gigas* and *macrophysa*, when more than two series the diameter of each layer becoming larger proceeding from secondary utricles to medulla; typically four primary utricles attached to a secondary utricle

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *tuna* | (25–)*34*–100(–125) | Laterally attached for *c.* 12–16 μm; sometimes two or three fuse | Subcuneate, discoid or reniform; 13 × 19, but for some specimens from deepish water to 25 × 40 | √ | √ | N | N S | N S | √ | Nodal filaments fuse in twos or threes either incompletely or completely |
| *scabra* | *26–55*(–66) | Laterally attached or separating slightly into hexagons; up to seven supported per secondary utricle; *spine* projects from surface | Subreniform to reniform, often with *bluish* colour on drying; 11 × 20 | | | | N | | 0 | Nodal fusion as for *tuna*; clean thalli of slightly roughish texture (=*spines*) |
| *cuneata* | *25–63*(–72) | Laterally attached for *c.* 35 μm; occasionally fuse in pairs | *Cuneate to subcuneate*; 16 × 18, but in some specimens to 21 × 27; a small "*cushion*" segment or an uncorticated "stalk" segment sometimes present beneath some segments, size 1·5 × 5·5 | N S | S | S | | | 0 | Nodal fusion as for *tuna*; this species essentially subtropical |

TABLE X (*cont.*)

| | *Peripheral utricles Surface diameter (μm)*[a] | *Other comment*[a] | *Predominant segment shape, and max. L × W* (mm), excluding basal or suprabasal segments[a] | *Distribution*[b] I w | P e w | A e w | M e | | *Other*[a] |
|---|---|---|---|---|---|---|---|---|---|
| *lacunalis* | *20–55*(–70) | Laterally attached for *c.* 13 μm; occasionally up to five per secondary utricle | *Subcuneate to obovate* 15 × 20 | √ | N | | | 0 | Complete fusion at node in twos and threes, resultant units entangled and adhering strongly |
| *gigas* | (84–)*96–130*(–170) | Laterally attached for *c.* 8 μm; sometimes fuse in twos and threes | Discoidal to reniform, surface tends to crack on drying when there is considerable shrinkage; 31 × 42 | | N | | | 0 | Nodal fusion in twos and threes, *usually for considerable distance* |
| *macrophysa* | *135–180* | *Separate readily* on decalcifying; *round* | Reniform or subreniform, also subcuneate; surface finely *stippled*; 15 × 28 | √ | √ N S | | | 0 | Nodal fusion as in *lacunalis*; occasionally larger units formed |
| | (ii) Two to three series of utricles with inner one considerably inflated and of fairly uniform diameter throughout | | | | | | | | |
| *discoidea* | (30–)*40–90* | Laterally attached for *c.* 42 μm, *up to 14 per secondary* utricle; sometimes fuse in twos to fours | Discoid to reniform, on drying often have a sunken appearance; 29 × 33 | √ R | √ N S | N S | N | 0 | Fusion as in *tuna*; *usually only two series of utricles and then inner ones (70–)95–155(–260) μm* |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *taenicola* | (20–)*40–75*(–86) | Laterally attached for c. 19 μm, *four* and *occasionally six per secondary utricle*; sometimes fuse in twos | Subcuneate to trapezoidal, on drying may have sunken appearance; 11 × 18 | | N S | | 0 | Nodal fusion as for *lacunalis*; *usually three series of utricles, with inner ones inflated, and 75–160(–190) μm* |
| | (iii) Two to three series of utricles with secondary ones expanded at apex, sometimes considerably so, and long, often continuing to medulla; commonly four supported by each secondary utricle | | | | | | | |
| *lacrimosa* | *31–42* | Generally adhere slightly; if separate remain hexagonal; *6–18 per secondary utricle* | *Tear-shaped*; may be somewhat *bluish* on drying; 5 × 5 × *5*; segments of all other species usually do not exceed 1·5 mm in thickness | | | N | 0 | Habit rather *straggling or decumbent*; thalli delicate to c. *5 cm long*; nodal fusion as in *tuna* but groups may include four filaments; *secondary utricles capitate, 66–110 μm at apical end.* |
| *gracilis* | *23–58*(–70) | Generally adhere slightly; if separate remain hexagonal; only up to eight per secondary utricle | Subcuneate to reniform; 9 × 15 | √ √ | N S | N S | 0 | Segments a glossy white; habit *often straggling and decumbent*; more than one place of holdfast attachment; nodal fusion complete, usually in twos, occasionally threes; secondary utricles club-shaped, 23–70(–125) μm at apical end. |

TABLE X (*cont.*)

| | *Peripheral utricles Surface diameter (μm)*[a] | *Other comment*[a] | *Predominant segment shape, and max. L × W* (mm), excluding basal or suprabasal segments[a] | *Distribution*[b] I w | I e | P w | P e | A w | A e | M | *Other*[a] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *bikinensis* | *23–47* | Lightly attached or separating, in both cases rounded; usually four but up to eight per secondary utricle | Subreniform to reniform; 16 × 25 | √ | | N | | | | 0 | Nodal fusion as in *tuna* except filaments occasionally remain separate; secondary utricles at most only slightly expanded at apex, *20–47* μm broad. |

[a] Characters diagnostic for the species or group are in italic.

[b] Categories of distribution are western (w) and eastern (e) Indian (I), Pacific (P) and Atlantic (A) Oceans and Mediterranean (M) Sea. The following symbols are used as appropriate: N = Northern Hemisphere; S = Southern Hemisphere; R = Red Sea; √ = present; 0 = definite absence. A blank indicates absence of substantiated data, and √ placed on line between "w" and "e" indicates a verified distribution which is central to west and east.

For the three species *borneensis*, *distorta* and *melanesica*, the material available is relatively scant and hence the data given are based on fewer than 100 measurements and 10 node dissections.

### 3. *Treatment of forms and varieties*

In the 1959 revision I placed a number of forms in synonymy, and discussed them in the text of the pertinent species. These details, therefore, are available in Hillis (1959). Since then I have encountered a number of variants in the reef which could be described as forms of species. This is not unexpected since a wide range of variation has occurred in the appearance of the species grown in the laboratory, including that shown in Fig. 16. To provide many of these variants with separate names, however, seems of questionable value to the taxonomist as well as to the ecologist who is probably working with Halimedae living under a different set of reef conditions, showing variations that are similar, yet not the same. In time we may know enough about the habitat of the different species and the variations encountered within a region to separate forms or varieties meaningfully by habitat, but we do not yet have his information.

### 4. *Synonymies*

For the earliest known *Halimeda* species such as *tuna* and *incrassata* the lists of synonymies are relatively extensive. The complete list to the time of Barton's monograph (1901) is given in that publication. I have provided in this section references to the type descriptions and species information since 1901.

### 5. *Geographic distribution*

This information is provided by general region in each ocean, and is discussed further in Section VIII. Detailed distributions are given in Hillis (1959).

### 6. *Type specimen depositories*

The abbreviations of Lanjouw and Stafleu (1964) are used to indicate the location of type material.

## B. *Species of the genus* Halimeda *Lamouroux, with index*

Section Rhipsalis J. Ag. *ex* De Toni 1889

*H. incrassata* (Ellis) Lamouroux .. .. .. .. .. p. 93
*H. favulosa* Howe .. .. .. .. .. .. .. p. 96
*H. monile* (Ellis and Solander) Lamouroux .. .. .. p. 98
*H. cylindracea* Decaisne .. .. .. .. .. .. p. 100
*H. stuposa* W. R. Taylor .. .. .. .. .. .. p. 101
*H. simulans* Howe .. .. .. .. .. .. .. p. 103
*H. borneensis* W. R. Taylor .. .. .. .. .. .. p. 105
*H. macroloba* Decaisne .. .. .. .. .. .. p. 108

Section Opuntia J. Ag. *ex* De Toni 1889

*H. opuntia* (Linnaeus) Lamouroux .. .. .. .. p. 110
*H. goreauii* W. R. Taylor .. .. .. .. .. .. p. 112
*H. minima* (W. R. Taylor) L. H. Colinvaux .. .. .. p. 113
*H. renschii* Hauck .. .. .. .. .. .. .. p. 115
*H. velasquezii* W. R. Taylor .. .. .. .. .. p. 117
*H. copiosa* Goreau and Graham .. .. .. .. .. p. 118
*H. distorta* (Yamada) L. H. Colinvaux .. .. .. .. p. 120

Section Halimeda J. Ag. *ex* De Toni 1889

*H. tuna* (Ellis and Solander) Lamouroux .. .. .. .. p. 122
*H. cuneata* Hering .. .. .. .. .. .. .. p. 124
*H. scabra* Howe .. .. .. .. .. .. .. p. 127
*H. lacunalis* W. R. Taylor .. .. .. .. .. .. p. 129
*H. gigas* W. R. Taylor .. .. .. .. .. .. p. 132
*H. macrophysa* Askenasy .. .. .. .. .. .. p. 134
*H. discoidea* Decaisne .. .. .. .. .. .. p. 136
*H. taenicola* W. R. Taylor .. .. .. .. .. .. p. 139
*H. bikinensis* W. R. Taylor .. .. .. .. .. .. p. 141
*H. gracilis* Harvey *ex* J. Agardh .. .. .. .. .. p. 144
*H. lacrimosa* Howe .. .. .. .. .. .. .. p. 147

Section Micronesicae *n. sect.*

*H. micronesica* Yamada .. .. .. .. .. .. p. 149
*H. fragilis* W. R. Taylor .. .. .. .. .. .. p. 151
*H. melanesica* Valet .. .. .. .. .. .. .. p. 153

Section Crypticae *n. sect.*

*H. cryptica* L. H. Colinvaux and Graham .. .. .. .. p. 154

### C. *Generic description of* Halimeda *Lamouroux,1812: the circumscription is emended to include uniaxial species*

*Halimedea* Lamouroux (1812), p. 186.
*Halimeda* Lamouroux (1816), p. 302, *nomen conservandum.*
*Ormus* Hill (1751), p. 12, Plate 3.
*Sertularia* Boehmer *ex* Ludwig (1760), p. 504.
*Corallina p.p.* Linnaeus (1758), p. 805; Pallas (1766), p. 420; Petiver (1767), Plate 20, Fig. 19; Ellis and Solander (1786), p. 108; Esper (1798–1806), Plate 11.
*Flabellaria p.p* Lamarck (1813), p. 302; Delle Chiaie (1829), p. 9, Plate 10.
*Fucus p.p.* Bertolini (1819), pp. 224, 316.
*Ulva p.p.* Pollinius (1824), p. 507.
*Codium p.p.* Springel (1827), p. 366.
*Opuntia p.p.* Naccari (1828), p. 104.
*Sertolara* Nardo (1834), p. 673.

Plants flaccid, prostrate or erect, and generally bushy, arising from a filamentous holdfast system, usually not exceeding 25 cm in height although to 1 m or more in sprawling specimens; branches composed of linear series of calcified segments, the nodes being uncalcified and flexible; segments plane or ribbed, spherical, tear-shaped, compressed-cylindrical, or cuneate to reniform in shape, with upper margins entire or lobed; organization consisting of coenocytic filaments which produce a multiaxial or occasionally a uniaxial core of medullary filaments surrounded by a cortex composed of layers of utricles, the outer walls of the peripheral utricles forming a continuous or slightly discontinuous surface; the medullary filaments, when more than one, remaining separate, or anastomosing in small groups, or into a single large unit at the nodes, their walls generally thickened in these regions; sexual reproduction by biciliate gametes produced in large globular to pyriform gametangia on stalks which are simple or branched, and arise from the node, segment margin or surface.

*Lectotype species. Halimeda tuna* (Ellis and Solander) Lamouroux.

### D. *Description of the sections*

Five sections of the genus were delimited in Section III (including Table V) on the basis of pattern of the medullary filaments at the node. Their formal descriptions are given below.

Section Rhipsalis J. Ag. *ex* De Toni 1889 as Rhipsales. Filaments of a node fusing briefly into a single unit.

Section Opuntia J. Ag. *ex* De Toni 1889 as Opuntiae.
Most or all of the filaments of a node fusing briefly in pairs; occasionally fusing in other units, or remaining single.

Section Halimeda J. Ag. *ex* De Toni 1889 as Tunae.
Filaments of a node most commonly fusing in both twos and threes; units occasionally may be larger, or filaments may remain single; fusion short or complete depending on the species.

Section Micronesicae *n. sect.*
Filaments of a node remaining completely separate, or a few may be joined briefly in *H. melanesica.*

Section Crypticae *n. sect.*
Single medullary filament unchanged at the node.

*Latin diagnoses for new sections*

Section Micronesicae
Filamenta nodi omnino discreta manentia, vel, in *H. melanesica,* aliquot interdum curte conjuncta.

Section Crypticae
Unicum filamentum medullosum ad nodos immutabile.

## E. *Taxonomic key to all species, and list of Indo-Pacific species*

### 1. *Composite key to all species*

1. Plants growing in sand or other loose substrates; holdfast usually well developed, rarely less than 1 cm long and frequently massive; nodal medullary filaments uniting into a single group, the adjacent filaments usually communicating by pores . . . section Rhipsalis . . 2
1. Plants generally attached to rock, or if associated with sand lacking a well-developed bulbous holdfast; holdfast rarely exceeding 1 cm in length, although sometimes it may spread laterally to this size or somewhat larger; more than one holdfast region may be present; nodal medullary filaments remaining separate or uniting in twos, threes and occasionally fours . . . . 10
2. Segments large, broad, flat, to 29 mm long and 40 mm broad . . 3
2. Segments smaller, flat or cylindrical, to 12 mm long and 16 mm broad (excluding basal or fusion segments) . . . . . 5
3. Segments predominantly large, subcuneate to reniform and little lobed, to 29 mm long, 40 mm broad; fan-shaped basal or suprabasal segment absent (Fig. 27); peripheral utricles sometimes separate and round . . . . . *H. macroloba*, p. 108
3 Segments rarely exceeding 12 mm long and 17 mm broad, margins often crenulated or lobed; if peripheral utricles separate on decalcification they remain hexagonal . . . . . 4

4. Fan-shaped basal or suprabasal segment present; plant heavy-set and somewhat squat with predominantly broad, reniform or ovate segments with crenulated margins, to 12 mm long, 17 mm broad *H. borneensis*, p. 105
4. Fan-shaped basal or suprabasal segment absent; basal portion of plant of two to three cylindrical to subcuneate or at times reniform segments, the upper one supporting several subcuneate segments which are often arranged in an *imbricated* fashion, or sometimes a stalk region present which has developed from the fusion of small adjacent segments; segments to 11 mm long, 15 mm broad, margins sometimes shallowly trilobed or undulating but usually not crenulated .. .. .. .. *H. simulans*, p. 103
5. Segment surface appearing pitted when viewed macroscopically; peripheral utricles generally exceeding 110 μm in surface diameter .. .. .. .. .. .. *H. favulosa*, p. 96
5. Segment surface not appearing pitted when viewed macroscopically; peripheral utricles generally less than 100 μm in surface diameter .. .. .. .. .. .. .. .. 6
6. Segments of the upper half of the plant, except those supporting branches, predominantly cylindrical, their length usually at least three to four times their diameter .. .. .. .. .. 7
6. Segments of the upper half of the plant flat, or if cylindrical the length usually not more than twice their diameter.. .. .. 8
7. Diameter of the cylindrical segments remaining fairly constant from base to apex of the plant and averaging 1·0–1·5 mm; stalk of thallus short, of one to two segments; plant of Atlantic distribution .. .. .. .. .. .. *H. monile*, p. 98
7. Diameter of the cylindrical segments decreasing from base to apex of the plant, averaging 3–4 mm near the base, and 1·0–1·5 mm towards the apex; caulescent, or in older plants a number of these cauline structures may be consolidated laterally into a basal fan-shaped structure; of Indo-Pacific distribution *H. cylindracea*, p. 100
8. Plants thick-set in appearance, the segments averaging 2 mm in thickness; segments subcuneate to cylindrical, often becoming subspherical towards the plant apex .. .. *H. stuposa*, p. 101
8. Plants not appearing thick-set, segments (excluding the basal ones) averaging 0·75–1·00 mm in thickness; segments generally subcuneate to reniform .. .. .. .. .. .. 9
9. Peripheral utricles generally 50 μm or less in surface diameter; segments predominantly subcuneate to reniform with outer margin entire to shallowly lobed; basal portion of plant commonly of two to three cylindrical to subcuneate or at times reniform segments, the upper one supporting several subcuneate segments often in an *imbricated* arrangement; plants to 10 cm tall .. .. *H. simulans*, p. 103

9. Peripheral utricles generally exceeding 50 μm in surface diameter; segments cylindrical to cuneate to discoidal and reniform with the outer margin often deeply lobed; plants to 24 cm tall *H. incrassata*, p. 93
10. Basal holdfast region appearing to involve several of the lowermost segments which consequently may be obscured by particles of sand adhering to the rhizoidal filaments of the region; entire holdfast area may spread laterally for 1 cm or more .. .. 11
10. Basal holdfast region restricted to a single segment, holdfast ranging from relatively conspicuous and about 1 cm in greatest dimension to almost negligible, any adhering particles of loose substrate usually can be scraped away readily to show a localized holdfast .. .. .. .. .. .. .. .. 12
11. Area of basal segments of thallus generally two or more times larger than those of rest of thallus so that a pronounced stalked effect is produced .. .. .. .. *H. melanesica*, p. 153
11. Segments of fairly uniform size (area) throughout, with maximum size approximately 4 mm long, 5 mm broad .. *H. renschii*, p. 115
12. Growth pattern often forming laterally spreading thalli to 25 m or more which may be accompanied by some erect growth, or growth pattern mostly erect producing densely branched clumps; branching often multidirectional so that thallus does not lie flat; holdfast attachment generally in several places rather than by a single basal holdfast attachment although these small attachments may be lost during collecting .. .. .. .. 13
12. Other than the above.. .. .. .. .. .. .. 15
13. Branching commonly in one plane so that thallus lies relatively flat; segments generally flat but sometimes arched, commonly white, glossy, broadly subcuneate, sometimes trilobed; cortex generally of two layers of utricles with secondary utricles slightly to distinctly clavate at apical end; secondary utricles supporting four to eight peripheral utricles .. .. .. *H. gracilis*, p. 144
13. Branching commonly multidirectional so that thallus does not lie flat; segments flat or contorted, their surfaces dull; cortex generally of three or more series of utricles which are not expanded at the apical end and which bear only four peripheral utricles at most .. .. .. .. .. .. .. .. .. 14
14. Segments relatively large, to 16 mm long, 19 mm broad; often contorted; peripheral utricles measuring 36–60 μm in surface diameter .. .. .. .. .. .. *H. distorta*, p. 120
14. Segments smaller, plane or somewhat contorted, to approximately 7 mm long, 11 mm broad; peripheral utricles measuring 12–41 μm in surface diameter .. .. .. .. .. *H. opuntia*, p. 110
15. Basal segment flabellate (Fig. 46), to approximately 12 mm long, 18 mm broad, supporting numerous branches *H. micronesica*, p. 149
15. Basal segment not flabellate .. .. .. .. .. 16

16. A small "cushion" segment to 1·5 mm long, 5·5 mm broad interposed between some or all of the segments (Figs 18, 61) *H. cuneata*, p. 124
16. Small "cushion" segments absent .. .. .. .. .. 17
17. Mature plants small, not exceeding 5 cm in length; the segments of at least the upper half of the plant spherical or tear-shaped, to 5 mm long, 5 mm broad and 5 mm thickness; secondary utricles capitate (Fig. 20, No. 12), supporting 6–18 peripheral utricles .. *H. lacrimosa*, p. 147
17. Mature plants larger; segments flat or somewhat contorted but not spherical .. .. .. .. .. .. .. .. 18
18. Average surface diameter of the peripheral utricles exceeding 120 μm .. .. .. .. .. .. .. .. 19
18. Average surface diameter of the peripheral utricles less than 120 μm .. .. .. .. .. .. .. .. 20
19. Segments large, to 31 mm long, 42 mm broad, not friable; colour on drying brownish-green; calcification rather light *H. gigas*, p. 132
19. Segments smaller, to 15 mm long, 24 mm broad, friable; colour on drying white or pale greenish-white; calcification moderate .. *H. macrophysa*, p. 134
20. Peripheral utricles each projecting into a central spine *H. scabra*, p. 127
20. Peripheral utricles with smooth outer surface .. .. .. 21
21. Node consisting of a single medullary filament .. *H. cryptica*, p. 154
21. Node consisting of several to many medullary filaments .. 22
22. Secondary utricles noticeably inflated, generally exceeding 90 μm in diameter (Fig. 20, No. 11) .. .. *H. discoidea*, p. 136
22. Secondary utricles less than 90 μm in diameter .. .. .. 23
23. Tertiary utricles averaging 110 μm or more in diameter, with length two to three or more times the diameter .. *H. taenicola*, p. 139
23. Tertiary utricles averaging less than 110 μm in diameter and length not more than twice the diameter of the utricles .. .. 24
24. Diameters of secondary and tertiary utricles swollen in comparison to diameters of medullary filaments, utricles noticeably contracted at their bases .. .. .. .. .. .. .. .. 25
24. Diameters of secondary and tertiary utricles not appreciably greater than diameters of medullary filaments, secondary and tertiary utricles not conspicuously contracted at their bases .. 26
25. Segments, at least those of the upper half of the plant, predominantly reniform to discoid; peripheral utricles generally exceeding 50 μm in surface diameter; nodal fusion in small units, for a short distance or complete .. .. .. .. .. *H. tuna*, p. 122
25. Segments predominantly subcuneate to obovate; peripheral utricles generally 50 μm or less in surface diameter; nodal units fusing completely in twos and threes; units entangled and adhering strongly for 80–150(–280) μm .. .. .. *H. lacunalis*, p. 129
26. Nodal filaments remaining separate although adjacent filaments may adhere slightly .. .. .. .. .. *H. fragilis*, p. 151

26. Nodal filaments fusing in small groups although the occasional filament may remain separate .. .. .. .. .. 27
27. Mature thalli relatively small, usually 13 cm or less in length; segments also relatively small, with length usually less than 6 mm, width usually less than 11 mm .. .. .. .. .. 29
27. Mature thalli larger, generally exceeding 13 cm in length; segments also larger with length to approximately 16 mm, width to about 25 mm .. .. .. .. .. .. .. .. 28
28. Plants to about 20 cm tall, generally growing erect, thallus somewhat heavy-set; nodal fusions mostly in twos or threes, the fusions within the units being for a short distance or complete .. .. *H. bikinensis*, p. 141
28. Plants to 70 cm long although they may be considerably shorter, frequently pendant from rock, branches relatively long and somewhat sparse so that overall appearance of thallus is of delicacy; nodal filaments most commonly fusing in small groups for a short distance only .. .. .. .. .. *H. copiosa*, p. 118
29. Segments predominantly slightly reniform or transversely oval; average diameter of peripheral utricles in surface view about 16 μm or less .. .. .. .. .. *H. velasquezii*, p. 117
29. Segments predominantly other shapes, average diameter of peripheral utricles in surface view 22 μm or greater .. .. 30
30. Segments generally longer than broad, except for those bearing branches; segments in upper part of plant flattened-cylindrical to cylindrical; plants often bushy and in shallow water tending to grow erect; nodal fusion mostly in pairs but also in threes with filaments occasionally separate; of Indo-Pacific distribution .. *H. minima*, p. 113
30. Segment length generally equalling width or somewhat broader in upper part of thallus; plant growth form somewhat pendant; fusion units of nodal filaments in pairs; of Atlantic distribution *H. goreauii*, p. 112

2. *List of Indo-Pacific species of* Halimeda

Section Rhipsalis

*H. incrassata*
*H. cylindracea*
*H. stuposa*
*H. borneensis*
*H. macroloba*

Section Opuntia

*H. opuntia*
*H. minima*
*H. renschii*
*H. velasquezii*
*H. copiosa*
*H. distorta*

Section Halimeda

*H. tuna*
*H. cuneata*
*H. lacunalis*
*H. gigas*

Section Halimeda (*cont.*)

*H. macrophysa*
*H. discoidea*
*H. taenicola*
*H. bikinensis*
*H. gracilis*

Section Micronesicae

*H. micronesica*
*H. fragilis*
*H. melanesica*

## F. *Key to Atlantic species, and list of Atlantic species*

### I. *Key to Atlantic species*

1. Plants growing in sand or other loose substrate; holdfast usually well developed, rarely less than 1 cm long and frequently massive; nodal medullary filaments uniting into a single group, the adjacent filaments usually communicating by pores . . . section Rhipsalis . . 2
1. Plants generally attached to rock or if associated with sand lacking a well-developed bulbous holdfast; holdfast rarely exceeding 1 cm in length, although sometimes it may spread laterally to this size or somewhat larger; more than one holdfast region may be present; nodal medullary filaments remaining separate or uniting in twos, threes and occasionally fours . . 5
2. Segment surface appearing pitted when viewed macroscopically; peripheral utricles generally exceeding 110 μm in surface diameter . . . . . *H. favulosa*, p. 96
2. Segment surface not appearing pitted when viewed macroscopically; peripheral utricles generally less than 100 μm in surface diameter . . . . . 3
3. Segments of the upper half of the plant, except those supporting branches, predominantly cylindrical, their length usually at least three to four times their diameter . . . . . *H. monile*, p. 98
3. Segments of the upper half of the plant flat, or if cylindrical the length usually not more than twice their diameter . . . . 4
4. Peripheral utricles generally 50 μm or less in surface diameter; segments predominantly subcuneate to reniform with outer margin entire to shallowly lobed; basal portion of plant commonly of two to three cylindrical to subcuneate or at times reniform segments, the upper one supporting several subcuneate segments often in an *imbricated* arrangement; plants to 10 cm tall . . *H. simulans*, p. 103
4. Peripheral utricles generally exceeding 50 μm in surface diameter; segments cylindrical to cuneate to discoidal and reniform with the outer margin often deeply lobed; plants to 24 cm tall . . . . *H. incrassata*, p. 93

5. Node consisting of a single medullary filament; plant growing at approximately −25 m and deeper .. .. .. *H. cryptica*, p. 154
5. Node consisting of several to many medullary filaments.. .. 6
6. Growth pattern often forming laterally spreading thalli to 0·25 m or more which may be accompanied by some erect growth, or growth pattern mostly erect producing densely branched clumps; branching often multidirectional so that thallus does not lie flat; holdfast attachment generally in several places rather than by a single basal holdfast attachment although these may be lost in the collecting .. .. .. .. .. .. .. .. 7
6. Other than the above.. .. .. .. .. .. .. 8
7. Branching commonly in one plane so that thallus lies relatively flat; segments generally flat but sometimes arched, commonly white, glossy, broadly subcuneate, sometimes trilobed; cortex generally of two layers of utricles with secondary utricles slightly to distinctly clavate at apical end; secondary utricles supporting four to eight peripheral utricles .. .. .. *H. gracilis*, p. 144
7. Branching commonly multidirectional so that thallus does not lie flat; segments flat or contorted, their surfaces dull; cortex generally of three or more series of utricles which are not expanded at the apical end and which bear only four peripheral utricles at most; the commonest species of many rocky areas in extremely shallow water (−0·3 m) where it grows as sprawling skeins, or as densely branched clumps .. .. .. .. *H. opuntia*, p. 110
8. Mature plants small, not exceeding 5 cm in length; the segments of at least the upper half of the plant spherical or tear-shaped, to 5 mm long, 5 mm broad and 5 mm thickness; secondary utricles capitate (Fig. 20, No. 12), supporting 6–18 peripheral utricles .. *H. lacrimosa*, p. 147
8. Mature plants larger; segments flat or somewhat contorted, but not spherical .. .. .. .. .. .. .. .. 9
9. Peripheral utricles each projecting into a central spine; surface of clean plants somewhat rough to the touch, colour on drying often bluish-green .. .. .. .. .. *H. scabra*, p. 127
9. Peripheral utricles with smooth surface, a central spine being absent .. .. .. .. .. .. .. .. .. 10
10. Secondary utricles noticeable inflated, generally exceeding 90 μm in diameter (Fig. 20, No. 11) .. .. *H. discoidea*, p. 136
10. Secondary utricles less than 90 μm in diameter .. .. .. 11
11. Diameters of secondary and tertiary utricles swollen in comparison to diameters of the medullary filaments, and utricles noticeably contracted at their bases .. .. .. .. *H. tuna*, p. 122
11. Diameters of secondary and tertiary utricles not appreciably greater than diameters of medullary filaments, secondary and tertiary utricles not conspicuously contracted at their bases .. 12

12. Mature plants relatively small and delicate, to approximately 13 cm long; segments commonly subcuneate and sometimes strongly trilobed, to 4 mm long and 5 mm broad; peripheral utricles averaging about 27 μm in diameter; commonly associated with *opuntia* in the reef .. .. .. .. *H. goreauii*, p. 112
12. Mature plants to 70 cm long although they may be considerably shorter; segments commonly transversely oblong to depressed ovate, to 13 mm long and 21 mm broad; peripheral utricles averaging approximately 37 μm; commonly associated with *cryptica* in deeper parts of the reef .. .. *H. copiosa*, p. 118

2. *List of Atlantic species of* Halimeda

Section Rhipsalis

*H. incrassata*
*H. simulans*
*H. favulosa*
*H. monile*

Section Opuntia

*H. opuntia*
*H. goreauii*
*H. copiosa*

Section Halimeda

*H. tuna*
*H. scabra*
*H. discoidea*
*H. gracilis*
*H. lacrimosa*

Section Crypticae

*H. cryptica*

## G. *Species descriptions*

### 1. *Section Rhipsalis J. Ag.* ex *De Toni*

### *Halimeda incrassata* (Ellis) Lamouroux

Figure 22.

*Corallina incrassata* Ellis (1767), Plate 17, Figs 20–27; Ellis and Solander (1786), p. 111, Plate 20, Figs $D_{1-6}$, d, $d_{1-3}$.
*Corallina tridens* Ellis and Solander (1786), p. 109, Plate 20, Fig. a.
*Halimedea incrassata* Lamouroux (1812), p. 186; *Halimeda incrassata* Lamouroux (1816), p. 307; Barton (1901), p. 25, Plate 4, Figs 39, 41–51; Hillis (1959), p. 365, Plates 4–6, 12.
*Halimeda incrassata* f. *gracilis* Børgesen (1913), p. 111, Fig. 89.
*Halimeda incrassata* f. *rotunda* Barton (1901), p. 28, Plate 4, Fig. 45.
? *Halimeda incrassata* f. *tridentata* Duchassaing *ex* J. Agardh (1887), p. 86.
*Halimeda incrassata* f. *tripartita* Barton (1901), p. 27, Plate 4, Fig. 43.

FIG. 22. *H. incrassata*. Basal portion of thallus shown is caulescent, and trilobed segments are common towards branch extremities. Basal third is also more heavily epiphytized, and appears to have functioned as perennating structure. Specimen from Curaçao, Spaanse Baai, south-east coast, 19 XI 62, Diaz-Piferrer. Scale bar is 2 cm long. (Photograph by The Ohio State University Department of Photography.)

*Halimedea tridens* Lamouroux (1812), p. 186; *Halimeda tridens* Lamouroux (1816), p. 308; Collins (1909–1918), p. 398; Taylor (1928), p. 84, Plate 10, Fig. 14; Taylor (1950), p. 92.

? *Halimeda brevicaulis* Kützing (1858), p. 11, Plate 25, Fig. 2.

Plants occasionally lax in habit, but more commonly erect and compact, to 24 cm tall excluding the holdfast region, which may extend to 9 cm in length; calcification rather heavy at the base, becoming moderate to light in the middle and upper portions; branching mainly di- to tetrachotomous, the lower part of the plant often remaining simple for some distance, or branching

immediately above the first to second basal segments, the resultant segments at times becoming consolidated laterally into a rather massive fan-shaped structure; the basal first to second segments cylindrical to subcuneate, others plane, ribbed or keeled, shape variable, from cylindrical to reniform, the outer margin entire, undulating or deeply lobed, to about 10 mm long, 14 mm broad, and averaging 0·75–1·00 mm in thickness.

Cortex of three to five layers of utricles; the outermost utricles generally remaining attached after decalcification for an average distance of 12 μm, their lateral and peripheral walls occasionally thickened, (34–)45–85(–105) μm in surface diameter, (40–)50–95(–125) μm long in section, two or four supported on each secondary utricle; secondary utricles often globose or subglobose, 23–70(–95) μm broad, 30–90(–118) μm long; innermost utricles (32–)46–100(–150) μm broad.

Nodal medullary filaments uniting as a single group for a distance of approximately 25–80 μm, the adjacent filaments communicating by pores or tubular processes; walls in this region thickened and often deeply pigmented.

*Type specimen.* Collected by Ellis in Jamaica; according to Barton (1901) this specimen has been lost.

*Habitat.* Grows in sand, mud or other unconsolidated substrate from just below low-tide line to about −65 m. In the Caribbean it may form very dense stands, often with *H. monile*, of more than 300 thalli of the two species per square metre just below low-tide line. In shallow environments that are somewhat exposed, as opposed to sheltered, the long axis of older plants is perpendicular to the direction of the wave motion.

*Halimeda incrassata* frequently is associated with sea grasses. In the Caribbean *H. monile* and *H. simulans* may occur with it. It is also associated with species of *Penicillus*, *Udotea* and *Rhipocephalus*.

At Enewetak Atoll it was found in moderately exposed to sheltered sites and in more exposed habitats than *cylindracea*. Extensive patches of it such as are common in the Caribbean were not observed.

*Geographic distribution.* Pantropical; includes western and eastern Indian Ocean; north and south in the western Pacific; north and south in the western Atlantic including Bermuda (western Atlantic).

This species is best known from the Caribbean where it appears to be the commonest of the Rhipsalian taxa, and often forms extensive populations in the shallow sandy regions of the reef.

Modifications other than those of segment shape occur in specimens of *incrassata*. These include an increase in the number or height of the cortical layers, either or both conditions producing thicker segments.

The firmness of the connections between the nodal medullary filaments also varies, the constituent filaments at times communicating mainly by a restricted number of narrow tubular processes which may be relatively easily severed, rather than by numerous well-developed broad short tubes. In addition, the general appearance of the basal portion of the plant may differ. Specimens from the Caribbean often appear distinctly caulescent, and in older plants from this region the lower branches may consolidate laterally to form a fan-shaped, erect basal portion. The stipe region in many Pacific specimens generally is restricted to one or two subcylindrical to subcuneate segments, the upper one supporting several branches.

## *Halimeda favulosa* Howe

Figure 23.

*Halimeda favulosa* Howe (1905b), p. 563, Plate 23, Fig. 2; Plate 24; Plate 26, Figs 1–6; Collins (1909–1918), p. 401; Hillis (1959), p. 370, Plates 4–6, 8, 12.

Plants attenuate, suberect or somewhat flaccid, to 22 cm tall excluding the holdfast, which is moderately well developed; calcification moderate; surface dull, rugose and appearing pitted; branching sparse, mainly ditrichotomous; basal segments commonly compressed-cylindrical to trapezoidal, often forming a short stipe and supporting several segments which remain separate or consolidate laterally, either entirely or in part, to form a fan-shaped unit; other segments friable, cylindrical to subcuneate, the upper margin two to five lobed, the resultant arms compressed or terete, to 9 mm long, 13 mm broad and averaging 1·0–1·5 mm in thickness.

Cortex of two to three layers of utricles; outermost utricles (110–)125–220(–260) μm in surface diameter, 170–280(–400) μm long in section, separating or remaining slightly attached after decalcification, appearing rounded in surface view, in section sometimes constricted basally forming a conspicuous bulb; one, two or four supported by each secondary utricle; secondary utricles 100–150(–190) μm broad, 170–275(–424) μm long.

Nodal medullary filaments uniting as a single group for a distance of approximately 28–50 μm, adjacent filaments communicating by pores; walls in this region thickened and pigmented.

*Type specimen.* Bahamas, Cave Cays, Exuma Chain, Howe 3981, 19 February, 1905 (NY).

*Habitat.* Grows in sand, mud, or other unconsolidated substrate.

*Geographic distribution.* North-western Atlantic; uncommon to rare.

FIG. 23. *H. favulosa. Holotype*, Bahamas, Cave Cays, Exuma Chain, Howe 3981. (Photograph courtesy of the New York Botanical Garden.)

Since *favulosa* fairly closely resembles the relatively common *monile* it may easily be passed over as such in the field. This perhaps partly explains its extremely restricted recorded distribution.

This species can be distinguished macroscopically from *monile* and other Rhipsalian species by the friable nature of its segments and their pitted surface. The pitted texture results from the large diameters of the peripheral utricles, and their partial or complete separation by calcium carbonate partitions. Histologically, *favulosa* is characterized by a relatively poorly developed inner cortex and by the large dimensions of the peripheral and secondary utricles.

## *Halimeda monile* (Ellis and Solander) Lamouroux

Figure 24.

*Corallina monile* Ellis and Solander (1786), p. 110, Plate 20, Fig. c.
*Halimedea monile* Lamouroux (1812), p. 186; *Halimeda monile* Lamouroux (1816), p. 306; Howe (1907), p. 501; Collins (1909–1918), p. 399; Taylor (1928), p. 82; Hillis (1959), p. 371, Plates 4–8, 12.
*Halimeda incrassata* v. *monilis* Harvey (1858), p. 24; Børgesen (1911), p. 138; Børgesen (1913), p. 112.
*Halimeda incrassata* v. *monilis* f. *cylindrica* Børgesen (1911), p. 143, Fig. 10; Børgesen (1913), p. 113, Fig. 91.
*Halimeda incrassata* v. *monilis* f. *robusta* Børgesen (1911), p. 143, Fig. 9; Børgesen (1913), p. 113, Fig. 90.
*Halimeda incrassata* f. *monilis* Barton (1901), p. 27, but not Plate 4, Fig. 40.

Plants sometimes elongate and sparsely branched, but more commonly compact and robust, to 16 cm tall excluding the holdfast which may extend to 4 cm in length; calcification moderate, becoming heavier towards the base, branching mainly ditrichotomous; basal first to second segments forming a short stipe, generally cylindrical to subcylindrical but becoming almost semicircular in densely branched plants, these supporting two to several segments which may consolidate laterally into a modified fan-shaped structure; other segments plane or ribbed, generally trilobed with terete arms, or cylindrical, the former usually predominating in regions of branching, the latter in the upper part of the plant, cylindrical ones to 8 mm long, 3 mm broad and averaging 1·5 mm in diameter, others excluding the modified basal ones to 8 mm long and 8 mm broad.

Cortex of three to five layers of utricles; outermost utricles remaining attached after decalcification for an average distance of 6 μm, (23–)30–60(–74) μm in surface diameter, 48–95(–116) μm long in section, two or four supported by each secondary utricle; secondary utricles 23–70 μm broad, 23–100(–140) μm long; tertiary utricles 30–90 μm broad.

Nodal medullary filaments usually uniting in twos, threes or larger groups for a distance of approximately 49–80 μm, these units held together by short narrow tubular processes which are easily broken; filament walls thickened and pigmented.

*Type specimen.* Collected by Ellis in Jamaica; according to Barton (1901) this plant has been lost.

*Habitat.* Grows in sand, mud or other unconsolidated substrate, from near low-tide line to about −13 m and possibly deeper. In water of about 0·3 m depth, low tides, it may form exceedingly dense stands, and one Jamaican quadrat I counted had 360 compressed *monile* thalli per square metre, together with 140 flattened *incrassata* thalli. Such dense growth may be restricted to very

FIG. 24. *H. monile.* Specimen from Jamaica, Glory Be reef top, IX 1967, Hillis-Colinvaux and Colinvaux. Scale bar is 2 cm long. (Photograph by The Ohio State University Department of Photography.)

shallow water. The thalli sometimes are partially buried by shifting sand.

*Halimeda monile* is associated with sea grasses and Rhipsalian Halimedae.

*Geographic distribution.* North-western Atlantic, where it is relatively common. Pacific material identified as *monile* (including Taylor, 1950) has thus far proved to belong to the species *cylindracea* (Hillis, 1959).

As seen from the preceding list of synonymy this species has had a rather varied taxonomic history since it was first described by Ellis and

Solander (1786). The earlier synonymy is given by Barton who, in addition to considering *monile* as a form of *incrassata*, equated with it *cylindracea* Decaisne and *polydactylis* J. Agardh.

Cylindrical segments, which are a characteristic of *monile*, also occur in other species. The predominance of them in *monile*, together with the general form of the plants, usually enables this taxon to be identified macroscopically. In doubtful cases, differences in nodal anatomy and in the diameters of the peripheral utricles, the latter averaging 46 μm in *monile* and 73 μm in *incrassata*, are diagnostic. The somewhat modified pattern of the nodal filaments in *monile* was discussed in Section III.

### *Halimeda cylindracea* Decaisne

Figures 4, 5, 104.

*Halimeda cylindracea* Decaisne (1842), p. 103; Hillis (1959), p. 373, Plates 4–7, 12.
*Halimeda polydactylis* J. Agardh (1887), p. 89.
*Halimeda incrassata* Harvey (1860), p. 125 *p.p.* including Plate 125.
*Halimeda incrassata* f. *monilis* Barton (1901), p. 27 *p.p.* including Plate 4, Fig. 40.

Plants erect, elongate, usually attenuated from base to apex, to 19 cm tall excluding the holdfast which may extend to over 12 cm in length; branching restricted, mainly ditrichotomous; basal segments cask-shaped, to 7 mm long, 12 mm broad and averaging 3–4 mm in thickness, forming a distinct terete or subterete stalk with the lower forkings often becoming consolidated laterally to form a fan-shaped structure in older plants; branch segments subcuneate with lobed upper margins, others generally plane and predominantly cylindrical, although at times becoming subspherical towards the plant apex, to 7 mm long, 4 mm broad and averaging 1·5 μm in thickness.

Cortex of three to five layers of utricles; outermost utricles tending to separate on decalcification, their lateral and peripheral walls sometimes thickened, 17–45(–55) μm in surface diameter, 24–62 μm long in section, two or four supported by each secondary utricle; secondary utricles 17–62 μm broad, 23–80(–100) μm long; tertiary utricles 30–90 μm broad.

Nodal medullary filaments uniting as a single group for a distance of approximately 34–72 μm, the adjacent filaments communicating by pores; walls in this region thickened and pigmented.

*Type specimen.* Madagascar, Nossi-Bé, Pervillé (PC).

*Habitat.* Grows in unconsolidated substrate, but its holdfast, which is sometimes massive, is frequently attached to one or more fragments of buried broken coral or rock; from about −0·3 m to

at least −58 m. At Enewetak Atoll it is sometimes associated with *stuposa*, and of three Rhipsalian Halimedae present (*incrassata*, *stuposa* and *cylindracea*), it was the commonest and grew in the least exposed habitats. At Enewetak it was commoner in sandy regions near coral patches than in open stretches of sand. This distributional pattern may partly result from bioturbation.

*Geographic distribution.* Western Indian Ocean, western Pacific, both north and south.

### *Halimeda stuposa* Taylor

Figure 25.

*Halimeda stuposa* Taylor (1950), p. 90, Plate 43, Fig. 1; Plate 49; Plate 50, Fig. 2; Hillis (1959), p. 374, Plates 3, 5–7, 11.

Plants erect, rather small, thick-set, compact, to 10 cm tall excluding the holdfast which is often massive, this generally extending to 5 cm in length but on occasion to 13 cm; calcification moderate; branching mainly ditrichotomous; basal segments subcuneate or compressed-cylindrical, often forming a stipe or else consolidating laterally with adjacent segments to form a short trunk-like structure; other segments plane or occasionally ribbed; subcylindrical or cylindrical, at times becoming subspherical towards the apex, the upper margins entire to slightly lobed, to 7 mm long, 11 mm broad and averaging 2 mm in thickness.

Cortex of three to five layers of utricles; outermost utricles separating slightly on decalcification or remaining attached for an average distance of 4 μm, their lateral and peripheral margins usually thickened, 21–48(–55) μm in surface diameter, 50–80(–100) μm long in section, two or more commonly four supported by each secondary utricle; secondary utricles (17–)25–50 μm broad, (23–)30–90(–125) μm long; tertiary utricles 38–65 μm broad.

Nodal medullary filaments uniting as a single group for a distance of approximately 30–50 μm, the adjacent filaments communicating by pores; walls in this region thickened and pigmented.

*Type specimen.* Marshall Islands, Rongelap Atoll, Naen Island, Taylor 46–591, 17 July, 1946 (MICH).

*Habitat.* Grows in sand, mud or other unconsolidated substrate from about low-tide line to at least −10 m, and sometimes develops extensive stands. In places, it may be partially buried in shifting sand, producing a very long holdfast which requires use of a trowel or knife to extract it completely. Sometimes it is associated with *cylindracea*.

FIG. 25. *H. stuposa.* Most of the lower half of this specimen was buried by shifting sand in 1–2·5 m of water, and holdfast filaments are present in the sand masses adhering to the segments. The basal holdfast is not massive as it is in some specimens (e.g. Taylor, 1950), and the thallus branching is less compact. Specimen from Enewetak Atoll, Enjebi Islet, lagoon, 20 XII 75, Hillis-Colinvaux and Colinvaux. Scale bar is 2 cm long. (Photograph by The Ohio State University Department of Photography.)

*Geographic distribution.* Western Indian Ocean, western Pacific, north and south.

This Rhipsalian *Halimeda* at times may resemble *monile* and certain forms of *incrassata*, but can usually be identified macroscopically by its short, rather thick-set appearance, the thickness of the segments averaging 2 mm. Also characteristic are the relative infrequence of deeply trilobed segments, and the presence of relatively short

cylindrical ones, the lengths of which rarely exceed twice the diameter, unlike similar segments in *monile* and *cylindracea* which, in general, are at least four times as long as broad.

Histologically, the thickened walls of the peripheral utricles of *stuposa* are generally fairly conspicuous in mature segments, particularly as viewed from the surface. This thickening is extremely well developed in basal segments where the utricles usually separate on decalcification. Towards the plant apex the induration is less pronounced and the utricles remain more firmly attached after decalcification. Although such thickening may occur in other species, particularly in basal segments, it is generally not as constant a feature as in *stuposa*.

## *Halimeda simulans* Howe

Figure 26.

*Halimeda simulans* Howe (1907), p. 503, Plate 29; Collins (1909–1918), p. 401; Taylor (1928), p. 84, Plate 10, Fig. 12; Plate 11, Figs 18–19; Hillis (1959), p. 368, Plates 3, 5, 6, 11.

*Halimeda incrassata* v. *simulans* Børgesen (1911), p. 144, Fig. 11; Børgesen (1913), p. 114, Fig. 92.

Plants erect, compact, forming cushion-like clumps, to 12 cm tall excluding the holdfast region which may extend to 4 cm; calcification moderately heavy; branching complanate, frequent, mainly di- to tetrachotomous; stalk region sometimes moderately well developed, resulting from the fusion of small adjacent segments, more commonly short and rather inconspicuous, of two to three cylindrical to subcuneate or at times reniform segments, the upper one supporting several subcuneate segments which often have an imbricated arrangement; other segments frequently ribbed, occasionally cylindrical but more commonly subcuneate to reniform, the outer margin entire, undulating or shallowly lobed, to 11 mm long, 15 mm broad, and averaging 0·75–1·00 mm in thickness.

Cortex of two to four layers of utricles with a fifth zone occasionally present; outermost utricles generally remaining attached after decalcification for an average distance of 7 μm, (26–)31–60 μm in surface diameter, 30–60(–90) μm long in section, two or four supported by each secondary utricle; secondary utricles 25–60(–78) μm broad, 28–70(–110) μm long; innermost utricles (34–)40–90 μm broad.

Nodal medullary filaments uniting as a single group for a distance of approximately 25–55 μm, the adjacent filaments communicating by pores; walls in this region thickened and pigmented.

*Type specimen.* Puerto Rico, Culebra Island, Howe 4332, 6 March, 1906 (NY).

FIG. 26. *H. simulans*. Imbricated arrangement of suprabasal segments is most readily seen in top plant. Specimens from less than 3 m depth, Jamaica, Sombra (smaller plant), and Runaway Bay, Spanish Cove (larger plant), IX 1967, Hillis-Colinvaux and Colinvaux. Scale bar is 2 cm long. (Photograph by The Ohio State University Department of Photography.)

*Habitat.* Grows in sand, mud or other unconsolidated substrate, from about −0·3 to −75 m, but is comparatively uncommon at the extreme depths. *Halimeda simulans* may be associated with *monile* in the Caribbean but is more commonly found in patches of *incrassata.* In the laboratory it sometimes can be initially mistaken for *incrassata* (see below), but in the reef it often seems fairly distinct, and sometimes can be readily spotted from above, by noting the rounder thalli in patches of Rhipsalian Halimedae. These individuals are generally *simulans,* since thalli of *incrassata* tend to have a more linear appearance. Relatively large populations of *simulans* may occur, or it may be present as a few thalli at the edge of a grove of *incrassata.*

*Geographic distribution.* Eastern Indian Ocean, north-western Pacific, north and south in the western Atlantic including Bermuda. It is best known from the Caribbean.

This species often may be distinguished from *incrassata* macroscopically by its substipitate or occasionally stipitate habit with basal segments of the lowermost branches commonly imbricated. Other distinguishing characteristics are the predominantly greenish-cream, reniform or slightly trilobed segments, and the smaller diameters of the peripheral utricles which average 45 μm in *simulans* as compared to 73 μm in *incrassata.* In *incrassata* the peripheral utricles adhere more firmly, whereas in *simulans* the corners often appear slightly rounded in surface view, the utricles nevertheless usually remaining attached. The pores between adjacent nodal medullary filaments in *simulans* at times may be relatively small and consequently not particularly conspicuous in longitudinal sections. Their presence then is more easily demonstrated by transverse section through the node.

The reniform segments of this species sometimes lead to confusion with *tuna* from which it is entirely distinct microscopically. Characteristics of habit, segment colour, the tendency for segments to be lobed in *simulans* rather than entire as in *tuna,* and particularly the presence of a more extensive holdfast with adhering particles of fine substrate distinguish these two species macroscopically.

### *Halimeda borneensis* W. R. Taylor

Figure 27.

*Halimeda borneensis* Taylor (1975), p. 81, Figs 1, 2.

Plants erect, compact and rather small, to 12 cm broad and 7 cm tall excluding the holdfast region which may extend to 3 cm in length; basal or

suprabasal segment fan-shaped, at times small, but also to 12 mm long, 20 mm broad, bearing a few to eight or more branching series of segments which tend to lie flat; other segments to about 12 cm long, 16 cm broad, ovate to reniform, their bases often a little contracted, the distal margins entire to frequently slightly three to seven crenate, to 12 mm long, 17 mm broad.

Cortex of three or more series of utricles; outermost utricles remaining attached after decalcification often by a very thin extension of the utricle, or separating slightly, 22–69 μm in surface diameter, two or four supported by each secondary utricle; secondary utricles of approximately the same diameter as the peripheral utricles, and two to seven times as long.

Nodal medullary filaments uniting as a single group for a distance about equal to the filament width, adjacent filaments communicating by pores; walls in the region thickened and pigmented.

*Type specimen.* North Borneo, Pulau Gaya off the east coast, Cleland, Station 10, 5 February, 1965 (MICH).

*Habitat.* Grows on unconsolidated substrates, in shallow water. The extent of its vertical range is, at present, not known.

*Geographic distribution.* South-western Pacific.

The Rhipsalian *Halimeda* this species most closely resembles is *simulans*. Although few samples of *borneensis* are presently available for an extensive evaluation of characters, the following comparisons can be made. The basal or suprabasal segment in *borneensis* is generally conspicuously broad, and the other segments often both broader and more reniform than those of *simulans*. The general appearance of *borneensis* is of a somewhat squatter, more heavy-set plant.

Microscopic differences include the peripheral utricles being somewhat larger and less firmly joined laterally in *borneensis* as compared to *simulans*. In addition, the secondary utricles of *borneensis* are generally longer, sometimes considerably more so, than those of *simulans*.

*Halimeda borneensis* is not known from the Atlantic where *simulans* is common, but there may be some overlap of ranges in the Indo-Pacific.

At times the species *borneensis* and *macroloba* could be confused, at least initially, and more data are needed on geographic and reef distribution to know the extent of overlap in their ranges. Differences between these two species are discussed under *macroloba*.

Both the habitat and habit of *borneensis* are distinctly different from those of *micronesica*, a species to which Taylor (1975) compared it, although there is a similarity in the especially large basal or suprabasal fan-shaped segments of the two.

FIG. 27. *H. borneensis.* Type specimen, North Borneo, Pulau Gaya, off the east coast, Cleland Station 10. Scale bar is 3 cm long. (Photograph by Jodi Grenga.)

The limited nodal material of *borneensis* I have been able to examine showed firm fusion of all the medullary filaments into a single unit for a short distance with well-developed pores. I did not find the filaments to separate more readily than in other Rhipsalian species, although Taylor (1975) reported a very light fusion, with filaments separating easily.

## *Halimeda macroloba* Decaisne

Figure 28.

*Halimeda macroloba* Decaisne (1841), p. 118; Decaisne (1842), p. 91; Barton (1901), p. 24, Plate 3, Figs 33–38; Hillis (1959), p. 375, Plates 3, 5, 6, 12.
*Halimeda macroloba* v. *ecalcarea* Weber-van Bosse (1926), p. 88.

Plants erect, flat or somewhat bushy, to 23 cm tall excluding the holdfast which is usually well developed and may extend to 5 cm in length; calcification moderate to rather light; branching relatively sparse, mainly ditrichotomous but often becoming polychotomous in the basal region; basal segments commonly compressed-cylindrical to trapezoidal, of a somewhat stipitate nature and supporting several segments which may remain separate or consolidate laterally, either entirely or in part, to form a fan-shaped unit which may lie flat or become somewhat undulated or folded; other segments plane or slightly ribbed, at times compressed-cylindrical but more commonly subcuneate, discoidal or subreniform, the upper margin entire, undulating or occasionally somewhat lobed, to 29 mm long, 40 mm broad and averaging 1 mm in thickness.

Cortex occasionally of two, but more commonly of three to four layers of utricles; outermost utricles separating on decalcification or remaining slightly attached, their lateral and peripheral margins occasionally thickened, 23–49 μm in surface diameter, (46–)62–110(–144) μm long in section, usually four or occasionally two supported by each secondary utricle; secondary utricles 20–58(–68) μm broad, (30–)40–80(–140) μm long; tertiary utricles 36–90(–110) μm broad.

Nodal medullary filaments uniting as a single group for a distance of approximately 44–80(–115) μm, the adjacent filaments communicating by pores; walls in this region thickened and pigmented.

*Type specimen.* Red Sea, Schimper 871, 1837; isotype material in several herbaria including the British Museum (Natural History) and the New York Botanical Garden.

*Habitat.* Grows in mud or other unconsolidated substrate, from above low-tide line to −12 m, sometimes developing extensive stands in the shallows. Its holdfast may also be associated with bits of coral rock and is then smaller. It often grows in the quiet waters

FIG. 28. *H. macroloba*. (Top) Specimen from Kenya, Malindi, on the reef flat, 4 IV 66, Isaac 2972. (Photograph by Jodi Grenga.) (Bottom) A grove of *macroloba* exposed at low tide, Nuku Alofa, Tonga, April. (Photograph by R. Lewin, reproduced with permission.)

associated with mangroves, and is associated with sea grasses and species of *Avrainvillea*, *Udotea* and sometimes with *H. opuntia*.

This is a well-known species of which many collections have been made. Hence, although it may grow somewhat more deeply than 12 m, it seems reasonable to consider this a species of very shallow to shallow waters, and one often achieving prominence in quiet mangrove waters.

*Geographic distribution.* Western and eastern Indian Ocean including the Red Sea; western Pacific, both north and south.

This species can usually be distinguished macroscopically from other Rhipsalian Halimedae by its broad, flat segments with distal margins usually very little lobed. These segments are relatively large, to 29 mm long and 40 mm broad, although in certain plants they do not exceed 11 mm in length and 20 mm in breadth. Histologically, the diameters of the utricles decrease towards the outer surface, those of the peripheral utricles being relatively small.

This species is at times confused with *discoidea* and *taenicola*, two members of section Halimeda. Although doubtful specimens can be readily identified on histological grounds, macroscopic criteria are usually adequate. These include the extent of development of the holdfast region, the general appearance of the basal part of the plant, and the size and appearance of the segments. In *discoidea* and *taenicola*, large segments, although often present, usually do not account for 50% or more of the segments as they often do in *macroloba*.

Of the Rhipsalian species, *macroloba* is most likely to be confused with *borneensis* because they both have relatively large, broad segments. In general, those of *macroloba* has a less-lobed distal margin and are larger. The mature thallus of *macroloba* is also larger than that of *borneensis*, and it lacks the distinctive fan-shaped basal or suprabasal segment which is characteristic of most thalli of *borneensis*.

Microscopically, the diameters of the peripheral utricles of *borneensis* tend to be somewhat larger than those of *macroloba*, and these utricles adhere, at least in some material, somewhat more firmly to each other. The secondary utricles of *borneensis* also tend to be longer than those of *macroloba*.

2. *Section Opuntia J. Ag.* ex *De Toni*

*Halimeda opuntia* (Linnaeus) Lamouroux

Figures 19, 51, 92.

*Corallina opuntia* Linnaeus (1758), p. 805 *p.p.*

*Halimedea opuntia* Lamouroux (1812), p. 186; *Halimeda opuntia* Barton (1901), p. 18, Plate 2, Figs 19–27; Collins (1909–1918), p. 400, Plate 17, Fig. 156; Taylor (1928), p. 82; Taylor (1950), p. 80, Plate 39, Fig. 1; Egerod (1952), p. 397, Plate 37, Figs 19a, e, f; Hillis (1959), p. 359, Plates 2, 5–7, 10.

*Halimeda multicaulis* (Lamarck) Lamouroux (1816), p. 307. *Flabellaria multicaulis* Lamarck (1813), p. 302.

*Halimeda opuntia* f. *typica* Barton (1901), p. 20, Plate 2, Fig. 19; Taylor (1928), p. 83, Plate 10, Figs 5–7, Plate 11, Fig. 17.

*Halimeda opuntia* f. *cordata* (J. Agardh) Barton (1901), p. 20, Plate 2, Fig. 21. *Halimeda cordata* J. Agardh (1887), p. 83.

*Halimeda opuntia* f. *triloba* (Decaisne) Barton (1901), p. 20, Plate 2, Fig. 20; Taylor (1928), p. 83, Plate 10, Fig. 2; Taylor (1950), p. 81, Plate 40, Fig. 2. *Halimeda triloba* Decaisne (1842), p. 102.

Plants compact or sprawling, often with both lateral and erect systems of growth, holdfast region not restricted to the initial area but diffuse, with patches of rhizoids occurring at intervals where the plant comes in contact with the substratum, to 1 m or more in length; calcification moderate to heavy; branches sometimes few but often numerous, arising in more than one plane from successive segments; segments extremely variable, flat or somewhat contorted, and frequently ribbed, cylindrical or oblong to auriculate, the upper margin entire, undulate or lobed, to 7 mm long, 11 mm broad, averaging 0·3–0·5 mm in thickness, with the occasional larger segment.

Cortex of up to five layers of utricles formed by dichotomies in the lateral branches of the medullary filaments (that is, not utriculiform); outermost utricles adhering slightly after decalcification or for as much as 6 μm, appearing somewhat rounded or hexagonal in surface view, 12–41 μm in surface diameter, 15–39(–50) μm long in section; secondary utricles 11–35 μm broad.

Nodal medullary filaments uniting most commonly in pairs for a distance of approximately 1·5 times the filament diameter, occasionally fusing in threes but rarely in fours, seldom remaining separate; adjacent fused units free or laterally attached for up to 25 μm.

*Type locality.* Jamaica.

*Habitat.* This species sprawls over rock surfaces, fills crevices, and produces ropes of thallus which grow at the bases of rocks or sometimes traverse patches of sand, with attachment provided by a multi-holdfast system. In water of about 0·3–0·5 m this species sometimes provides about 90% cover of rock surfaces.

In deeper water it may be associated with *H. goreauii*. It also grows as clumps on *Acropora*.

It is known from close to the surface to −90 m.

*Geographic distribution.* Pantropical; western and eastern Indian Ocean including Red Sea; western Pacific both north and south; north-eastern Pacific; western Atlantic, both north and south. Not in Bermuda.

Special features of the thallus of this species include segments with a wide range of shapes, the occasional termination of a branch with rhizoidal rope-like strands rather than segments, a feature also of a few other species particularly *micronesica,* and the development in certain specimens of two fairly dissimilar growth systems, an upright (cushion) pattern and a spreading (axial) pattern. Of these, the spreading system, which is somewhat loosely organized and composed of cylindrical and deeply trilobed segments or occasionally subcuneate ones, often produces discrete clumps of intense erect growth at intervals, in which flat, relatively broad segments with entire slightly lobed margins are often the most common.

*Halimeda goreauii* W. R. Taylor

Figure 29.

FIG. 29. *H. goreauii. Isotype* specimen, Jamaica, St Ann Parish, reef off Cardiff Hall beach at about −30 m, T. F. Goreau *et al.* 3337. Scale bar is 2 cm. (Photograph by The Ohio State University Department of Photography.)

*Halimeda goreauii* Taylor (1962), p. 173, Figs 1–7.
*Halimeda opuntia* f. *minor* Vickers (1905), p. 57; Taylor (1928), p. 83, Plate 10.

Plants at least to 13 cm tall from a small stupose base, simple below, a few of the lower segments subterete, above abundantly loosely branched, with branches lying essentially in a plane; segments at the bases of the lower branches subterete to subcuneate, those above and in all the upper branching deltoid to most characteristically strongly trilobed, the lobes terete in the central parts of the plant, more flattened above, the segment faces shiny, often slightly ribbed, the margins minutely erose, in length 2·5–4·0 mm, in width 2·5–5·0 mm, the upper segments generally wider in proportion than the lower ones.

Cortex generally of three or more series of utricles, not utriculiform; peripheral utricles remaining attached for a distance of up to 5 μm, appearing somewhat rounded or hexagonal in surface view, (12–)16–37 μm in surface diameter, (12–)17–40 μm long in section; secondary utricles 10–30 μm broad.

Nodal medullary filaments uniting in pairs for a distance of approximately 1·5 times the filament diameter, at times adhering strongly with other pairs.

A separate form has been described.

### f. *compacta* W. R. Taylor

*Halimeda goreauii* f. *compacta* Taylor (1962), p. 174.

Plants to 4 cm tall, short stalked and very densely branched, the upper segments a little smaller and less sharply trilobed than in typical plants.

*Type specimens*. For *H. goreauii* f. *goreauii* Jamaica, St Ann Parish, reef off Cardiff Hall beach at about −30 m, T. F. Goreau *et al.* 3337, 21 July, 1961; for f. *compacta* Jamaica, St Ann Parish, Llandovery, on the reef sill at −33 m to −57 m, T. F. Goreau A3362, 31 December, 1960. Both in Museum of Science, Institute of Jamaica (isotypes MICH).

*Habitat*. Growing attached to rocks from near low-tide line to −65 m or more, in places associated with *H. opuntia*.

*Geographic distribution*. Western Atlantic.

### *Halimeda minima* (W. R. Taylor) Colinvaux

Figure 30.

*Halimeda minima* (W. R. Taylor) Colinvaux (1968a), p. 32, Figs 5, 6.
*Halimeda opuntia* f. *minima* Taylor (1950), p. 82, Plate 39, Fig. 2.

FIG. 30. *H. minima*. Small holdfast is present on upper specimen. Material from Enewetak Atoll, Enewetak Islet, Quarry, 4 XII 75, Hillis-Colinvaux. Scale bar is 2 cm. (Photograph by The Ohio State University Department of Photography.)

Plants to at least 9 cm tall, usually bushy, from a single tiny holdfast although at least occasionally there may be additional points of attachment; calcification moderate to heavy; branching in a single plane except possibly near the base, most commonly trichotomous, less commonly dichotomous; segments may be brittle and glossy, hardly ribbed, frequently trilobed in the lower half of the plant, trilobed to flattened-cylindrical to cylindrical in the upper half, trilobed segments to 5 mm long and 4·5 mm wide, others to 4 mm long and 3 mm wide.

Cortex of up to four series of utricles with inner ones usually not utriculiform; outermost utricles generally adhering slightly after decalcification, in surface view most commonly polygonal although occasionally somewhat rounded with a covering lamella (Section I) sometimes evident, diameter in surface view 14–30(–39) μm, in section 14–32 μm long, more than four supported by each secondary utricle; secondary utricles 10–18(–25) μm broad.

Medullary filaments numerous in mature segments, most commonly united at the node in pairs or sometimes in threes for (52–)56–75(–87) μm, occasionally completely separate; nodal units sometimes adhering slightly.

*Type specimen.* Marshall Islands, Bikini Atoll, Bikini Lagoon, dredged at −55 m, W. R. Taylor 46–108, 29 March, 1946 (MICH; isotypes in C, L, PC).

*Habitat.* Known from −1 m low tide to −55 m. At the shallowest depths it grows erect on shallow ledges of coral rock, appearing like a miniature bush. Sometimes growing in the vicinity are *H. distorta*, *H. gracilis* and *H. macrophysa*.

*Geographic distribution.* Northern Pacific Ocean.

In a re-evaluation of some of the entities assigned to *opuntia*, this and two other species were separated out by Colinvaux (1968a). A discussion of characters is provided in that paper.

### *Halimeda renschii* Hauck

Figure 31.

*Halimeda renschii* Hauck (1886), p. 167; Hillis-Colinvaux (1975), p. 93.
*Halimeda batanensis* W. R. Taylor (1973), p. 34.
*Halimeda opuntia* f. *renschii* (Hauck) Barton (1901), p. 21, Plate 2.

Plants compact, erect or somewhat repent, to 8 cm tall, from a non-discrete base of matted filaments and sometimes loose particles of substrate which may exceed 1 cm in largest dimension, but is not bulbous as in typical Rhipsalian species; branching tending to produce a flat (plane) thallus; lower segments of thallus may be obscured by the matted base, segments commonly obtrianglar but sometimes transversely oval towards the apex particularly in Pacific specimens, flat or faintly ribbed, to 4 mm long, 5 mm broad.

Cortex of three or more series of utricles formed by dichotomies of the lateral branches of the medullary filaments and hence not particularly utriculiform; outermost utricles adhering only slightly and sometimes separating after decalcification, polygonal, but sometimes rounded with a covering lamella sometimes present, (11–)15–28(–38) μm in surface diameter, 20–33 μm long in section; secondary utricles 14·8–22 μm broad.

FIG. 31. *H. renschii.* Basal portion of specimen is extensively matted. Specimen from Kenya, Diani, Isaac 3193. Scale bar is 2 cm. (Photograph from Hillis-Colinvaux, 1975.)

Nodal medullary filaments uniting in pairs for a distance of 1–1·5 times the filament diameter, sometimes fusing in groups of three, or filaments remaining single.

*Lectotype specimen.* Comoro Islands, Johannes Island, J. M. Hildebrandt No. 1889 (L), designated by Hillis-Colinvaux (1975); isotype material BM, C, PC, NY. The epithet *brevicaulis* appears on some of this material, and its use cannot be readily explained for macroscopically and microscopically the specimens so named are the same as *renschii*. The taxon *H. renschii* is distinct from *H. brevicaulis* from the Bahamas described by Kützing (1858). Some sheets are also labelled with the orthographic variant *H. reinshcii*.

*Habitat.* Growing in outer reef pools under moderate wave wash, where it forms dense masses (Womersley and Bailey, 1970; Isaac, 1971).

*Geographic distribution.* Eastern Indian Ocean; western Pacific both north and south, south-eastern Pacific.

## *Halimeda velasquezii* W. R. Taylor

Figure 32.

*Halimeda velasquezii* W. R. Taylor (1962), p. 176, Figs 8–14.
*Halimeda opuntia* f. *intermedia* Yamada (1934), p. 81, Figs 50, 51.

Plants compact, to 7 cm tall, from a very small stupose base; branching producing a flat (plane) thallus; the lower one to four segments small,

FIG. 32. *H. velasquezii*. Specimen from Ryuku Island, Waha, Yamada V–1933 = holotype of *opuntia* f. *intermedia*. Scale bar is 2 cm. (Photograph by The Ohio State University Department of Photography.)

subterete or compressed, other segments transversely oval to reniform, to 6 mm long, 11 mm broad, the margins entire, surface often glossy, sometimes with a faint trace of a midrib.

Cortex of three or more series of utricles formed by dichotomies of the lateral branches of the medullary filaments and hence not particularly utriculiform; outermost utricles adhering only slightly and sometimes separating after decalcification, in surface view round or somewhat compressed, a distinct covering lamella usually present which parts in a polygonal pattern when slight pressure is applied to the utricles; 9–22 μm in surface diameter, 15–34 μm long in section; secondary utricles 8·5–15(–22) μm broad.

Nodal medullary filaments uniting in pairs for a distance of 1–1·5 times the filament diameter, also fusing for a short distance in threes, rarely fours, and sometimes remaining single; the fusion units commonly adhering firmly in one or a few groups.

*Type specimen.* Philippines, Sta. Ana, Prov. Cayagan, Luzon Island, Velasquez 2379, 17 July, 1950 (MICH); isotype material at the University of the Philippines.

*Habitat.* From about −3 m to −100 m. The shallow records are from rock tidepools and surge channels in Guam, both with strong currents (R. Tsuda, personal communication); the deep records were obtained by dredging during the *Sealark* Expedition, 1905, with specimens housed in the British Museum (Natural History).

*Geographic distribution.* Western Indian Ocean; western Pacific, both north and south.

### *Halimeda copiosa* Goreau and Graham

Figures 33, 101.

*Halimeda copiosa* Goreau and Graham (1967), p. 433, Figs 1–10.
*Halimeda hederacea* L. H. Colinvaux (1968a), p. 30, Figs 1–3, 6; (1969a), p. 88.
*Halimeda opuntia* f. *hederacea* Barton (1901), p. 21, Plate 3.
*Halimeda opuntia* v. *hederacea* (Barton) Hillis *p.p.* (1959), p. 360.

Plants to 70 cm long, loose or compact of habit, from a single holdfast; calcification moderate; branching in a single plane, most commonly dichotomous but also trichotomous; segments commonly one to three ribbed although not strongly so, a "skin" of peripheral utricles sometimes separating from the rest of the cortex when the segment dries; the first two or three segments at the base of the thallus and often the first on a branch small, trilobed, terete or rhombic, other segments transversely oblong to depressed ovate with upper margin entire, three-lobed or crenate, and basal margin truncate to cordate, often forming a short stalk at the nodal junction, to 13 mm long, 21 mm broad, and 0·3–1·0 mm thick when dried.

Cortex of three to four series of utricles with subperipheral ones usually not utriculiform; outermost utricles adhering firmly for about 1–5 μm; in surface view polygonal with polygons measuring (22–)28–46(–64) μm in diameter or if only the utricles with hexagonal surface appearance considered then (27–)32–46(–64) μm; in section outermost utricles (22–)30–50(–68) μm long, not more than four supported by each secondary utricle; secondary utricles (16–)19–30(–45) μm broad.

Medullary filaments numerous in mature segments, most commonly united at the node in pairs, less commonly in threes to sixes, all for a short distance; occasionally fused in pairs for about two to three times this

FIG. 33. *H. copiosa*, from approximately −37 m to −50 m on rock. Specimen from Jamaica, Maria Buena, 5 V 62, Goreau and Graham. Scale bar is 2 cm. (Photograph by The Ohio State University Department of Photography.)

distance, or completely separate; nodal filaments sometimes adhering slightly to somewhat firmly but usually not much entangled.

*Type specimen.* Jamaica, Parish of St Ann, Runaway Bay, from −30 m, Graham and Goreau, 10 April, 1964 (IJ; isotypes BM, NY, UWI, UM).

One special form has been described.

f. *elongata* (Barton) L. H. Colinvaux

*Halimeda cuneata* v. *elongata* Barton (1900), p. 480, Plate 18.
*Halimeda copiosa* f. *elongata* (Barton) L. H. Colinvaux (1969a), p. 88.
*Halimeda opuntia* f. *elongata* (Barton) Barton (1901), p. 21, Plate 2.
*Halimeda hederacea* f. *elongata* (Barton) L. H. Colinvaux (1968a), p. 32, Fig. 2.

Segments predominantly longer than broad, although the two dimensions may be equal; in shape elliptical, rhombic and obtrullate, to 12 mm long, 10·5 mm broad.

*Type specimen.* Ellice Islands, Funamanu, dredged −72 m, No. A 54, Funafuti Expedition, 1896–1898 (BM box coll. 196, as *H. opuntia* f. *elongata*).

*Habitat.* Attached to rock surfaces where it may grow from between the plates of corals, or as pendant fronds beneath coral overhangs. Its range is from about −10 m to −100 m. In Jamaica it reaches its greatest development on the fore-reef slope (Goreau and Goreau, 1973), and is associated with *H. cryptica* at this and greater depths. In the lagoon of Enewetak Atoll, it is a common *Halimeda* of the pinnacles.

*Geographic distribution.* Western Indian Ocean; western Pacific, both north and south; north-western Atlantic.

### *Halimeda distorta* (Yamada) L. H. Colinvaux

Figure 34.

*Halimeda distorta* L. H. Colinvaux (1968a), p. 33, Figs 4, 6.
*Halimeda incrassata* f. *distorta* Yamada (1941), p. 119, Fig. p. 120; Yamada (1944), p. 28, Plate 4.
*Halimeda opuntia* v. *hederacea* (Barton) Hillis *p.p.* (1959), p. 360.

Plants to at least 26 cm long, sometimes bushy, with prostrate and erect portions and a diffuse holdfast region (i.e. not restricted to single basal region); calcification heavy; branching in more than one plane from successive segments, usually di- and trichotomous; segments often ribbed, sometimes keeled, very commonly contorted, brittle; segment shape commonly broadly ovate to discoidal, the lower margins truncate to auriculate and sometimes somewhat cuneate, upper margins smooth to moderately lobed; segments to 16 mm long, 19 mm wide.

Cortex of up to several series of utricles with inner ones usually not utriculiform; outermost utricles attached but slightly after decalcification, frequently tending to separate at least in patches, but retaining their polygonal shape in surface view, diameter in surface view 36–60 μm, in section outermost utricles 39–54(–62) μm long, not more than four supported by each secondary utricle; secondary utricles 17–37 μm broad.

Medullary filaments numerous in mature segments, commonly united at the node in pairs for a relatively short distance; complete fusion in pairs, short and complete fusion in threes and occasionally other groupings, or the filaments completely separate; short fusion for the distance of (66–)100–160(–193) μm; nodal units may be entangled and adhere firmly; medullary filaments above the node sometimes not developing a cortex but continuing as long, sometimes tangled, threads.

*Type specimen.* Caroline Islands, near Ponape, lagoon of Ants Atoll, Y. Yamada, S 15–1 (SAP).

FIG. 34. *H. distorta. Holotype*, Caroline Islands, near Ponape, lagoon of Ants Atoll, Yamada S 15–I. Hair-like strands from outer margin of some segments in lower part of photograph are rope-like uncorticated medullary filaments. Scale bar is 2 cm. (Photograph from Colinvaux, 1968a.)

*Habitat.* A spreading alga, growing on rock, in and through its crevices, and around the bases where it may extend into sand. Attachment is provided by a multi-holdfast system. This species grows in regions of strong currents such as the inter-island passes and quarry at Enewetak. The limited depth records are all from water of −0·6 m to −3 m.

*Geographic distribution.* Western Pacific Ocean, both north and south.

### 3. *Section Halimeda J. Ag.* ex *De Toni*

#### *Halimeda tuna* (Ellis and Solander) Lamouroux

Figure 35.

*Corallina tuna* Ellis and Solander (1786), p. 111, Plate 20, Fig. e.
*Halimedea tuna* Lamouroux (1812), p. 186; *Halimeda tuna* Lamouroux (1816), p. 309, Plate 11, Fig. 8; Barton (1901), p. 11, Plate 1, Figs 1–6; Collins (1909–1918), p. 400; Taylor (1928), p. 85; Hillis (1959), p. 342, Plates 1, 5, 6, 9.
? *Halimeda tuna* f. *albertisii* Piccone (1879), p. 23, Fig. 2; Barton (1901), p. 14, Plate 1, Fig. 3.
*Halimeda tuna* f. *platydisca* (Decaisne) Barton (1901), p. 14, Plate 1, Fig. 2; *Halimeda platydisca* Decaisne (1842), p. 102.
*Halimeda tuna* v. *platydisca* Børgesen (1911), p. 134; Børgesen (1913), p. 106, Collins (1909–1918), p. 102; Taylor (1928), p. 85, Plate 10, Fig. 13.

Plants spreading or compact, often forming cushion-like clumps, arising from an inconspicuous holdfast, to 15 cm tall; calcification moderate to light, sometimes becoming heavier towards the base; branching generally ditrichotomous; basal segments often subcuneate, the others plane or sometimes ribbed, mainly subcuneate, discoid or reniform, commonly relatively small, to 13 mm long, 19 mm broad, and averaging 0·50–0·75 mm in thickness, but in other specimens, often from deep water, to 25 mm long and 40 mm broad.

Cortex of two to four layers of utricles; outermost utricles remaining firmly attached after decalcification for a distance of approximately 12–16 μm, sometimes fusing laterally in twos or threes for this same distance; lateral and peripheral walls occasionally somewhat thickened; unfused peripheral utricles measuring (25–)34–100(–125) μm in surface diameter, (46–)60–130(–230) μm long in section, two to four or occasionally up to seven supported by each secondary utricle; secondary utricles (20–)30–80(–110) μm broad; tertiary utricles 40–130 μm broad.

Nodal medullary filaments uniting in twos and threes, the length of fusion usually 1·5 times the filament diameter or else complete; resultant units

FIG. 35. *H. tuna*. Densely branched, slightly stipitate plant with holdfast slash-shaped and immediately above centimetre scale. Specimen from Jamaica, Boscobel, IX 62, Hillis-Colinvaux and Colinvaux. Scale bar is 2 cm. (Photograph by The Ohio State University Department of Photography.)

usually densely entangled and remaining separate or laterally adhering for an average distance of 85 μm.

*Type locality*. Mediterranean Sea. This species is the type for the genus.

*Habitat*. Grows attached to coral rock or other hard surface, from just below low-tide to about −80 m. Apart from *opuntia* it is probably the commonest rock-growing *Halimeda* of the Caribbean.

*Geographic distribution*. Pantropical; western and eastern Indian Ocean; north-western Pacific; western Atlantic, both north and south including Bermuda; eastern Atlantic, both north and south; Mediterranean.

This species, which was first described for the Mediterranean, has subsequently been attributed to most tropical areas. The specimens from these other regions, however, usually differ in one or more respects from the small-segmented Mediterranean plants which represent the type.

In habit, the typical small-segmented Mediterranean plants seem small and cushion-like, whereas specimens with small segments from the Atlantic and Indian Oceans are often larger and less compact. The lower segments of western Atlantic plants are commonly subcuneate in shape rather than reniform, and the surface diameters of peripheral utricles in western Atlantic and Indian Ocean material average approximately 50 μm as opposed to 65 μm for the Mediterranean plants. The *tuna* plants of Bermuda, a region at the extreme edge of the tropical range, resemble the Mediterranean *tuna* more closely than do Caribbean plants (Howe, 1905a), an observation well substantiated by herbarium specimens. Some of the observed differences may be a response to a stress environment as well as to geographical isolation. The range encountered in the various characters has been considered within the range of the species.

Large-segmented plants occur throughout the entire range of *tuna* and are sometimes assigned to f. *platydisca*. The surface diameters of their peripheral utricles are at the larger end of the range given.

## *Halimeda cuneata* Hering

Figures 36, 61.

*Halimeda cuneata* Hering *in* Krauss (1846), p. 214; Barton (1901), p. 15, Plate 1, Fig. 7, but not Plate 2, Fig. 9, or Plate 1, Fig. 10; Hillis (1959), p. 345, Plates 1, 5–7, 9.
*Halimeda obovata* Kützing (1858), p. 11, Plate 25, Fig. 1.
*Halimeda versatilis* J. Agardh (1887), p. 86.

Plants rather loosely organized or occasionally compact, arising from a small but distinct holdfast region, to 25 cm tall; calcification light; the surface smooth and usually somewhat glossy; branching mainly dichotomous but with up to six segments arising from a single one; the basal first to second segments cylindrical to subcylindrical, often giving the appearance of a short stipe; other segments plane, mostly cuneate, sometimes discoid, generally to 16 mm long, 18 mm broad and averaging 0·50–0·75 mm in thickness, but in some specimens reaching 21 mm in length and 27 mm in breadth; many of the segments supported by a cushion segment, to 1·5 mm long, 5·5 mm broad, or a stalk region of uncorticated medullary filaments, or both.

FIG. 36. *H. cuneata*. A stalk region of uncorticated medullary filaments occurs between some of the segments shown. Specimen from East Africa, Inhaca Island, 24 IV 56, Isaac 799. (Photograph by Jodi Grenga.)

Cortex of two to four layers of utricles; outermost utricles remaining firmly attached after decalcification for an average distance of 35 μm, occasionally fusing laterally in pairs for this same distance; unfused peripheral utricles 25–63(–72) μm in diameter, (43–)58–100(–135) μm long in section, usually four but occasionally two supported by each secondary utricle; secondary utricles 20–67(–79) μm broad, 20–67 μm long; tertiary utricles (40–)50–80(–94) μm broad.

Nodal medullary filaments united in twos and threes, the length of fusion usually 1·5 or several times the filament diameter; fused units densely

entangled but at most adhering only slightly; filament walls thickened and pigmented at the node, and in the cushion joint and stalk region.

*Lectotype specimen.* Collected by Krauss at Durban (Natal Bay), South Africa (BM).

*Habitat.* Growing on rocks near low-water mark and under ledges of reef pools, also dredged to −40 m.

*Geographical distribution.* Subtropical; western Indian Ocean, both north and south; south-eastern Indian Ocean; south-western Pacific.

This range includes the first authentic material I have seen from the northern hemisphere. It was collected by R. Norris at Okah, Gujarat State, India, 9 March, 1963 (Smithsonian Oceanographic Sorting Center No. 28).

This species differs from all other species of the genus in the presence of what have been called "stalked" as opposed to "sessile" segments at the base of a few segments of the thallus. The "stalk" consists of either a small cushion segment or a stalk region or both.

The medullary filaments, subsequent to fusion in twos and threes in the node region of a typical segment, may extend into a "cushion" segment which consists of cortical layers as in a regular segment. However, the inner layers are usually not as regular in appearance or as extensively developed. In cushion segments near the base of the plant the cortex may be replaced by rhizoidal filaments. Such segments are readily recognized by their looser, rather disorganized appearance. The walls of the main filaments in cushion segments and often those of their branches are somewhat indurated. This is evident in section, and also in surface view of the peripheral utricles, although care must be taken in the latter to distinguish between actual thickening and the effects of shrinkage.

At the apex of these cushion segments, the medullary filaments commonly branch dichotomously, but may also remain unforked. Either way they usually become torulose and proceed uncorticated for some distance. This represents the stalk. These filaments ultimately branch, generally trichotomously, and their rami develop the cortical layers of the new segment.

The preceding account describes the complete expression of the "stalk" region between segments. The extent of its development varies with the individual specimen, and it may be influenced by age since it was rather uncommon in the few young plants observed. Rarely does a plant occur without either of these structures being interposed between some of its segments.

A second prominent characteristic of *H. cuneata* is the extensive attachment of adjacent peripheral utricles which is for approximately 0·3–0·5 of their length. Extensive attachment, however, is not unique for *cuneata*. The peripheral utricles also adhere for a considerable distance in *H. discoidea*, and for somewhat shorter distances in *H. tuna*, and *H. incrassata*. When working with dried material this region is generally compressed and, as a result, the utricles may present the illusion in surface view of being thick-walled.

The concept of this species as presented by Barton was broad, and included both "stalked" and "sessile" plants such as *discoidea*. Hence, the reported geographic range of *cuneata* has sometimes been considerably extended as has been noted by Gilbert (1947), Papenfuss and Egerod (1957) and Hillis (1959).

Two forms of this species, f. *digitata* and f. *undulata*, have been designated (Barton, 1901, p. 16, Plate 1, Fig. 9, Plate 2, Fig. 10), the type specimens of which have not been located. However, since these are based on "sessile" plants which are not included in the present concept of the genus, they no longer seem applicable to *H. cuneata*.

### *Halimeda scabra* Howe

Figure 37.

*Halimeda scabra* Howe (1905a), p. 241, Plates 11, 12; Collins (1909–1918), p. 401; Taylor (1928), p. 84, Plates 10, 11; Hillis (1959), p. 348, Plates 1, 5, 6, 8, 9.

Plants generally compact forming cushion-like clumps, or somewhat spreading, occasionally lax and decumbent and then to 25 cm in length but more commonly not exceeding 9 cm; calcification moderate; colour on drying bluish-green, olive or whitish, the surface dull and somewhat rough; branching frequent, usually dichotomous; basal segments often subcuneate, others plane or slightly ribbed, most commonly subreniform to reniform but also subcuneate and discoidal, to 11 mm long, 20 mm broad and averaging 0·50–0·75 mm in thickness.

Cortex of two to three layers of utricles with a fourth zone occasionally present; outermost utricles remaining attached after decalcification, or separating slightly but retaining their hexagonal shape as viewed from the surface, each bearing a central indurated spine which may extend to two-thirds the length of the rest of the utricle, 26–55(–66) μm in surface diameter, (50–)70–165(–240) μm long in section including the spine, up to seven supported by each secondary utricle; secondary utricles 30–60(–70) μm broad, their length variable and often extending to the medulla; tertiary utricles when present approximately 39–65 μm broad.

Nodal medullary filaments united in twos and threes, the length of fusion approximately 1·5 times the filament diameter or complete; resultant units entangled and sometimes adhering for up to 60 μm.

FIG. 37. *H. scabra*. Specimen from Florida, IX 1895, Curtiss. Scale bar is 2 cm.

*Type specimen*. Florida, Sands Key, Howe 2905, 30 March, 1904 (NY).

*Habitat*. Growing on rocks from near low-tide line to at least −20 m.

*Geographic distribution*. North-western Atlantic.

In general form and anatomy *H. scabra* is closely allied to *H. tuna*, particularly to the somewhat modified plants of the Caribbean, and has frequently been identified as *tuna* in herbaria. From this species it can often be distinguished macroscopically by the rather bluish cast which commonly occurs towards the apices of the branches, and by the rough texture which results from the indurated spines which project from the peripheral utricles, their length varying to a limited extent with the age of the segment. When well developed, the spines are usually visible with a good handlens. The relative ease of separation of the peripheral utricles after decalcification and their small surface diameters are also characteristic of this species, the latter averaging 42 μm in *H. scabra* as opposed to 70 μm in *H. tuna*. Adjacent fused nodal units may remain

separate or else adhere for an average distance of 30 μm, whereas in the Caribbean *H. tuna* the filaments are usually attached laterally for an average length of 85 μm.

### *Halimeda lacunalis* Taylor

Figure 38.

*Halimeda lacunalis* Taylor (1950), p. 91, Plate 51; Hillis (1959), p. 349, Plates 1, 5–7, 9.

Plants erect or somewhat flaccid, arising from a small holdfast region, to 18 cm tall; calcification light to moderate; the surface often glossy; branching complanate, sometimes sparse, commonly dichotomous but with up to four segments arising from a single one; basal segments often relatively small and subcylindrical to subcuneate; suprabasal segments at times fusing laterally, others occasionally ribbed, most commonly subcuneate or obovate, but also discoidal or reniform, to 15 mm long, 20 mm broad, and averaging 0·50–0·75 mm in thickness.

Cortex of two to four layers of utricles; outermost utricles sometimes thickened towards the periphery, remaining attached after decalcification for an average distance of 13 μm, 20–55(–70) μm in surface diameter, 45–100(–190 in subcylindrical segments) μm long in section; two, four or occasionally five borne on each secondary utricle; secondary utricles 15–50(–60) μm broad, (15–)23–80 μm long, these small utricles absent at times; innermost utricles 35–80 μm broad.

Nodal medullary filaments fusing completely in twos and threes; resultant units entangled and adhering strongly for approximately 80–150(–280) μm.

*Type specimen.* Marshall Islands, Enewetak Atoll, Taylor 46–464, 6 June, 1946 (MICH).

One special form has been described.

### f. *lacunalis* f. *lata* (W. R. Taylor) Hillis

*Halimeda lacunalis* f. *lata* (W. R. Taylor) Hillis (1959), p. 349.
*Halimeda gracilis* f. *lata* Taylor (1950), p. 83, Plate 42.

Plants sometimes rather lax, but generally compact; segments usually broader than long, occasionally subcuneate but more generally discoid to reniform, to 15 mm long, 20 mm broad, and averaging 0·75–1·00 mm in thickness.

*Type specimen.* Marshall Islands, Bikini Atoll, Enyu Island, Taylor 46–21, 15 March, 1946 (MICH).

*Habitat.* The known depth range for the genus is 1–55 m. At Enewetak, the form f. *lata* was relatively common in the fast-flowing

FIG. 38a. *H. lacunalis* f. *lacunalis*. *Holotype*, Marshall Islands, Enewetak Atoll, Taylor 46–424. Height of axis on right-hand side from bottom to top of broken segment is 13·2 cm. (Photograph courtesy of the Division of Biological Sciences, University of Michigan.)

FIG. 38b. *H. lacunalis* f. *lata*, showing small holdfast, thickened basal segments and multi-branching near the base, all characteristic features. (Specimen from the Marshall Islands, Enewetak Atoll, pass between Alembel and Lojwa Islets, −2 m to −3 m, 18 XII 75, Hillis-Colinvaux. Scale bar is 2 cm. (Photograph by The Ohio State University Department of Photography.)

waters of an inter-island channel (Section X) where it grew erect on the seaward and leeward faces of the rock substrate, or protruded slightly from rock crevices. The thalli were also attached near the eroded bases of rock, under miniature overhangs. Dwarf forms of f. *lata* occurred at these sites also.

*Halimeda lacunalis* f. *lacunalis* was not encountered at these sites, and seems to be the rarer of the two.

*Geographic distribution.* For *lacunalis* f. *lacunalis* north-western Pacific Ocean; for f. *lata* western Indian Ocean; north-western Pacific Ocean.

This species can be fairly readily distinguished from other Halimedae, except possibly *cuneata*, by the frequent occurrence of subcuneate or obovate segments. The absence of stalk or cushion segments separates it from this one species. Any confusion with *discoidea* or *taenicola* can be resolved microscopically by the absence of swollen secondary or tertiary utricles in *lacunalis*.

Histologically, the commonness of small secondary utricles is fairly characteristic of mature segments of this species. These small utricles are absent, however, when the cortex is composed of only two layers.

In other anatomical aspects *lacunalis* resembles *tuna*, particularly the Atlantic and Indian Ocean specimens. Features the two species have in common are the lateral adhesion of the nodal fusion units, the regular surface appearance of the peripheral utricles and the apparent absence of lateral fusions among them.

*Halimeda lacunalis* differs from *tuna* in the significantly smaller diameters of its peripheral utricles, with those of f. *lata* generally towards the lower limit of the broad *tuna* range.

The adherence of the nodal groups is usually fairly considerable, the rigidity of the resulting nodal structure sometimes leading to confusion with the Rhipsalian pattern. From this type of nodal union it is, nevertheless, entirely distinct, the units in *lacunalis* separating on teasing. *Halimeda lacunalis* also lacks the well-developed bulbous holdfast of Rhipsalian species.

### *Halimeda gigas* W. R. Taylor

Figure 39.

*Halimeda gigas* Taylor (1950), p. 84, Plate 44; Hillis (1959), p. 350, Plates 1, 5, 6, 9.

Plants loosely organized, to 15 cm tall; calcification rather light; colour brownish-green, the surface slightly glossy, rugose, tending to crack somewhat on drying; branching complanate and sparse, although up to six segments may arise from a single segment; basal segments subterete, the others plane, mainly discoidal to reniform, the outer margin entire or very slightly undulating, to 31 mm long, 42 mm broad and averaging 0·75–1·00 mm in thickness; shrinkage on drying fairly considerable, leaving a brown stain on paper.

Cortex of two, occasionally three layers of utricles; outermost utricles remaining attached after decalcification for an average distance of 8 μm, at times fusing laterally in twos and occasionally threes for this same distance; unfused peripheral utricles (84–)96–130(–170) μm in surface diameter, 130–240 μm long in section, borne two or four on each secondary utricle; secondary utricles 60–120(–160) μm.

FIG. 39. *H. gigas. Holotype,* Marshall Islands, Enewetak Atoll, Taylor 46–419. Actual width of specimen is 14·3 cm. (Photograph courtesy of the Division of Biological Sciences, University of Michigan.)

Nodal medullary filaments fusing completely in twos and threes, although occasionally and most particularly towards the periphery of the node uniting for only a short distance (incomplete fusion); fused groups entangled but at most adhering only slightly.

*Type specimen.* Marshall Islands, Enewetak Atoll, Taylor 46–419, 6 June, 1946 (MICH).

*Habitat.* Pendant on rocks in relatively quiet water, and growing from approximately −1·5 m to −46 m. In shallow water it is sometimes relatively common and at some sites it is associated with *H. macrophysa.*

*Geographic distribution.* North-western Pacific Ocean.

This species may initially be mistaken for a large segmented *tuna* or *discoidea.* Microscopic differences with *tuna* include the large surface diameters of the peripheral utricles, these averaging 115 μm in *gigas* as compared to 70 μm in *tuna* and a less extensive development of the cortex in *gigas* as opposed to *tuna.*

In comparing it with *discoidea*, the surface utricles of *discoidea* are smaller (average diameter 65 μm), and the secondary utricles larger (average 125 μm as compared to 90 μm in *gigas*).

### *Halimeda macrophysa* Askenasy

Figures 40, 99.

*Halimeda macrophysa* Askenasy (1888), p. 14, Plate 4, Figs 1–4; Barton (1901), p. 17, Plate 2, Figs 15–18; Hillis (1959), p. 351, Plates 2, 5, 6, 11.

FIG. 40a. *H. macrophysa*. Habit. Scale bar is 2 cm. (Photograph by The Ohio State University Department of Photography.)

Plants fragile, compact and erect, arising from a single small holdfast region, to 10 cm tall; calcification moderate; the surface dull, rugose and appearing pitted; branching complanate, mainly ditrichotomous but with several segments arising from some of the larger ones; basal segments often subcuneate, the others friable, plane, commonly reniform or subreniform but also subcuneate, the upper margin entire, to 15 mm long, 24 mm broad and averaging 0·5 mm in thickness.

Cortex most commonly of two layers of utricles; outermost utricles separating readily on decalcification, appearing round in surface view, 135–180 μm in surface diameter, 170–230(–290) μm long, most commonly two but also one or four supported by each secondary utricle; secondary utricles 40–100 μm broad, 73–140(–230) μm long.

Nodal medullary filaments fusing completely in twos, threes and occasionally larger units; resultant units densely entangled and often adhering slightly.

*Type locality.* Matuku, Fiji Islands, South Pacific.

FIG. 40b. *H. macrophysa.* Close-up of segments showing pitted surface which, macroscopically, often gives a stippled appearance to the segment. Specimen from Mentawei Islands west of Sumatra, Pulau Stupai north of Sanding Island, 4 XII 63, Hillis-Colinvaux LH–29c. Scale bar is 1 cm. (Photograph by The Ohio State University Department of Photography.)

*Habitat.* Hanging from rocks, filling crevices, or growing more openly as compact clumps; from approximately −1·5 m to −50 m. At Enewetak it formed relatively dense populations on flat surfaces on the tops of pinnacles and on a buttress on the seaward site of Mut Island. It was a very common species in the lagoon, and was at times associated with *H. gigas*, *H. distorta* and *H. gracilis* (Section X).

*Geographic distribution.* Western and eastern Indian Ocean; western Pacific, both north and south.

This species is readily distinguished from all species of the genus other than *favulosa* by its friable nature, and the pitted condition of the

segment surface, the latter resulting from the extremely large peripheral utricles and their separation by calcium carbonate partitions. From *favulosa* it can be separated macroscopically by its habit including the absence of the bulbous holdfast of the Rhipsalian species, and by the morphology of its segments. Reniform segments commonly occur in *macrophysa*, the plants themselves usually being compact and less than

FIG. 40c. *H. macrophysa*. Fertile specimen, pendant from coral rock, Pulau Stupai. "Growths" on most of the segments are gametangia supported by gametophores (Fig. 64). Average width of segments is 13 mm. (Photograph by K. Rützler, reproduced with permission.)

10 cm tall, whereas in *favulosa* trilobed or cylindrical segments predominate, and the plants are attenuate and to 22 cm in height. In microscopic details the cortex in both species is rather poorly developed, but the node structure is different.

### *Halimeda discoidea* Decaisne

Figure 41.

*Halimeda discoidea* Decaisne (1842), p. 91; De Toni (1889), p. 527; Collins (1909–1918), p. 400; Howe (1907), p. 495, Plate 25, Figs 11–20, Plate 26; Taylor (1928), p. 82, Plate 10, Fig. 17; Plate 11, Fig. 23; Taylor (1950),

p. 85, Plate 45, Figs 1–2; Egerod (1952), p. 398, Plate 38, Figs 19b–d; Hillis (1959), p. 352, Plates 2, 5–8, 11.

*Halimeda discoidea* v. *platyloba* Børgesen (1911), p. 134, Fig. 3; Børgesen (1913), p. 107, Fig. 86.

*Halimeda discoidea* f. *intermedia* Gilbert (1947), p. 126.

*Halimeda discoidea* f. *subdigitata* Gilbert (1947), p. 125.

*Halimeda tuna* Barton (1901), p. 11 *p.p.*

? *Halimeda cuneata* f. *digitata* Barton (1901), p. 16, Plate 2, Fig. 9.

FIG. 41. *H. discoidea*. A densely branched plant with some of the relatively large segments which commonly occur in the lower portion of robust, mature thalli. Specimen from Florida, 31 III 04, Howe 2964.

Plants generally compact, forming cushion-like clumps but occasionally loose, arising from a small but distinct holdfast region, to 18 cm tall; calcification light; branching mainly ditrichotomous but polychotomous from large segments; the basal first or second segments subcylindrical or broadly cuneate and often of a substipitate nature; other segments usually plane, commonly discoidal to reniform but also compressed-cylindrical, cuneate or subcuneate, the outer margin entire, undulating or occasionally somewhat deeply cleft, to 29 mm long, 33 mm broad and averaging 0·75–1·25 mm in thickness.

Cortex of two, occasionally three layers of utricles; outermost utricles remaining firmly attached after decalcification for an average distance of

42 μm, often fusing laterally in twos, threes and occasionally fours for this same distance, unfused peripheral utricles (30–)40–90 μm in surface diameter, 45–120(–210) μm long in section, up to 14 being supported by each secondary utricle; innermost utricles somewhat contiguous at their apical end, or when well developed for most of their length, (70–)95–155(–260) μm broad, 100–350(–435) μm long.

Nodal medullary filaments united in twos and threes, the fusion both complete and incomplete; fused units entangled but at most adhering only slightly.

*Type specimen.* In the Musée National d'Histoire Naturelle, Paris; label indicates the plant was collected at Kamtschatka during voyage of the *Venus*; at least locality incorrect.

*Habitat.* Growing erect; associated with rock surfaces which sometimes may be veneered or partly buried with sand; from slightly below low-tide line to −50 m.

*Geographic distribution.* Pantropical; western and eastern Indian Ocean including Red Sea; western Pacific both north and south; north-eastern Pacific, western Atlantic, both north and south; north-eastern Atlantic.

The epithet *discoidea* was first applied by Esper (1798–1806, Plate 11) to a drawing of *Halimeda* labelled *Corallina discoidea*. This plant, apparently Mediterranean, was later placed in synonymy under *tuna* by Hammer (1830) in his continuation of Esper's work. Even were this relationship not accepted, Esper does not qualify as author of *discoidea*, since a plate unaccompanied by analysis of parts does not constitute valid publication (Lanjouw *et al.*, 1966). The species *discoidea* was later described by Decaisne (1842).

This species, although frequently mistaken for *tuna* and *cuneata*, is microscopically distinct, and is characterized in particular by the swollen utricles of the inner cortex, one layer being the most common. When an additional zone is present, it rarely occurs uniformly throughout the segment, the innermost utricles then tending towards the lower limit of the size range. Relatively small secondary utricles often occur in Pacific–Mexican plants, and in some of the Hawaiian *discoidea*. This irregularity was also noted by Howe (1911).

Subsequent to the removal, by Howe (1907), of this species from synonymy under *tuna* where it had been relegated by Barton (1901), three subspecific taxa have been described: v. *platyloba* (Børgesen, 1911) from deep water, f. *subdigitata* (Gilbert, 1947) including plants which resemble *cuneata*, and f. *intermedia* (Gilbert, 1947) containing

specimens intermediate between f. *discoidea* and f. *subdigitata*. Consistent with the treatment accorded entities based mainly on modifications of habit or segment morphology which seem unaccompanied by significant histological differences, these three have not been given separate taxonomic standing. The type of the subspecific taxon *H. cuneata* f. *digitata* has not been located with certainty. It does not appear to belong to *cuneata*, as already mentioned, and is retained in synonymy with *discoidea* where it was tentatively placed by Hillis (1959).

### *Halimeda taenicola* W. R. Taylor

Figure 42.

*Halimeda taenicola* Taylor (1950), p. 86, Plate 46. Fig. 1; Hillis (1959), p. 354, Plates 2, 5, 6, 11.

Plants erect and compact, arising from a small holdfast region, to 15 cm tall; calcification moderate; the surface generally glossy and smooth but sometimes rugose; branches numerous with up to five arising from a single segment; the lowermost one to two segments usually compressed-cylindrical to subcuneate and often of a substipitate nature, others plane, often becoming concave on drying, generally subcuneate to trapezoidal, less commonly subcylindrical or reniform, the upper margin entire, to 11 mm long, 18 mm broad, and averaging 1·0–1·5 mm in thickness.

Cortex of two to three layers of utricles; outermost utricles remaining firmly attached after decalcification for an average distance of 19 μm, sometimes fusing laterally in twos and threes for this same distance, unfused peripheral utricles (20–)40–75(–86) μm in surface diameter, (45–)56–125(–140) μm long in section, their lateral and peripheral margins sometimes thickened, four or occasionally up to six supported by each secondary utricle; if three layers of utricles present the secondary ones relatively small, 26–60(–80) μm broad, (30–)40–90 μm long; innermost utricles usually relatively large, 75–160(–190) μm broad.

Nodal medullary filaments generally uniting completely in twos and threes; fused units entangled and adhering laterally for 40–70 μm.

*Type specimen.* Marshall Islands, Rongerick, Enyvertik Island, Taylor 46–551, 29 June, 1946 (MICH).

*Habitat.* The known depth range is −1 m to −47 m. At Enewetak this species occupied microsites in the fast-flowing inter-island channels similar to those filled by *lacunalis* f. *lata*, but *taenicola* was less common. These sites were the seaward and leeward faces of the coral rock on which the thalli were growing, often tucked into microcaves or attached near the eroded bases of the rock, under miniature overhangs (Section X).

FIG. 42. *H. taenicola*, with single basal holdfast, from approximately −4 m to −6 m. Specimen from Enewetak Atoll, lagoon side of pass between Alembel and Lojwa Islets, 18 XII 75, Hillis-Colinvaux and Colinvaux. Scale bar is 2 cm. (Photograph by The Ohio State University Department of Photography.)

*Geographic distribution.* Western Pacific Ocean, both north and south.

In general form, *taenicola* frequently appears like a Caribbean *discoidea* with thick segments, from which it can sometimes be

distinguished macroscopically by its trapezoidal-shaped segments which are often somewhat greenish on drying. Thalli of *discoidea* often possess relatively large *discoidal* segments which dry to a brownish colour. The segments of *taenicola* also appear to be somewhat more heavily calcified than those of *discoidea*.

Microscopically it also shows resemblances to *discoidea*, with the rather characteristically expanded utricles of the innermost, usually tertiary, layer of the cortex, although somewhat smaller in average diameter, suggesting the secondary utricles of *discoidea*. In *taenicola* these utricles often support five or six relatively small secondary utricles, as opposed to only four or two which are the more usual numbers for most species with a three-layered cortex. Occasionally the intermediate zone may be absent, but this rarely happens uniformly throughout the segment.

In more basal segments of *taenicola* an additional layer of utricles is frequently present, the length of the peripheral and secondary utricles is often greater, and the breadth of the innermost utricles is towards the lower limit of the range. These modifications, however, occur fairly commonly throughout the genus.

Microscopically, *taenicola* differs from *discoidea* in the somewhat smaller surface diameters of the peripheral utricles, these averaging 57 μm in *taenicola* and 65 μm in *discoidea*. Other differences include the relatively fewer lateral fusions of these utricles, and the degree of their lateral attachment, which in *taenicola* is approximately half that occurring in *discoidea*. Although the basic nodal structure is similar in these two species, incomplete fusion is considerably commoner in *discoidea* with the fusion groups at most adhering only slightly. In *taenicola* groups of fused filaments adhere for an appreciable distance.

The external appearance of this species sometimes leads to confusion with *macroloba*. These two species can be distinguished macroscopically on the basis of the bulbous holdfast and the somewhat fused condition of the basal or suprabasal segments in *macroloba*. These features are absent in *taenicola*. Histologically also, the two species are entirely distinct. The peripheral utricles in *macroloba* often separate after decalcification, and the pattern of its nodal filaments is that of the section Rhipsalis.

### *Halimeda bikinensis* Taylor

Figure 43.

*Halimeda bikinensis* Taylor (1950), p. 87, Plate 48, Fig. 1; Hillis (1959), p. 358, Plates 2, 5, 6, 10.

Plants erect, moderately compact or somewhat loose, arising from a small holdfast region, to 20 cm tall; calcification relatively heavy; branching somewhat sparse with up to four or five segments and occasionally more arising from a single one; basal segments subcylindrical, subcuneate to subreniform, the three to four lowermost ones often devoid of branches; the others brittle, sometimes discoid but more commonly subreniform to reniform with subcuneate segments frequently occurring at the bases of the branches, the outer margin entire or slightly undulating, frequently raised and infolded, measuring to 16 mm long, 25 mm broad, and averaging 0·7–1·0 mm in thickness.

Cortex of two to three layers of utricles produced by dichotomies in the lateral branches of the medullary filaments; the outermost utricles remaining slightly attached or separating on decalcification, appearing rounded in surface view, 23–47 μm in surface diameter, (48–)60–105(–125) μm long in section, most commonly four but up to eight borne on each secondary utricle; secondary utricles usually not constricted at their origin, 20–47 μm broad.

Nodal medullary filaments occasionally remaining separate but more commonly uniting in twos and threes, the fusions within these units being complete or incomplete; fusion units not particularly entangled, and at most adhering only slightly.

*Type specimen.* Marshall Islands, Namu Islands, Bikini Atoll, Taylor 46–156, 3 April, 1946 (MICH).

*Habitat.* In deep holes of inner reef flats (Taylor, 1950); it is also known to −90 m from material dredged during the *Sealark* Expedition, 1905 (Hillis, 1959).

*Geographic distribution.* Western Indian Ocean; north Pacific.

In external appearance this species is most commonly confused with specimens of *tuna* with large segments, with *discoidea*, and to a lesser extent with *gigas*. A number of well-defined distinctions exist for *bikinensis*, however, including the greater degree of calcification of its segments, the dichotomous nature of the inner cortex, the smaller surface diameters of the peripheral utricles, and the relative ease of separation of these utricles. This last characteristic varies somewhat with age.

Microscopically, this species appears to have most in common with *gracilis* and *lacrimosa*. Characteristic of these two species and most particularly *lacrimosa* are the somewhat swollen apical ends of the secondary utricles which in turn support several, usually 6–18, peripheral utricles. These are absent in *bikinensis*, although the appearance is somewhat simulated by some of the broader secondary utricles which may bear up to eight peripheral utricles rather than the more usual two or four.

FIG. 43. *H. bikinensis*. Specimen from 48 m, Saya de Malha.

## *Halimeda gracilis* Harvey *ex* J. Agardh

Figure 44.

*Halimeda gracilis* Harvey *ex* J. Agardh, 1887, p. 82; Harvey's Ceylon Algae No. 72; Barton (1901), p. 22, Plate 3, Figs 28–32; Vickers and Shaw (1908), p. 24, Plate 34; Collins (1909–1918), p. 399; Hillis (1959), p. 356, Plates 2, 5, 6, 7, 10.

*Halimeda gracilis* v. *opuntioides* Børgesen (1911), p. 144, Fig. 11; Børgesen (1913), p. 108, Fig. 87.

*Halimeda gracilis* f. *laxa* (Barton) Barton (1901), p. 22, Plate 3, Fig. 29; *Halimeda laxa* Barton (1900), p. 479, Plate 18, Figs 1–3.

*Halimeda gracilis* f. *elegans* Yamada (1941), p. 20, Fig. p. 21; Yamada (1944), p. 28, Plate 3.

*Halimeda cuneata* Kützing (1857), p. 8, Plate 21, Fig. 3.

FIG. 44a. *H. gracilis*. Photograph shows spreading habit characteristic of many thalli. Specimen from Saya de Malha.

Plants flaccid, straggling and decumbent, sometimes to over 1 m long; holdfast attachment not restricted to a single basal region but at several places where the sprawling thallus contacts substrate; calcification moderate to heavy; the surface usually glossy; branching sometimes sparse but usually frequent with up to five branches arising from a single segment; segments ribbed, chalky to brittle, at times subcylindrical but more commonly subcuneate to reniform, the upper margin entire, undulate or lobed, to 9 mm long, 15 mm broad, and averaging 0·50–0·75 mm in thickness.

Cortex of two, sometimes three, layers of utricles, these generally produced by dichotomies in the lateral branches of the medullary filaments; outermost

FIG. 44b. *H. gracilis* showing a more compact, broader segmented habit than that in Fig. 44a. Both are relatively common. Specimen from Mentawei Islands, west of Sumatra, Pulau Stupai, northern edge of Sanding Islands, in *c.* −1·1 m to −5 m, 4 XII 63, Hillis-Colinvaux LH 29c. Scale bar is 2 cm. (Photograph by The Ohio State University Department of Photography.)

utricles usually remaining slightly attached on decalcification, occasionally separating but still appearing hexagonal rather than rounded in surface view, 23–58(–70) μm in surface diameter, 40–90(–110) μm long in section, up to eight supported by each secondary utricle; secondary utricles clavate, 23–70(–125) μm broad, usually relatively long and frequently extending to the medulla.

Nodal medullary filaments fused most commonly in twos but occasionally in threes, fusion complete; fusion groups not entangled and at most adhering only slightly.

*Type specimen.* Harvey's Ceylon Algae No. 72; isotype material in several herbaria including BM, NY.

*Habitat.* This species, which is often straggling and sprawling frequently grows at the bases of coral rock and therefore may be associated with sand as well as rock. Attachment is provided by a multi-holdfast system. At Enewetak Atoll *gracilis* was most commonly associated with *distorta* and *macrophysa*, occasionally with *minima*. The known vertical range for the species is −1 m to −70 m.

*Geographical distribution.* Pantropical; western and eastern Indian Ocean; western Pacific, both north and south; western Atlantic, both north and south.

This species seems closely related to *lacrimosa* and probably also to *bikinensis*. From *bikinensis*, a taxon of relatively compact specimens with large segments, to 16 mm long and 25 mm broad, *gracilis* is often readily distinguished by its loose straggling habit which reaches a length of 1 m or more, and by its smaller segments, to 9 mm long and 15 mm broad. In contrast, plants of *lacrimosa* reach about 5 cm in length and are composed of spherical or tear-shaped segments rather than flat ones.

Although *gracilis* is pantropical, its known distribution is extremely limited as compared to that of *discoidea* or *opuntia*. The paucity of records can be partly attributed to the relatively frequent misidentifications of material of this species as *opuntia*, and less commonly as *incrassata* or *tuna*. Identity problems can be resolved microscopically because nodal medullary filament pattern and appearance of the cortical layers are both distinctive for *gracilis*.

The peripheral utricles in plants of this species may initially appear rounded in surface view and give the impression of being separate. A more careful examination, however, usually reveals that they are at least slightly attached, though often by only the thin platform-like extensions of the outer surface. The different optical properties of these edges and the slightly convex outer face of the utricles combine to

produce the illusion of roundness. These edges, in addition, may sometimes create the impression of a matrix, perhaps formed of the covering lamella, surrounding the utricles. This may represent the condition described by Barton for some of these plants.

Four infraspecific categories have been designated for this species: v. *opuntioides* (Børgesen, 1911), f. *laxa* (Barton, 1901), f. *elegans* (Yamada, 1941), and f. *lata* (Taylor, 1950). The latter has been transferred to *lacunalis* (Hillis, 1959). Since the variations in appearance on which the other three forms are based also occur in typical plants, these three forms were placed in synonymy under *gracilis* (Hillis, 1959).

## *Halimeda lacrimosa* Howe

Figure 45.

*Halimeda lacrimosa* Howe (1909), p. 93, Plate 4, Fig. 1; Plate 6, Figs 3–11; Collins (1909–1918), p. 399; Hillis (1959), p. 357, Plates 2, 5–7, 10.

Plants fragile, straggling and decumbent, to 5 cm long; calcification heavy; colour on drying white, often becoming bluish-green towards the apex, the surface smooth and usually glossy; branching restricted, generally di- or trichotomous; segments easily crushed on drying, the basal ones usually cylindrical, often moniloid; others and particularly the more apical ones commonly spherical or tear-shaped, to 5 mm in the three dimensions.

Cortex of two to three layers of utricles, these often produced by dichotomies or tetrachotomies in the lateral branches of the medullary filaments; outermost utricles usually remaining slightly attached on decalcification, occasionally separating but still appearing hexagonal rather than rounded in surface view, 31–42 μm in surface diameter, 40–110 μm long in section, generally 6–18 supported by each secondary utricle; secondary utricles capitate, 66–110 μm broad at the apical end, 105–340(–400) μm long.

Nodal medullary filaments uniting in twos, threes and fours, incompletely or completely, short and complete fusions often mixed so that fewer filaments may emerge than participate in the fusion; resultant units not particularly entangled and at most adhering only slightly.

*Type specimen.* Bahamas, Mariguana, Howe 5524, 11 December, 1907 (NY).

*Habitat.* Howe (1909) reports this tiny species growing on stones, in sand, and on the stipes of *Avrainvillea*. It is also associated with *Pocockiella* (Diaz–Piferrer collection). Its known vertical range is −1 m to −20 m.

*Geographic distribution.* North-western Atlantic.

FIG. 45. *H. lacrimosa.* Specimen from Florida, Content Key, 23 IV 66, Croley 1061. (Photograph by The Ohio State University Department of Photography.)

This delicate species is readily distinguished from all other species of the genus by its small size and by the presence of spherical or pyriform (tear-shaped) segments. It shares with one of the commonest growth forms of *gracilis*, apparently the most closely related species, several features including a lax decumbent habit and an essentially dichotomous inner cortex. The general appearance and degree of attachment of the peripheral utricles are also common to the two species.

Microscopically, *lacrimosa* is characterized by capitate secondary utricles which appear circular in cross-section and support up to 18 peripheral utricles. The pattern of nodal medullary filaments is complex, and is perhaps best interpreted as a combination of short and complete fusion with, for example, two filaments sometimes resulting from a fusion of three or four. The usual type of complete fusion also occurs.

The restricted distribution of this species may be partly accounted for by the ease with which such small specimens are overlooked.

4. *Section Micronesicae* n. sect.

*Halimeda micronesica* Yamada

Figure 46.

*Halimeda micronesica* Yamada (1941), p. 121, Fig. 15; Yamada (1944), p. 29, Plate 5; Taylor (1950), p. 89, Plate 46, Fig. 2; Plate 47; Hillis (1959), p. 364, Plates 3, 5, 6, 9.
*Halimeda orientalis* Gilbert (1947), p. 126, Fig. 1.
? *Halimeda incrassata* f. *pusilla* Barton (1901), p. 28, Plate 4, Fig. 44.

Plants compact, spreading, to 10 cm tall excluding the rhizoidal region which is often small but sometimes long and fibrous, the rhizoids not noticeably interlaced with sand particles; calcification moderate; colour on drying white or steel-grey, the surface usually dull; branching, except for the basal region, mainly trichotomous and complanate; basal segment larger than the others and more or less reniform, its outer margin frequently undulate, to 12 mm long, 18 mm broad, supporting numerous cylindrical to subcuneate segments; other segments occasionally slightly ribbed, sometimes cylindrical but more commonly subcuneate to discoidal, the upper margin entire to trilobed, to 7 mm long, 9 mm broad and averaging to 0·5 mm in thickness.

Cortex mainly of three or occasionally four layers of utricles produced by successive dichotomies in the lateral branches of the medullary filaments; outermost utricles usually separating on decalcification but in young segments often slightly attached, usually appearing rounded in surface view, 28–48(–55) μm in surface diameter, 40–82(–94) μm long in section, borne two or four on each secondary utricle; secondary utricles generally not constricted at their origin, 15–45 μm broad.

Nodal medullary filaments remaining unfused although sometimes adhering slightly with adjacent ones; filament walls in nodal region thickened and usually somewhat pigmented.

*Type locality.* Ants Atoll, near Ponape Island in the east Caroline Islands.

*Habitat.* Growing attached to rock in relatively exposed sites such as inter-island channels of Enewetak Atoll. Rope-like non-corticated extensions from segments provide additional attachment and the resultant growth form is semi-prostrate. Known vertical range for this species is −1 m to −37 m.

*Geographic distribution.* Western and eastern Indian Ocean; western Pacific, both north and south.

This was the first species described in which the medullary filaments continued unfused through the node. Barton (1901) mentioned such a

FIG. 46. *H. micronesica*, showing small holdfast, and much enlarged basal segment which is somewhat contorted and bears many branches. In the specimen shown the nodal medullary filaments of a segment near the base (bottom photograph) have remained uncorticated, forming a rope-like strand which terminates in a young plant. This is an example of asexual reproduction by runners which are above the substrate. Specimen from vicinity of South Pagi Island, west of Sumatra, 2 XII 63, Hillis-Colinvaux LH 27a, b, c. Scale bars are 2 cm. (Photographs by The Ohio State University Department of Photography.)

condition but felt that it occurred largely in stunted plants. She assigned some of them to *incrassata* f. *ovata*.

In addition to having this special nodal pattern, *micronesica* is characterized by peripheral utricles which usually separate readily, and by an extremely modified basal, rarely suprabasal, segment which may become very large in some specimens but is less distinctive in others. In well-developed plants the growth is prostrate, with branches projecting in all lateral directions from the greatly enlarged basal (suprabasal) segment. These branches occasionally terminate in rope-like extensions to approximately 6 cm in length, which consist of intertwined rhizoidal filaments.

### *Halimeda fragilis* W. R. Taylor

Figure 47.

*Halimeda fragilis* Taylor (1950), p. 88, Plate 48, Fig. 2; Hillis (1959), p. 363, Plates 3, 5–9.

FIG. 47. *H. fragilis*, with holdfast. From Enewetak Atoll, pass between Alembel and Lojwa Islets, towards seaward side, 18 XII 75, Hillis-Colinvaux. Scale bar is 2 cm. (Photograph by The Ohio State University Department of Photography.)

Plants compact, often cushion-like, to 8 cm tall including the rather small holdfast region, rhizoids not noticeably interlaced with sand particles; calcification heavy; colour on drying white, cream or greyish-green, the surface dull; branches occurring in more than one plane with up to four arising from a single segment; basal segment generally inconspicuous, cylindrical to reniform; others brittle, frequently ribbed and sometimes

keeled, occasionally cylindrical, these usually occurring as the basal segments of branches, sometimes subcuneate but more commonly subreniform to reniform, the lower margin truncate to auriculate, the upper margin entire to trilobed, to 9 mm long, 16 mm broad, and averaging 0·50–0·75 mm in thickness.

Cortex of three to four layers of utricles produced by successive dichotomies in the lateral branches of the medullary filaments; outermost utricles separating on decalcification, appearing rounded in surface view and at times thickened along the peripheral margin, 21–52 μm in surface diameter, (32–)43–81 μm long in section, borne two or four on each secondary utricle; secondary utricles usually not constricted at their origin; 15–46 μm broad.

Nodal medullary filaments remaining unfused although adjacent filaments may adhere slightly; filament walls in this region usually extremely thickened and deeply pigmented.

*Type specimen.* Marshall Islands, Enewetak Atoll, Taylor 46–394, 2 June, 1946 (MICH).

*Habitat.* Growing on rock in the fast-moving waters of inter-island passes at Enewetak where it seemed to be rare; reported commoner in the deeper waters of the lagoon attached to pinnacles (Gilmartin, 1960). The known vertical range of the species of −1·5 m to −57 m.

*Geographic distribution.* Central Indian Ocean; north-western Pacific.

Macroscopically, *fragilis* is most frequently confused with *opuntia*, *gracilis* and to a lesser extent *bikinensis*. In all four species the cortex is formed essentially by dichotomous branching of the lateral medullary filaments and thus internally there are also similarities. Difficulties in macroscopic determination, however, can always be resolved by an examination of the nodal medullary filaments which remain separate in *fragilis*, but fuse in twos and threes in the other species. The separate peripheral utricles in *fragilis* are also distinctive. In *bikinensis* the peripheral utricles separate only with pressure, whereas they generally remain attached in *opuntia* and *gracilis*.

From *micronesica*, a second species in which the nodal filaments remain separate, *fragilis* can be distinguished macroscopically by its heavier calcification and by its often complanate branching. In addition, the segments are somewhat thicker, larger, more brittle and commonly reniform in shape rather than discoid or trilobed, and the lowermost segment is usually smaller than the others rather than being generally much larger and flabellate as is typical for *micronesica*.

## *Halimeda melanesica* Valet

Figure 48.

*Halimeda melanesica* Valet (1966), p. 680, Figs 1, 2, Plate 1.

FIG. 48. *H. melanesica. Isotype*, New Caledonia, region of Luengöni, Loyalty Islands, Isle Lifou, 10 I 64, Valet 1853. Discrete holdfast absent although photograph shows rhizoidal filaments with sand associated with lower segments. (Photograph by Jodi Grenga.)

Plants forming flaccid clumps, to about 12 cm tall; holdfast function appears to be served by aggregates of basal segments and adhering particles of sand and shell which fix the thallus firmly to hard (rock) substrate, this holdfast mass to 1 cm and possibly more in width; calcification light; basal segment reniform, to 5 mm long, 9 mm broad, bearing two to four branches

of which the first segments are cylindrical to cuneate and often conspicuously larger than those above although not as large as basal segment; other segments cuneate, with lobed or entire margins, to 4 mm long, 3 mm broad and 0·5 mm thick.

Cortex generally of three series of utricles which are often constricted at their bases; outermost utricles remaining attached after decalcification and appearing polygonal in surface view, (20–)56–72 μm in surface diameter, 62–90 μm long; secondary utricles 47–72 μm in diameter.

Nodal medullary filaments remaining unfused, or at times fusing in pairs for a distance of 1–1·5 times the diameter of the filaments.

*Type specimen.* Loyalty Islands, vicinity of Luengoni, Lifou, Valet, 1853, 1 October, 1964 (PC; an isotype in Hillis-Colinvaux herbarium).

*Habitat.* Growing on coral rock in agitated water at −3 m.

*Geographic distribution.* South-western Pacific.

5. *Section Crypticae* n. sect.

*Halimeda cryptica* L. H. Colinvaux and Graham

Figures 3, 15, 49.

*Halimeda cryptica* L. H. Colinvaux and Graham (1964), p. 5, Plates 3–5.

Plants to about 9 cm tall, loosely to somewhat compactly organized, with a small distinct holdfast which is usually less than 1 cm long; calcification heavy to moderate; colour of lighted and umbral surfaces of plant distinctly different, the lighted surface on drying usually green but sometimes greenish-cream to off-white, the umbral surface white to cream, both surfaces generally dull though sometimes glossy in younger segments; branching usually di- or trichotomous; segments generally plane but occasionally slightly ribbed, brittle, the bases of all but the basal segment attenuated into a short narrow beak or stalk; basal segment usually turbinate, the others most commonly very broadly to depressed ovate or transversely broadly to transversely elliptic, sometimes with upper margins shallowly trilobed and lower margins auriculate to truncate, occasionally and particularly in the lower third of the plant the segments broadly to transversely rhombic or angular-obovate; segments often largest in the middle third of the plant measuring when dried to 11 mm long, 15 mm broad and about 0·33–0·66 mm thick.

Cortex of two to three, less commonly to four series of utricles, with the inner utricles often not particularly expanded at the apices or constricted at their bases; outermost utricles very broadly obovate to depressed obovate, remaining attached after decalcification or separating slightly, although still

FIG. 49. *H. cryptica*. (Top) A vertical, heavily-shaded rock wall at about −43 m with attached pendant clumps of *H. cryptica*. (Photograph by T. F. Goreau, Jamaica, Maria Buena Bay, Duncans; from Colinvaux and Graham (1964).) (Bottom) Habit to two plants, each with a basal segment. The plant on the left also has a typical small holdfast. Scale bar is 2 cm. (Left-hand plant = isotype, NY; from Colinvaux and Graham, 1964.)

generally retaining their hexagonal appearance in surface view, (36–)56–76(–103) μm in surface diameter, (42–)54–69(–83) μm long in section including the sometimes prolonged pedicels, usually four supported by each secondary utricle; secondary utricles (20–)27–40(–65) μm broad.

Plants uniaxial, the single medullary filament generally broadest in the node region where the wall is often yellowish and (11–)18–45(–58) μm in maximum thickness.

*Type specimen.* Jamaica, Parish of St Ann, Runaway Bay off Cardiff Hall beach, from a depth of 34–41 m, T. F. Goreau and E. A. Graham, 26 August, 1962 (IJ; isotypes in BM, NY, UC, UCWI, UM).

*Habitat.* Hanging from rock surfaces or flattened against them, on the fore-reef, fore-reef slope and deep fore-reef, this species develops its largest populations in the deep fore-reef (Goreau and Goreau, 1973; Moore *et al.*, 1976). Down to −100 m it is associated with *copiosa*, but *cryptica* is much the commoner. Its vertical range is −25 m to −100 m.

*Geographic distribution.* Western Atlantic Ocean.

The external aspect of these plants suggests the Indo-Pacific species *fragilis*. Yet *cryptica* is readily separated from this and all other described species of *Halimeda*, with the possible exception of some specimens of *copiosa*, by the consistently different colour of its lighted and umbral surfaces, the light-exposed surfaces usually being green, the umbral ones white or off-white. Less striking but equally characteristic of *cryptica* is the especial delicacy of the nodes, an expression of this species' uniaxial construction (Figs 3, 15). All other described Halimedae are multiaxial (Hillis, 1959). Smallish utricles from the upper, and to a lesser extent from the lower, of two adjoining segments form a collar (Fig. 3) which almost covers the medullary filament at the node, and produces the beaked or stalked macroscopic appearance of the upper of the segments.

The lighted and umbral surfaces of mature segments can be readily distinguished microscopically also. The peripheral cortical utricles of the umbral surface generally seem delicate. They collapse easily, and seem to become detached readily from the secondary utricles. To observe them satisfactorily the mature segments must usually be very slowly decalcified. Preparations to show the surface of the peripheral utricles of the umbral surface are more easily made from immature segments. In contrast, the peripheral utricles of the lighted surface and of the edge of the segment continuing slightly into the umbral surface

are well developed, and retain their shape on decalcification as do those of other *Halimeda* species. The plastids in the material studied were generally conspicuously denser in the utricles of the lighted surface.

### H. *Species of uncertain systematic position*

Authentic specimens have not been located for four described species which can therefore not be placed in the system.

#### *Halimeda irregularis* Lamouroux

*Halimeda irregularis* Lamouroux (1816), p. 307, Fig. 7.

*Type locality.* Antilles, West Indies.

#### *Halimeda nervata* Zanardini

*Halimeda nervata* Zanardini (1858), p. 289, Plate 12, Fig. 2.

*Type specimen.* Collected by Portier in the Red Sea.

#### *Halimeda papyracea* Zanardini

*Halimeda papyracea* Zanardini (1851), p. 37; Zanardini (1858), p. 288, Plate 13, Fig. 2.

*Type specimen.* Collected by Portier in the Red Sea.

#### *Halimeda rectangularis* J. Agardh

*Halimeda rectangularis* J. Agardh (1894), p. 100.

*Type locality.* Australia.

## V. Culture

Serious attempts to culture Halimedae and their relatives apparently date from the 1960s. Techet (1908) showed that *tuna* could be kept in aquaria supplied with seawater at a marine station. In addition, very many coral reef organisms, including Halimedae, were kept for short times in aquaria at the Discovery Bay Laboratory in Jamaica by Dr T. F. Goreau in the early 1960s. This suggested that Halimedae could be grown in aquaria, if necessary, far from the sea. This has been done (Colinvaux *et al.*, 1965), and Halimedae have been maintained at inland laboratories for over two years, in both natural and artificial seawater,

with the production of more than one vegetative generation. Only the completion of the sexual cycle, with the development of the characteristic segmented thallus from the loose filaments obtained by the germination of zygotes (Meinesz, 1972b), still remains to be carried out in culture.

The basic approach, which can be modified in many ways to suit facilities and the particular problem being investigated, is given in the following subsections. Considerably more elaborate arrangements are possible and may at times be feasible, but much can be done simply. Halimedae and their calcareous relatives such as *Penicillus*, *Udotea*, *Rhipocephalus*, *Acetabularia* and *Batophora* all seem relatively hardy. They can be transported for several days in dim light and at temperatures of 20 °C or less, and still grow satisfactorily in the laboratory.

It is not yet possible to begin *Halimeda* cultures with clean zygotes, not only because fertile plants of most species are hard to find, but also because it is not yet known how to germinate and grow the mature thallus from zygotes. It is only with *tuna* from the Mediterranean that development beyond the zygote has been obtained (Meinesz, 1972b), and this has not been the adult plant as we know it (Section VII). It is necessary, therefore, to begin cultures with direct transplants from the sea, a procedure that unavoidably introduces troublesome contaminants into the cultures. The basic procedure is to collect good field material, to clean it by hand, to plant it in simple aquaria, to bubble air into the water, to provide light and to combat epiphytes.

### A. *Field procedure*

It is obviously important to select healthy vigorous specimens; the difficulty is to identify the signs of vigour and health. It seems natural to avoid thalli with segments which tend to fall off when touched, with white segments, or with large numbers of epiphytes. The thalli selected should be collected with minimal damage to the holdfast, and rock-growing species should have a portion of the rock to which the holdfast is attached included if possible.

After collecting, the thalli are carefully cleaned of as much associated plant or animal material as is possible without breaking the segment surface or pulling away the holdfast filaments. Then, until the algae can be transported to home base, they are maintained in three to four times their volume of clear seawater at about 24–25 °C with a bubbler, and exposed to diffuse light. For travel, the water is replaced with fresh clean seawater, the amount being decreased to that manageable for the journey, and the containers closed. If accessible, compressed air is

bubbled in at this stage. Large heavy-gauge plastic bags are useful for separating different collections, those with and without attached pieces of rock, for example. The bags can then be tied off and arranged carefully in styrofoam chests to minimize damage. Buckets with fitted lids and collapsible carboys are also suitable containers, and can be carried in the pressurized cabins of aircraft. About 50 sand-dwelling Halimedae can be transported in a 4·5 l carboy half-full of seawater. They survive up to 3 days of travel in this way.

The algae are replanted as soon as possible after arrival. If time and facilities permit, it is a good plan to check for smaller epiphytes with a dissecting microscope and remove them.

## B. *Basic laboratory procedure*

The Halimedae are grown in closed aquaria without recirculating water, lighted for part of the day, provided with about 2·5 cm of calcareous gravel, and equipped with an air bubbler (Fig. 50). Sand-dwelling forms with bulbous holdfasts are simply planted in aquaria containing about 2·5 cm of sand over the calcareous gravel. Rock-attached forms are anchored to the bottom or suspended from an arrangement of rocks or pieces of clean dead coral in a manner that resembles their normal growth habit. Species with a sprawling growth pattern such as *opuntia* are merely placed in an aquarium without sand but which usually contains chunks of rock or coral (Fig. 51). The aquaria are covered with glass or a thin sheet of transparent plastic. The thalli are regularly cleaned by hand of epiphytes and animals as far as is possible without damaging them.

### 1. *Culture medium*

Natural seawater and the commercial artificial seawater "Instant Ocean" have been the main media used.

Natural seawater is collected from areas free of wastes and filtered through a Millipore filter with average pore size 0·45 μm.

Commercial artificial seawaters were not available when I first started culturing. They are now readily obtainable, however, and have proved as satisfactory for this work as natural seawater. The composition of "Instant Ocean" is given in Table XI. Some minor elements are missing from it, but results seem comparable to those with natural seawater.

No nutrients are added directly to either medium in routine culturing. Some nutrients are probably introduced by the sand substrates,

FIG. 50. *Halimeda* cultures in glass aquaria, showing arrangement of lights and aeration system. Compressed air is filtered through glass wool (in tube at far upper right) and enters a manifold (suspended from top shelf). From there is passes through Teflon tubing to a bubbler in each aquarium. The rate of flow to each aquarium is controlled by a tubing clamp. Arrangements similar to this can line the walls of a controlled environment chamber. A *Udotea* plant is in the left-hand corner of the middle aquarium in the upper row. (From Colinvaux *et al.*, 1964.)

FIG. 51. An aquarium planted with a *Halimeda* of sprawling growth form, the species *opuntia*. Five separate clumps can be seen. When introduced into the aquarium the clumps were tidy rounded cushions. All the straggling branches, which roughly double the height of the left-hand clump, were produced in about 38 days. The long air bubbler was removed from the aquarium before photographing. The labels are 2·25 cm square.

TABLE XI. CHEMICAL ANALYSIS OF THE COMMERCIAL ARTIFICIAL SEAWATER "INSTANT OCEAN"[a]

| *Component* | *Percentage by weight* |
|---|---|
| $NaCl$ | 65·226 |
| $MgSO_4.7H_2O$ | 16·307 |
| $MgCl_2.6H_2O$ | 12·762 |
| $CaCl_2$ | 3 261 |
| $KCl$ | 1·737 |
| $NaHCO_3$ | 0·4963 |
| $KBr$ | 0·07206 |
| $H_3BO_3$ | 0·06214 |
| $SrCl_2.6H_2O$ | 0·04689 |
| $MnSO_4.H_2O$ | 0·009379 |
| $Na_2HPO_4.7H_2O$ | 0·009379 |
| $LiCl$ | 0·002343 |
| $Na_2MoO_4.2H_2O$ | 0·002343 |
| $Na_2S_2O_3.5H_2O$ | 0·002343 |
| $Ca(C_6H_{11}O_7)_2.H_2O$ | 0·001669 |
| $Al_2(SO_4)_3.18H_2O$ | 0·001202 |
| $RbCl$ | 0·0004005 |
| $ZnSO_4.7H_2O$ | 0·0002563 |
| $KI$ | 0·0002403 |
| EDTA NaFe | 0·0001936 |
| $CoSO_4.7H_2O$ | 0·0001335 |
| $CuSO_4.5H_2O$ | 0 00002670 |

[a] Data from Aquarium Systems, Inc., Wickliffe, Ohio.

while the bulbous holdfast system of sand-growers may supply their own.

When the aquaria are filled with seawater to the desired level and the plants added, the level of the medium is marked on each aquarium wall. Water evaporated from the system is replaced every few days by topping up to the level marked with distilled or glass-distilled water. This maintains a constant volume and accordingly a constant salinity. If the aquaria are maintained for six months or longer, the salinity is monitored. The seawater is siphoned out and replaced every six to nine months.

### 2. *Substrates*

(a) *Unconsolidated.* About 2·5 cm of a calcareous material and another 2·5 cm of a readily available sand are used, with, for convenience, the larger-grained material providing the bottom layer.

Suitable calcareous materials are quartz gravel, calcareous filtrant material as used in many aquarium systems, *Halimeda* sand and pieces of cuttle bone. The first two can be obtained from aquarium suppliers, and the second one, the calcareous filtrant, is also available from the suppliers of "Instant Ocean". *Halimeda* sand is collected in the reef. Cuttle bone, which is only practicable on a small scale, can usually be obtained from pet shops.

It is not known if a calcareous substrate is necessary for *Halimeda* growth, but their possession of a calcareous structure suggests that it may be important. The natural populations commonly grow in sand which is largely composed of old *Halimeda* segments and which is usually highly calcareous.

Calcareous substrates are washed several times in distilled water before use.

Sand materials which have been used include reef sand, beach sand and playbox sand. The stand is autoclaved at 15 lb pressure for 20 minutes before using.

(b) *Rock substrates.* Dead and cleaned coral rock or other soft rock is used partly for substrate, partly for the support and anchorage of rock-growing Halimedae collected with holdfast intact on their own small piece of rock. The rock-growing Halimedae are arranged and supported in a rock framework in such a way that they simulate their natural position in the reef.

Before being used the rock is washed, and autoclaved for 20 minutes at 15 lb pressure.

3. *Aquaria*

The most used sizes have been 9·5, 11·5 and 19 l aquaria which preferably are all-glass. These small sizes are manoeuvrable, and growth can be readily seen and photographed from all sides. Height is a critical dimension in selecting aquaria. One that is too shallow will seriously restrict the size of the thalli selected. A 30 cm height or slightly more would seem close to the ideal unless one is working only with small squat species. This height permits a reasonably thick sand–gravel layer as well as air space at the top which decreases the amount of water bubbling over from changes of pressure in compressed air lines of the circulation system.

Between uses, aquaria are scrubbed with 10% hydrochloric acid, then filled with tap water and allowed to stand for at least 24 hours. This operation is repeated at least twice more. If possible aquaria are not reused immediately.

4. *Circulation system*

In the small 11·5 l aquaria used most frequently, circulation is provided by aquarium air-bubblers, sometimes with the addition of an outside or inside water-filtering system.

Long air bubblers (approximately 14 cm) are connected to a compressed air system by Teflon tubing. An air-filter system of glass-wool is interposed, and a manifold is used so that several aquaria may feed off the system. Rate of flow to individual aquaria is regulated by C-clamps on the Teflon leads to each aquarium. The particular bubblers used function well after autoclaving.

A closed-circuit water-filtering system is sometimes used by adding the standard inside or outside aquarium filter, fitted only with glass-wool, which fits against the vertical walls of the aquaria. Bottom or under-gravel filters might be feasible for Halimedae which grow on rocks or sprawl but are not suitable for sand-growing species. The Rhipsalian Halimedae do not normally have water circulating past their holdfast systems, which, in some reef sites, even grow in an anoxic environment. The reducing environment may facilitate the exchange of certain ions between substrate and holdfast, with such reactions being important to the successful growth of these particular species.

5. *Temperature control*

Kinsman (1964) gives a range of 25–29 °C as the temperature at which reef corals best flourish, while indicating that these organisms can withstand limited exposure to 16–17 °C, and that some corals continue to grow at temperatures as high as 36 °C.

For *Halimeda*, temperatures of 27–29 °C are probably about optimal, although these plants are exposed to higher and lower temperatures in the reef. A range of approximately 25–29 °C is acceptable.

Lighting will increase the water temperature of the small aquaria by 2 °C and more, depending on the intensity and duration.

6. *Light intensity and cycle*

Light intensities for much of the *Halimeda* culturing have ranged from 375 to 780 foot-candles, measured just above the sand–water interface. Intensities as low as 100 ft-c have been used, but growth is very slow or absent.

Lighting on a 12-hour light : 12-hour dark cycle is provided by cool-white fluorescent light placed about 22 cm above the aquaria. The lighting cycle was chosen because it is that of the tropics.

The lower intensities of this range were initially chosen because they were similar to those commonly used in algal culture including work with siphonaceous algae. Puiseux-Dao (1970) gives a range of approximately 100–300 ft-c for *Acetabularia*, and Chen and Jacobs (1966) used 100 ft-c in their culture of *Caulerpa*.

Better growth is obtained, at least initially, at intensities such as 700 ft-c. This improvement is often paralleled by increased epiphyte growth, and the epiphytes can become very difficult to control. The water of small self-contained aquaria also becomes overheated at the higher intensities, necessitating a cooling system.

Light intensities of approximately 375–500 ft-c are somewhat of a compromise in the range given. Growth as well as vegetative and sexual reproduction occur at these intensities. It is realized, however, that they are considerably below the light intensities of the shallow reef, some of which are recorded in Table XII, using a Gossen Tri-Lux foot-candle meter in an underwater case at two of our north shore Jamaican work sites, Runaway Bay and Glory Be (Section X). They indicate that plants growing at −1·5 m to −2 m receive approximately 47–73% of the surface light which, on three sunny Jamaican days, about midday, averaged 7530 ft-c.

It is realized too that the unusual segment shapes often obtained in culture (Fig. 16; Colinvaux *et al.*, 1965, Fig. 3) may be the result of growing these plants in intensities equivalent to those of the blue-lighted regions in the reef at about −40 m to −50 m.

### 7. *Epiphyte control*

A wide range of organisms, plant and animal, are introduced on the cleaned Halimedae thalli. A number of them grow very well in the system, and if uncontrolled will usually overgrow the *Halimeda* population eventually. Some of the introduced organisms also grow on the sand and rock substrates, as well as on the glass sides of the aquaria. Epiphyte control is important for aquaria which will be maintained longer than about six weeks, and for shorter-term aquaria when light intensities are 1000 ft-c or higher.

The contaminant plants include a number of soft red and green, as well as blue-green, algae. There have also been occasional dense dinoflagellate blooms.

Phytoplankton blooms, if troublesome, can be controlled by changing the water and using a filter system. Since some inoculum remains on the Halimedae and on the sand or rock substrate, the improvement may only be temporary.

TABLE XII. LIGHT INTENSITIES AT GLORY BE REEF, NORTH SHORE OF JAMAICA[a,b]

| *Date* | *Time* | *Depth (m)* | *Light intensity (ft-c) (meter in case)* | *Ratio water to air (%)* | *Location* |
|---|---|---|---|---|---|
| 16.6.69 | 0728 | +2 | 440 | 73 | Shaded beach steps |
| | 0735 | −1·5 | 320 | | Shaded quadrat site ($Q_1$) |
| | 0812 | —1·5 | 200–300 | | Shaded quadrat site ($Q_1$) |
| | 0735 | —1·5 | 1000 | | Patch of light north of $Q_1$ |
| | 0820 | −1·5 | 700 | | Patch of light north of $Q_1$ |
| | 9745 | −3·7 | 600–1000 | | Range on sand patches outside zooanthid reef |
| | 0825 | −3·7 | 1500 | | Dune sand pass in zooanthid reef |
| | 0747 | −3·1 | 1000–1200 | | Urchin barren |
| | 0810 | −1·5 | <200 | | Red algal patch under rock |
| | 0830 | −1·8 | 2000 | 67 | *Halimeda* sand without plants |
| | 0836 | 0 | 3000 | | *Halimeda* sand without plants |
| 16.9.68 | 1115 | +2·5 | 6400–7200 | 47–69 (−78) | Sun in and out of clouds |
| | 1230 | −2 | 3000–5000 | | $Q_1$, sun in and out of clouds |
| | 1250 | +2·5 | 6400 | | |
| August | | 0 | 1500 | 53 | Odum and Odum (1954), with Weston light meter, Enewetak Atoll |
| | | −0·5 | 800 | | Odum and Odum (1954), with Weston light meter, Enewetak Atoll |

[a] For description of sites see Section X.
[b] Intensities were measured with a Gossen Tri-Lux foot-candle meter in an underwater case.

The most successful method for controlling the other epiphytes, once established, has been by hand cleaning, an operation which is tedious and time-consuming. The soft red and green algae can usually be plucked off their hosts fairly easily, but many of the blue-greens, with their slimy coatings and mats, must be scraped off, using tools such as a fingernail for the thalli, or a long-handled aquarium cleaner with razor blade for the sides of the aquarium. Tissues also are helpful for cleaning aquarium sides and retaining some of the material. Mats and slime coatings on the sand can be lifted off.

External or internal water filters, which may be initially useful for avoiding phytoplankton blooms or eliminating or minimizing successful

development of new organisms from released zoospores or gametes, are of minimum help in controlling attached organisms, a number of which reproduce by non-motile means.

Other methods tried include the use of the invertebrate poison Lindane, and the antibiotic Penicillin. Lindane had previously been found helpful in *Ulva* culture (Strand *et al.*, 1966). Halimedae were immersed for 15 minutes in seawater containing Lindane at a concentration of 15 parts per million. The results for the limited number of thalli available for experimental treatment were inconclusive.

For the testing of Penicillin the antibiotic was added to two aquaria at a concentration of 1000 units $ml^{-1}$ for one and 3000 units $ml^{-1}$ for the other. The higher concentration killed the vegetative stage of many epiphytes and they dropped off within the first two weeks. By the end of about two months, however, epiphytes, particularly blue-greens, were again abundant (Hillis–Colinvaux, 1972). When the treatment was repeated, it was not as effective. Penicillin may be helpful in short-term epiphyte control, particularly if added to the medium initially.

### 8. *New approaches to epiphyte control*

Two additional techniques could be helpful. Sand-growing species might initially be planted in trays which could then be transferred out of one aquarium to a cleaner one, or used for experimental purposes. The trays could also be suspended over bottom filters since the circulation pattern would not then interfere with any reducing environment established by the holdfasts in the trays.

Epiphyte-free stock also can provide cleaner cultures. One source of such plants is the young Halimedae developing in the aquaria by vegetative multiplication. They can be successfully transplanted into fresh aquaria. Another potential source of clean thalli are individuals produced by regeneration. The basic procedure is to remove branches of several segments from robust thalli by cutting at the node (where there are fewer filaments), briefly pressing the cut ends together to induce wall formation (Jacobs, 1958), thereby preventing excessive loss of cytoplasmic materials, and then anchoring or planting the cuttings in substrate. I have had limited success with such cuttings which have ranged from two to a dozen segments. The longer cuttings were the most successful, and although none grew into a large thallus (all tended to get overgrown with epiphytes), a few produced new plants from rhizoidal runners in the sand (Section VII), and others produced rhizoids and segments.

9. *Controlled environment room*

A walk-in controlled environment room, if available, permits a finer control of both the temperature and lighting cycles, and some investigation of environmental effects which are not possible if aquaria are maintained in a multi-use room. Such a room, however, may restrict sizes of aquaria and intensity of lighting.

### C. *Some experiences with* Halimeda *culture*

Table XIII lists the species of *Halimeda* cultured, together with other plants that have been introduced intentionally or inadvertently.

TABLE XIII. PARTIAL LIST OF ORGANISMS MAINTAINED IN AQUARIA FOR TWO MONTHS TO OVER ONE YEAR

| | | |
|---|---|---|
| 1. HALIMEDA SPECIES | | |
| *incrassata* | *tuna* | *opuntia* |
| *cylindracea* | *discoidea* | *copiosa* |
| *macroloba* | *gigas* | *goreauii* |
| *monile* | | |
| *simulans* | | |
| 2. OTHER CAULERPALES | | |
| *Boodleopsis* | *Rhipocephalus* | |
| *Caulerpa* | *Udotea* | |
| *Penicillus* | *Tydemania* | |
| 3. DASYCLADALES | | |
| *Cladophoropsis* | *Cymopolia* | |

4. PARTIAL LIST OF EPIPHYTES

| CYANOPHYTA | CHLOROPHYTA | | DIATOMS |
|---|---|---|---|
| | Dasycladales | Cladophorales | |
| *Aphanocapsa* | *Acetabularia* | *Rhizoclonium* | *Navicula* |
| *Calothrix* | *Batophora* | *Cladophora* | |
| *Lyngbya* | *Dictyosphaeria* | | |
| *Oscillatoria* | *Valonia* | | |
| *Spirulina* | | | |

Using the approach described, sand-growing Halimedae have settled in and grown well, with the first obvious growth of the transplants often appearing in about five days (Section VI). On the few occasions that some Rhipsalian Halimedae have been kept in seawater and not planted immediately, rhizoidal growth has been noted on about the third day,

followed by new segments two or so days later. Non-rhipsalian species have not grown as well, at least initially, and *tuna* has been the most difficult to maintain under these conditions.

At the beginning of the culture work, when looking for evidence of success, some growth observations were especially troubling. Examples include the turning white of segments or branches which then fall off, and the overburdening of thalli with epiphytes, the latter being distinct from the problem of maintaining *Halimeda* in culture with a minimum number of epiphytes. Both developments, however, are part of the *Halimeda* growth cycle.

Segments and branches are shed, at least in some species, rather like leaves being dropped from a bush or tree in the autumn, and the growth of *Halimeda* is thereby different from that of *Penicillus capitatus* Lamarck and *Udotea flabellum* (Ellis and Solander) Lamouroux (Colinvaux *et al.*, 1965) in which there are no dehisceable units. The shedding of segments or branches also relieves the *Halimeda* thallus of a crop of epiphytes, and produces sites where vigorous new growth can occur.

In the reef, epiphytes are, at times, very evident on *Halimeda*. Blue-green algae may cover much of the *Halimeda* thallus and contribute a coating or matting to the surrounding sand. Matheison *et al.* (1971), in a transect study at −17·3 m to −21·5 m in the Virgin Islands, reported 17 species of epiphytes, mostly red algae, on *H. incrassata*. These workers did not seriously include blue-green algae in their study, so Cyanophyta may have occurred as well. It may be that massive imposition of epiphytes is a hazard to which *Halimeda* populations are adapted, and that their reproductive and persistence strategies will be influenced by this recurrent event. It is also possible that patterns of grazing on the *Halimeda* beds may be reflected in blooms of epiphytes. That the phenomenon occurs in nature suggests that it is an ecosystem event of some significance. It is also one such event that we can study in our cultures.

A number of animals, introduced inadvertently with the thalli, live successfully in the culture systems described, and some of the grazers, particularly the snails, may clean the plants and aquaria of some growths. Introduced animals include tube worms, anemones and polychaetes, with occasional snails, bivalves and brittle stars. From time to time there also have been blooms of small medusae of about 2 mm diameter. What are presumed to be different species of opisthobranch molluscs, both identified as *Elysia* spp., have fed, one type on *Tydemania*, the other on *Halimeda incrassata*. The *Tydemania* lived only about three months, and too little is known of its growth pattern to have assessed the impact of *Elysia* grazing. However, the other

*Elysia*, a lone specimen, appeared to feed mostly on one individual *Halimeda* although there were others of the same species in the aquarium. This it did for a year, when it was preserved and sent off for identification. During the year it was alive, new segments started to form many times on the host *Halimeda* plant, but they generally did not complete their development.

These observations show that it is possible to maintain simple marine grazing systems in the laboratory.

### D. *Summary of* Halimeda *culturing*

Eleven species of *Halimeda* have been grown in the laboratory, some through one or more vegetative generations, while individuals have been maintained for more than two years.

It is not yet possible to start cultures with clean zygotes since the segmented *Halimeda* has not been grown from them in the laboratory. Cultures, therefore, must be started with direct transplants from the sea, a technique that introduces troublesome contaminants.

The basic procedure is to collect good field material, to clean it by hand, to plant it in simple aquaria, to light it, to bubble air into the water and to combat epiphytes.

Other Caulerpacean and various Dasycladalean genera also grow satisfactorily in this system, as well as a number of inadvertently introduced animals, showing that it is possible to maintain simple marine grazing systems in the laboratory.

Although large numbers of epiphytes in laboratory culture usually lead to the swamping of *Halimeda* thalli, on the reef this may be a hazard to which *Halimeda* populations are adapted, and the reproductive and persistence strategies of Halimedae may be influenced by this recurrent population event.

## VI. Growth and Calcification

Patterns of growth in Halimedae must result in fronds which may be likened to strings of beads because each frond is a linear array of segments fastened at the nodes by a string-like structure of filaments. This string-of-beads structure is constructed from a non-cellular syncitium. The segmental "beads" of each species tend to have characteristic shape, suggesting a rather refined system for controlling the web of growing filaments; and this system operates as nuclei are spread along the filament, without obvious physical separation of individual

nuclear domain. Furthermore, the shape imposed on a filament becomes fixed in a matrix of mineral calcium carbonate. Clearly, there are interesting questions to ask about the patterns of growth in Halimedae that concern control of growth, rates of growth, maintenance of structure and the process of calcification.

One of the reasons *Acetabularia*, a relative of *Halimeda* with a single nucleus instead of many, has yielded so many data about the nucleo-cytoplasmic control of growth is that it could be cultured. *Halimeda* can be easily grown too, if initial care is taken in obtaining clean starting plants. But nucleo-cytoplasmic and chemical aspects of its growth have not yet been approached. Our information on growth is at the thallus, filament and ultrastructural levels.

The classical accounts of growth are basically three. Askenasy (1888) provided the first short description when he noted that after a "rest period" the nodal filaments of an apical segment produced filamentous extensions which branched many times. The branches in turn branched and rebranched to the tips or peripheral utricles, which adhered, forming an outer surface and, as a result a new segment.

Barton's (1901) account of the development of a new segment varied from that of Askenasy only in the branching pattern of the medullary filaments. The initial branching was trichotomous, with the middle branch continuing as part of the medulla while the two side branches divided and redivided until they terminated in the peripheral utricles. A demonstration of this pattern can be seen in *cryptica* (Figs 3, 15) with its single medullary filament.

The first field datum on rate of growth was obtained about this time too, and appears to have been originally published by Barton (1901). This was the observation by Finckh (1904), at Funafuti, that a branch of *Halimeda* growing through a hole in a submerged board of wood on the reefs added three inches of height and thickness in six weeks, or 14·38 g of calcareous matter. Thereafter, until these algae were grown in the laboratory (Colinvaux *et al.*, 1965) little more was known about growth of *Halimeda* or, indeed, of any of the calcareous Caulerpales.

### A. *Macroscopic growth*

Much of the following account uses hitherto unpublished data and some reported by Colinvaux *et al.* (1965). It is based mostly on the species *incrassata, simulans* and *monile* from the Caribbean, and although many of the developments described have been observed in the field, all of the quantitative data, particularly those on rates, are of

growth in laboratory culture at approximately 27 °C, with light intensities mostly of 310–560 ft-c for 12 hours, followed by 12 hours of darkness. The only field study of some duration is that of Merten (1971), working in Guam. She reported growth rates in *macroloba* over a period of 10 months, and included some laboratory study of it as well. Like *incrassata*, *macroloba* is a Rhipsalian *Halimeda*, but the appearance and size of its segments are very different (Figs 22 and 28, respectively). The maximum length × width × thickness measurements for an *incrassata* segment are 10 × 14 × 0·75–1·0 mm. For *macroloba* they are 29 × 40 × 1 mm. The two species also have different habitats within the reef, with *macroloba* seemingly restricted to water of −12 m or shallower and growing best in waters of −2 m or less.

In *incrassata* transplanted to the laboratory, the first obvious growth is usually in the holdfast, as delicate new filaments extend out into the surrounding medium. It can be readily observed in unplanted thalli lying horizontally in seawater. In thalli so arranged most of the first new rhizoidal growth is oriented downwards.

Within the next few days there are also obvious signs of the development of new segments, as white, conical protrusions appear from the apical edges of terminal segments (Figs 16, 52, 53). These are the extensions of the medullary filaments which branch and ramify as they grow. The branches develop into the cortical series of utricles of which the outermost ones are contiguous. Within about 24 hours, the albino protrusions from an apical segment develop a fairly complete, somewhat greenish segment. The outer surface, however, is spongy and disconnected, for the peripheral utricles have not yet formed a continuous outer surface. This separateness of the peripheral utricles is unlike the pattern encountered in mature segments of most species (Sections III, IV). The very young filaments of a segment, therefore, may have a different environment before and after being enclosed within the segment since at the earliest stages of growth they are in direct contact with seawater. The resulting closed or almost enclosed spaces may be important in calcification (Colinvaux *et al.*, 1965; Wilbur *et al.*, 1969; Böhm and Goreau, 1973; Borowitzka and Larkum, 1976a, b, c, 1977; Borowitzka, 1977). Within the next 12–24 hours or somewhat longer, adhesion of peripheral utricles occurs in most species at least, and it is at about this stage that the first granules of calcium carbonate appear.

The pattern of a segment, its length and width are essentially set within the first couple of days. Subsequent development is mostly in the calcification of the segment, with some change in thickness, depending on the location of the segment within the thallus and the species.

| Days | 0 | 13 | 21 | 56 | 72 |
|---|---|---|---|---|---|
| No. segs added | | +35 | | | +96 |
| Growth (mm.) | | +114 | | | +265 |
| Growth $wk^{-1}$ (mm.) | | +61.4 | | | +25.8 |

FIG. 52. *H. incrassata*, record of growth in culture for 72 days. (1) Plant with several branch stubs where old, dead segments have fallen off. New segments have developed in the regions indicated. (2) Thirteen days later. Plant is turned 180°. Many new segments and branches have developed in the same regions indicated in No. 1. The small whitish segments at the tips of the branches (left-hand side of picture) are about 24 hours old. The large, very white segment at the right-hand edge is heavily calcified and dead. (3) Eight days later. Both types of development indicated for No. 2 have continued. More new segments have been added to the new branches started in No. 1, and more segments on the right-hand branch have died. (4) Thirty-five days later. Plant has been turned 180°. The white, dead segments have fallen off. (5) Sixteen days later. A few new segments have formed since No. 4, while others appear dead and very white. Ninety-six segments or 265 mm have been added in the 72 days. The diameter of the unnumbered white discs is 0·85 cm.

| Days | 0 | 12 | 15 | 18 | 21 | 29 | 61 |
|---|---|---|---|---|---|---|---|
| No. segs added | | | | +16 | | +31 | +43 |
| Growth (mm.) | | | | +48.3 | | +87.3 | +116.5 |
| Growth $wk^{-1}$ (mm.) | | | | +18.8 | | +21.1 | +13.4 |

FIG. 53. *H. incrassata*, record of growth in culture for 61 days. (1) A plant which has already produced and shed branches. The third branch from the left has two very young segments. Other branches show whitish dead segments. (2) Twelve days later. The two-segmented branch in No. 1 is now composed of six segments. Two of the dead white segments have been shed. (3) Three days later. The developing branches of branch 1 show more clearly. (4) Three days later. Two other branches, to left and right, have started to grow. The left-hand one has two segments, the right-hand one six. The remainder of the white dead segments of No. 1 have dropped off. (5–6) Further development of branches 1, 2 and 3. Number 5 is three days later; No. 6 is eight days later. (7) Thirty-two days later. Two more branches have developed. Since the first photograph 43 segments or 116·5 mm have been added. Twenty-two days after No. 7, a new *Halimeda* was produced from rhizoidal development in the sand (Section VII). The diameter of the unnumbered white discs is 0·85 cm.

In very old segments the peripheral utricles may separate more readily or may be somewhat thickened.

New segments may develop daily or every other day on each branch so that many new segments can be added in a relatively short time. This growth pattern has been observed also with *cylindracea*, *opuntia* and *gigas*, growing in running seawater aquaria maintained for three weeks in the roofed open-air wet laboratory of the Mid-Pacific Marine Laboratory at Enewetak.

The growth which occurred on two thalli of *incrassata* over a time span of 72 and 61 days is shown in Figs 52 and 53, respectively. Thirteen days after the photographic series was started for the plant of Fig. 52 it had added 35 segments or 114 mm. Seventy-two days after the beginning of the series it has added 96 segments or 265 mm. These figures represent a rate of growth of 6·1 cm $wk^{-1}$ for the first two weeks, and 2·6 cm $wk^{-1}$ at the end of the tenth week. For the plant of Fig. 53, 16 segments or 48·3 mm were added in 18 days yielding a growth rate of 1·9 cm $wk^{-1}$, after 29 days 31 segments or 87·3 mm had been added representing a rate of 2·1 cm $wk^{-1}$, and by 61 days 43 segments or 116·5 mm had been added making the growth rate 1·3 cm $wk^{-1}$. Twenty-two days later a new plant as well as new segments had been produced, and some segments had been shed. These rates and other similar ones from my cultures indicate some of the growth potential of *incrassata* at low light intensities, as does the growth analysis by Chen and Jacobs (1966) on *Caulerpa prolifera* (Forsskål) Lamouroux. They cultured *Caulerpa* on supplemented seawater at $24 \pm 1$ °C at 100 ft-c on a 12-hour light : 12-hour dark cycle, and found that rhizomes, rhizoid clusters and "leaves" elongated at the rate of approximately 4·4 mm $d^{-1}$ or 3·1 cm $wk^{-1}$. It seems likely that the incrassatae of the reef, when actively growing, may have a growth rate which is at least comparable to the best of those reported, that is, to 6 cm $wk^{-1}$.

Merten (1971), in Guam, worked with 200 plants of *macroloba* in both field and laboratory environments. The average growth rates for her four populations followed the same pattern, and all four were of the same general order of magnitude. For the 200 plants she gives an average growth rate of 5·8 cm for the first month, and 1·5–3·0 cm for the other months, with the laboratory populations performing as well or slightly better than the three field populations in overall height, although the plants were less branched and the segments irregular. The higher rate obtained is of the same order of magnitude as the opportunistic growth measure of Finckh (1904) on an unknown species of *Halimeda*.

Marten's rates are lower than those given for the *incrassata* plants although three-quarters of her measurements were of reef plants, under

supposedly good to optimal conditions of growth. The comparison may not be meaningful, however. These are two widely distinct species of *Halimeda* and different growth rates can be expected. In addition, a linear measure is perhaps not the best for either comparing or measuring their growth, although for these two species it is considerably more meaningful than the number of segments produced.

This growth activity of relatively rapid segment formation has, in the laboratory, generally been followed by a quiescent period of a week or two to a month or more, in which no new segments form. Goreau (1963), observing a number of representative species of calcareous algae over a period of 15 months, also noted this pattern of growth in spurts in cultured Halimedae. A quiescent phase may be a laboratory phenomenon, although many of the thalli I have observed in the reef have not given the impression of active growth at that particular time. It also may be a species-related phenomenon. Merten (1971) calculated the life-span for the shallow-water *macroloba* populations she worked with to be four months. The pattern for them appeared to be one of growth, sexual reproduction and death.

Growth of many of the species has another component as well, that of "negative growth". Some of the mature segments turn white or yellowish, and eventually fall off, to be added to the calcareous sediments (Figs 52, 53). In culture their death and final dehiscence may take a month or so, depending upon the presence and extent of grazing activity, intensity of water flow around the thallus and weight of epiphytes. The first losses of segments are generally restricted to the apical portion of the thallus, and vigorous new branches generally develop to replace fallen ones (Figs 52, 53). Occasionally there has been a massive whitening in a laboratory aquarium, with the segments of the upper third or half of the thalli of an aquarium population falling off a week or so after transplanting. New branches routinely develop at these sites.

In some taxa this decay of segments or "negative growth" may occur just as commonly, or even more so, in basal portions. The species *opuntia*, and probably others with sprawling or prostrate habit such as *macrophysa*, *micronesica*, *distorta*, *gracilis* and possibly *copiosa*, at times show signs of decay in the lower regions of their thalli. The younger and more vigorous segments and branches above them have initiated rhizoidal development and attachment and continue as separate plants when the older segments fall away. This pattern of growth thereby also functions as a method of vegetative reproduction. In some species or environments, thalli being buried in shifting sand behave similarly. The buried basal portions whiten and loosen, while a new holdfast system is

established above them; then new segments are produced by the apical branches of unburied portions (Section VII).

Some species, or the thalli of some sites, may not lose segments as part of their growth pattern. Merten (1971) does not mention segment loss in the Guam *macroloba* populations, but one would expect few losses if the life-span is four months. And Feldmann (1968), writing briefly of the Mediterranean *tuna*, speaks of ageing the thallus by the length of the branches. "Les individus bien développés, qui présentent souvent 8 à 10 articles successifs, doivent donc être agés d'une dizaine d'années." This does not imply much loss of segments, if the growth rate is as implied.

Certainly dead whitish segments would be more apparent in the laboratory because they remain on the thallus rather than being removed by currents. It is possible, too, that they may be commoner in laboratory culture.

In a few *incrassata* I followed this pattern of gain and loss of segments several times for up to 2½ years. During that time branches and segments closer and closer to the base of the thallus were shed, until all but a few basal segments had been lost. A stump, or markedly reduced thallus, remained which was composed of whitish or yellowish, very heavily calcified, segments. Holdfast filaments stopped growing, and the thallus stump was loose in the substrate. Eventually the remaining segments fell off, or the remnants of the alga toppled over, and that individual had died.

This pattern of growth is characterized by what could be called a "perennating thallus", from which new segments and branches arise. This perennating thallus not only consists of a well-anchored holdfast, but also a few to several basal segments, together with a few vigorous segments possibly of a younger generation (Figs 52, 53, first photographs). Very reduced, old, basal portions do not appear to be able to develop new growth.

### 1. *Growth axis*

Depending upon the species, the addition of new segments may result mostly in either a horizontal or a vertical extension of the thallus. In Rhipsalian species the main growth axis is vertical, and a thallus that is generally erect results. In *gracilis* the predominant axis is commonly horizontal and a spreading or creeping habit is produced. In *opuntia* and *distorta* both types of growth are common, and the resulting habit is frequently a spreading cushion of many centimetres thickness.

The size of the resulting thalli is partly determined by this direction of growth, with mature erect thalli such as *incrassata* generally being

shorter than mature pendant thalli such as *copiosa*, some plants of which are 1 m long (Goreau and Goreau, 1973). The confines of a spreading thallus such as *opuntia* are often exceedingly large. Hence, precise boundaries for this species may be difficult to determine, making field counts meaningless.

*Halimeda*, in its ability to continue adding to its thallus over a relatively long period of time, resembles *Udotea* which periodically resumes growth, adding onto the margins of its fan-shaped thallus (Colinvaux *et al.*, 1965) and *Tydemania*, which adds new glomeruli (unpublished data). Both genera differ from *Penicillus* (Colinvaux *et al.*, 1965) and *Rhipocephalus* (unpublished data) for which extensive new growth from the mature photosynthetic portion of the thallus is unusual. Although the filaments of the brush may elongate, another capitulum is not formed and the original thallus dies within a few months.

## 2. *Perennating structures and the systems of Raunkiaer and Feldmann*

Feldmann (1968) has modified for algae the Raunkiaer (1934) system of classifying life-forms of terrestrial plants on the basis of the position of the perennating bud, but did not develop the system to define communities by life-form spectra as Raunkiaer did. This system may have little interest to contemporary community analysts (Whittaker, 1975), and this doubtful utility becomes apparent when we attempt to apply Feldmann's version to *Halimeda*. We find that a single species can behave as two or more of the categories.

A *Halimeda* with a perennating thallus as described earlier would fit the *hemiphanerophyte* category in Feldmann's (1968) description of life-forms, that is, only a part of the erect frond persisting. Some Atlantic populations of *tuna* appear to fall into this category. The Mediterranean *tuna* Feldmann considered a *phanerophyte*, that is, an alga in which the entire thallus functions as the perennating structure, and very young *Halimeda* thalli of many species after their initial bout of growth would also fit this category.

It is possible too, although there is no evidence as yet, that some species, including *tuna*, may have rhizoidal structures functioning as perennating structures. As such they would be classified as *hemicryptophytes*. Feldmann placed the Mediterranean *Caulerpa prolifera* and *Udotea petiolata* (= *U. minima*) in this last category because they live through the winter without their leaf-like parts. Other populations or individuals of *tuna* may be annuals, thereby fitting another category.

What any system of classifying life-forms is bound to do is to recognize common adaptations to common environmental constraints. But these systems can easily mislead. Raunkiaer (1934), for instance, remarks on an absence of phanerophytes (essentially trees) from the tundra. This absence of trees in the Arctic may be accounted for by arguments based on heat balance, desiccation or maintenance of biomass, yet Raunkiaer's classification must have convinced many students that the critical difficulty is exposing buds to cold air, a proposition for which there is no evidence. In the same way there seems to be no reason for suggesting that the environmental range of a species of *Halimeda* is directly responsible for imposing a particular system of perennation. The showing in at least two of Feldmann's perennating taxa of a single species of *Halimeda* is evidence that this approach is of limited use.

### 3. *Some conclusions about macroscopic growth*

Halimedae grow a segment at a time. A segment begins from the medullary (nodal) filaments of the preceding segment which grow out as whitish filaments. These filaments branch and rebranch forming first a whitish cone, then a segment-shaped mass of branching bundles of filaments. The tips of these outgrowing filaments become the peripheral utricles and the external surface of the plant. A new segment may be fairly completely formed in about a day. It turns noticeably green by the end of the second day, and by this time has started to calcify. The length and width of the segment are essentially fixed at this stage, but the segment becomes increasingly calcified with age within certain limits, and also may thicken somewhat. Several segments may be produced by a frond in a week, although this varies with the species. Rates of growth for some *incrassata* thalli of 61·4 mm $wk^{-1}$ were obtained.

The youngest segments are at the periphery of the plant, the oldest at the base. Therefore, a gradient of segment ages exists in the alga.

A *Halimeda* thallus may lose some fronds even as others are actively growing. The moribund segments first lose their colour, turn white, may attract epiphytes, then fall off, a process reminiscent of the shedding of leaves by terrestrial plants. The resulting *Halimeda* litter is responsible for much of the mass of carbonate in coral reefs.

Whole *Halimeda* plants may die, and the process is essentially the same as the death of a frond. In addition, the holdfast becomes loose in the sand, if the species is a Rhipsalian one, because rhizoidal filaments have stopped growing. For species like *incrassata*, *simulans* and *monile* there seems to be a definite pattern of youth, growth, old age and death.

These thalli may persist, however, as offspring from asexual reproduction (Section VII). Spreading forms such as *opuntia* appear to persist as senile portions of the plant fall away only to be replaced in the spreading mass by younger fronds which make their own attachments to the substrate with rhizoids from between younger segments (Section V). *Halimeda* thalli may appear senile and dehisce many of their segments only to regenerate later from the remaining segments and possibly from buried rhizoidal filaments (Section VII). These patterns of growth, life and death obviously raise questions of the strategies of *Halimeda* species. One of the most striking of the aspects of growth in *Halimeda* is that individual thalli have life-spans; they die like so many other organisms, after a life-span typical to the species.

### B. *Ultrastructural events*

The basic ultrastructure of *Halimeda* has been described in Section I. The approach in this subsection is to consider aspects of the ultrastructure of the filaments that are associated with the growth of a segment. Two of the studies, Wilbur *et al.* (1969) and Borowitzka and Larkum (1977), were undertaken initially to provide data on calcification. Borowitzka and Larkum (1974b) provide additional information on chloroplast development, and Colombo and Orsenigo (1977) give some information on distribution of organelles within the mature segment.

From the descriptions of the preceding section three stages of segments can be delimited. They are:

the young developing segment;
the mature segment;
the old basal segment.

Some of the ultrastructural features of these three ages of segment are given in Table XIV.

#### 1. *Young developing segment*

Embodied in the young segment are all the stages in the development of a new segment, from the first filamentous extensions of the medullary filaments of the preceding segment to the establishment of lateral branch filaments (cortex), to the peripheral filaments (utricles) making contact and eventually adhering, at least in most species. This whole process takes about 24–48 hours, and seems to start early in the day or light cycle. In about the last 12 hours, which corresponds to the

TABLE XIV. SUMMARY OF ULTRASTRUCTURAL CHANGES IN SEGMENTS

| | | |
|---|---|---|
| DEVELOPING SEGMENT (Processes of Phases I–IV take *c.* 24 h or 48 h, but additional variation with species) | | Position mostly terminal<br>Walls *c.* 0·1–1 μm thick, of three parts (Section I): fibrillar layer, covering lamella and amorphous main portion<br>Golgi present in all phases |
| | Phase I | Medullary filaments develop. Their growing tips have (i) region of small vesicles, (ii) mitochondrial region and (iii) region of small vacuoles<br>This growth and development continues during Phase II |
| | Phase II | Initiation of cortex. Growing tips of cortical filaments have same three regions as tips of medullary filaments |
| | Phase III | Peripheral utricles delimited but unattached |
| | Phase IV | Peripheral utricle walls adhere—many mature chloroplasts present; segment is greenish<br>Calcification begins |
| MATURE SEGMENT | | Occurs anywhere on alga<br>Peripheral region, inner cortex and medulla fully differentiated; pilose layer absent from peripheral walls; may be limited growth by elongation of cortical filaments<br>Calcification continues |
| OLD BASAL SEGMENT | | Basal region of some but not all plants<br>Wall is thickened (to 2 μm), and stratified<br>Peripheral utricles may not adhere<br>Cytoplasmic components reduced in numbers |

dark cycle but is not necessarily related, noticeable greening occurs. Adhesion of the peripheral utricles also takes place at about this time, and the first granules of calcium carbonate appear.

The growing medullary filaments are thin-walled (0·1–1 μm). Their tips show a gradient of organelles, and three regions have been delimited (Borowitzka and Larkum, 1977). At the very apex and extending sometimes for a length of about 4 μm is a region of numerous small vesicles, some with granular material resembling wall components, others with osmiophilic material.

The region below the tip is characterized by much endoplasmic reticulum and many mitochondria with DNA-like fibrils in part of their matrix. Some of the mitochondria are several times the length of mitochondria elsewhere in the thallus. There is also much nuclear division.

The third growing-tip region contains many small vacuoles together with microtubules, mitochondria and young plastids with and without starch depending on the age of the filament.

Golgi bodies are present throughout the three regions although not uniformly so. Migration of organelles from the preceding segment and their participation in the development of the new segment have not been studied.

The tips of the filaments forming the cortex show a similar differentiation into three regions (Borowitzka and Larkum, 1977).

The remainder of the filaments of the developing segment may be somewhat more vacuolate, and other organelles may be present such as amyloplasts (Fig. 54). The spherical and electron-dense bodies (Section I) may occur in some material (Wilbur *et al.*, 1969).

Young peripheral utricles, when their walls become laterally attached, possess many well-developed chloroplasts as well as young plastids, amyloplasts and a vacuole which may contain many spherical bodies (Borowitzka and Larkum, 1977). Calcification begins at about this stage.

(a) *Adhesion of peripheral utricles.* In *cylindracea* the osmiophilic covering lamella bulges outwards, away from the rest of the filament wall, and appears to fuse with the covering lamella of the neighbouring peripheral utricle (Borowitzka and Larkum, 1977). The resulting space between covering lamella and filament wall contains a granular material.

This is the only species for which lateral adhesion has been studied and reported at the ultrastructural level. The process is probably similar in most other species, but interesting variations may occur. In some species, particularly *macrophysa* (Sections III, IV), the peripheral

FIG. 54. *H. monile.* Filament from a segment less than 24 hours old, showing a variety of sizes of vesicles (v) near the wall, and amyloplasts (a) towards the centre. Approximately half the filament width is shown. Aragonite deposition has not begun, and the fibrous coating of the wall can be seen. Stained with lead tartrate. Scale bar is 1 μm.

utricles are free in mature segments. What happens in the developing segment has not been investigated. In other species where peripheral utricles barely touch each other (*gracilis*, Section IV) the covering lamella would provide the matrix to hold the utricles together and also provide the continuous outer covering of the segment.

## 2. *Mature segment*

In these segments, which may be *all* the segments on many thalli, the growth process is essentially complete, and the three regions of the segment (peripheral utricles representing the exterior, the inner cortex and the medulla) are fully delimited. Some subsequent elongation of these regions may occur, with possibly the addition of another layer of inner cortex in much older segments. There may be increased vacuolation of the filaments, and calcification continues, although the full extent of it varies with the species and with depth.

The outer surface of a mature segment shows some physical differences from the walls of the filaments within them. The outer pilose layer has been lost, and in *cylindracea* a second layer of covering lamella develops beneath the original one, which then becomes detached except in the corners where it appears to reinforce utricle adhesion (Borowitzka and Larkum, 1977).

FIG. 55. *H. monile.* Filament from a mature segment but one which is less than 48 hours old. There appears to be much cytoplasmic activity in material of this age. Mature chloroplasts (c) are present as well as immature ones, although the latter are not present in the photomicrograph. Calcification has begun, but the crystals (cr) were lost in sectioning. a = Amyloplast, e = electron-dense body, m = mitochondrion. Stained with lead tartrate. Scale bar is 1 μm.

Although the full range of organelles may occur (Fig. 55), there is also a gradient in the kinds of organelles predominating from periphery to centre of the mature segment, the chloroplasts being commonest towards the periphery and amyloplasts commoner in inner regions, but since the chloroplasts migrate inward at night (Stark *et al.*, 1969) and amyloplasts presumably migrate too, the picture is not so simple.

FIG. 56. *H. monile*. Cross-section of a filament from an old, white suprabasal segment, showing the much thickened wall of some of the filaments, spherical body (s), and aragonite crystals filling the segment space. The density of cytoplasmic organelles appears to be comparatively low in old, white, heavily calcified segments. A portion of a filament with wall of more usual thickness appears on right-hand side. Stained with lead tartrate. Scale bar is 0·1 μm.

### 3. *Old basal segments*

In these segments, which occur mostly on perennating thalli or old thalli, the filament wall may be considerably thickened, up to at least 2 μm, and stratified (Fig. 56), although there is also local thickening in younger material. Amyloplasts are relatively prominent in some of the material as are spherical bodies (Wilbur *et al.*, 1969).

### 4. *Wounding response*

Siphonaceous algae, when wounded, quickly produce a yellowish material often referred to as a callose or mucilagenous substance

(Mirande, 1913) which clots at the site of the injury. Burr and West (1971b) have studied this process in *Bryopsis* where proteinaceous schizogenous bodies are involved. Wounding has not been examined in *Halimeda*. The spherical bodies may be involved in this process.

5. *Summary of ultrastructural changes*

In the developing segment a gradient of organelles and activities occurs in the tips of the growing medullary filaments and their lateral branches. At the extreme tip is a region of small vesicles. This region may be up to about 4 μm long. Behind it is a mitochondrial region, followed by a region of small vacuoles.

By the time utricle adhesion takes place, which in some species occurs by the fusion of the osmiophilic covering lamellae of adjacent walls, the utricles contain many mature chloroplasts, as well as some amyloplasts.

Migration of organelles from the preceding segment and their participation in the development of the new segment have not been studied.

When utricle adhesion occurs growth is essentially complete. Thereafter utricle surfaces on the outside of the plant slough off much of the pilose layer of their walls, utricle layers may elongate somewhat, and calcium carbonate deposits build up.

In very old segments the walls may be much thickened, up to at least 2 μm, and stratified. In some specimens or species the peripheral utricles do not adhere in these segments although they adhere elsewhere on the plant (Hillis, 1959). In the limited material examined cytoplasmic components of old basal segments are much reduced.

## C. *Calcification*

Somewhat over 100 genera of algae calcify, and there are calcareous representatives in most algal divisions (Table XV). Two species of calcium carbonate are deposited, aragonite and calcite, and the type is constant for the species. Aragonite rather than calcite precipitation is avoured by high temperatures, high pH and the presence of sodium succinate, chondroitin sulphate and the cations of strontium, barium and lead (Milliman, 1974). The precipitation of calcite but not aragonite is inhibited by the presence of magnesium in solution, while sulphate ions may inhibit precipitation as aragonite (Milliman, 1974).

In *Halimeda*, as the new segment is completing its development calcification begins, and the process continues for much or all of the life of the segment. X-ray diffraction studies (McConnell and Colinvaux,

TABLE XV. THE TAXONOMY OF CALCAREOUS ALGAE AND THEIR CARBONATE SPECIES[a]

| *Algae* | *Polymorph of $CaCO_3$ deposited* | *Site of deposition* | *Habitat* |
|---|---|---|---|
| Cyanophyta | | | |
| Cyanophyceae | Calcite (usually) | Extracellular in mucilage | Freshwater and marine |
| Rhodophyta | | | |
| Rhodophyceae | | | |
| Nemalionales | Aragonite | Extracellular in intercellular space | Marine |
| Cryptonemiales | | | |
| Peysonelliaceae | Aragonite | In cell wall (?) | Marine |
| Corallinaceae | Calcite | In cell wall | |
| Dinophyta | | | |
| Dinophyceae | | | |
| Peridiniales | Calcite[b] | In cell wall | Marine |
| Chrysophyta | | | |
| Haptophyceae | Calcite | In the Golgi[c] | Marine and freshwater |
| | Calcite (?) | In external mucilage | |
| Phaeophyta | | | |
| Phaeophyceae | | | |
| Dictyotaceae (*Padina*)[d] | Aragonite | Extracellular | Marine |
| Charophyta | | | |
| Charophyceae | | | |
| Charales (internodal cells) | Calcite | Extracellular | Freshwater |
| (oogonia) | Calcite | Extracellular and in cell wall | |

TABLE XV (*cont.*)

| *Algae* | *Polymorph of $CaCo_3$ deposited* | *Site of deposition* | *Habitat* |
|---|---|---|---|
| Chlorophyta | | | |
| Chlorophyceae | | | |
| Dasycladales | Aragonite | Extracellular in intercellular space | Marine |
| Caulerpales | Aragonite | Extracellular in intercellular space | Marine |
| Derbesiales (*Pedobesia*)[d] | Aragonite | In cell wall[e] | Marine |
| Conjugatophyceae | | | |
| Desmidiales (*Oocardium*)[d] | Calcite | Extracellular in mucilage | Freshwater (soils) |

[a] Modified from Borowitzka (1977).
[b] Calcite is deposited only in the resting cysts.
[c] The coccoliths are formed within the Golgi and then excreted.
[d] The generic name in parentheses indicates that this is the only genus reported to be calcareous.
[e] Only in the disc-like stage of the life-cycle.

1967) have shown that only aragonite is deposited in the genus, all the then known species being tested.

The crystals are generally needle-shaped, reaching about 10 μm in length, 0·08–0·60 μm in width and 0·01 μm and less in thickness (Wilbur *et al.*, 1969; Marszalek, 1971; Borowitzka *et al.*, 1974). Wilbur *et al.* (1969) observed granular and polygonal crystals, up to 0·6 μm in diameter, in some material of *incrassata*. The size and numbers of crystals vary with the age of segment, with the species and to some extent from specimen to specimen of the same species, particularly specimens from different sites.

Carbonate deposition seems to be an important function in the metabolism of *Halimeda*, and needs to be understood both as a physiological process, and as an adaptation to life in a reef.

In its simplest form the reaction of calcification is the following:

$$Ca^{2+} + 2HCO_3^- \rightleftharpoons CaCO_3\downarrow + H_2O + CO_2$$

That more than a physical precipitation from a supersaturated solution is involved for many organisms is shown by the isotopic composition of the algal carbonate. That of *Halimeda* is enriched in $^{13}C$ and poor in $^{18}O$ as compared to natural limestone (Fig. 57), and the organic matter of this alga is enriched in $^{12}C$ (Milliman, 1974). These differences indicate metabolic involvement of the plant in calcification.

### 1. *Aragonite deposition: a process working outside filament walls*

Askenasy (1888) in an early microscopical study of the calcium carbonate deposits in *Halimeda* observed that deposits were present soon after the segment was completed, that they increased with age, and that deposition began on the outer surface of the lateral walls of the peripheral utricles and soon spread over the entire space between them.

Few further studies were made of the calcification of any alga until the 1960s (Lewin, 1962), by which time new techniques and equipment, particularly radiocarbon isotopes and the electron microscope, had become available.

These new tools, however, had already been applied, in the years before Lewin's review of the subject, to studies of animal calcification, and research by two workers into calcification included algae as well. Goreau, working on the reefs of Jamaica and calcification in corals, included the calcareous red and green algae, and Wilbur at Duke University, working with molluscs, included coccolithophorids.

It was known from the work of Wilbur and others that calcium carbonate deposition in molluscs was associated with an external

FIG. 57. Comparison of the deviations of $^{18}O$ and $^{13}C$ in *Halimeda* (green algae) with those of other calcareous organisms and natural carbonates. (From Milliman (1974), reproduced with permission.)

organic matrix, and that crystallization was internal in coccolithophorids, the crystals subsequently being extruded onto the cell surface. One might, therefore, anticipate a matrix or internal precipitation in

*Halimeda*. An electron microscope study of calcification in *Halimeda* (Wilbur *et al.*, 1969), however, showed that the pattern was different.

Working with cultured *incrassata* and *monile*, Wilbur *et al.* (1969) noted that aragonite crystals were first formed on the outer surface of the utricle walls when the segment was about 36 hours old (Fig. 55), although this varies somewhat with the material, and that the crystals formed in the immediate vicinity of the fine fibrils of the filament wall. No organic matrix was observed at the site of crystallization (Fig. 58)

FIG. 58. *H. monile*. An early stage in the development of aragonite crystals. Both granular crystals and needles occur in the region of the fibres of the filament wall. The needles extend at various angles into the interutricular spaces. Scale bar is 0·1 μm.

and in contrast to other calcification systems it also was not evident in sections decalcificated with uranyl acetate which retains an organic matrix in molluscan shell. Crystal orientation was random. These aspects have subsequently been confirmed with *cylindracea* (Borowitzka and Larkum, 1977).

Sections through older material showed that following the formation of crystals within the fibrous matting of the walls of the peripheral

utricles, the crystals grow into the spaces (Fig. 58) until eventually the interutricular space is completely filled (Figs 56, 59). The crystals also extend, depending somewhat on species, into the spaces between the central medullary filaments with, in old segments, some secondary

FIG. 59. *H. incrassata*. Cross-section of a filament from a mature green segment near the base of the thallus showing amyloplast (a), chloroplasts (c), chloroplasts with starch ($c_s$), and spherical bodies (s). The segment is well calcified, with aragonite crystals filling the spaces of the segment. Stained with lead tartrate. Scale bar is 1 μm.

crystal formation around the aragonite needles (Borowitzka and Larkum, 1977).

This work by Wilbur and his coworkers (1969) demonstrated that the process of calcification in *Halimeda* occurs in the spaces of the segments, and they pointed out that since the peripheral utricles usually

adhere laterally, the solution filling these spaces is not in free communication with the surrounding seawater except in the very youngest segments. They considered that a completely enclosed volume within the segment would favour crystallization, but that crystallization might also occur without complete isolation from the seawater outside.

### 2. *Calcium-binding properties of the filament wall*

With the first aragonite crystals being formed in close proximity to the filament wall, it would seem natural to scrutinize the nature and activities of the wall more closely. Böhm (1972) reported the presence of a calcium-binding polysaccharide fraction in the wall of *opuntia*. In a more detailed study of the mucilages (water-soluble polysaccharides) the calcium-binding strength was described as low and of the same order of magnitude as succinate (Böhm, 1973b).

The fibrous matting layer, on the basis of tests with ruthenium red and proteolytic enzymes, appears to be polysaccharide (Borowitzka and Larkum, 1977).

### 3. *Calcification and metabolic activity*

The enhancement of calcification by light was initially demonstrated by Goreau (1963) working with eight species of *Halimeda*, and later by Stark *et al.* (1969), the latter group working with *opuntia* and *discoidea* in the reefs of Puerto Rico and the laboratory of the University of Maryland. Goreau's results were, however, somewhat clouded by greater rates being obtained for deposition of calcium carbonate in the dark with four of the eight species. The overall average for the eight species, however, gave a greater light : dark ratio. The difficulty appears to lie in the $^{45}Ca$ methodology which included a short labelling time followed by a long wash in unlabelled medium (Borowitzka and Larkum, 1976a).

Calcium pathways were first worked on by Stark *et al.* (1969) and Böhm and Goreau (1973). By comparing the differential washout rates for $^{45}Ca$ absorbed in the light with those obtained in the dark, Stark *et al.* (1969) suggested a two-step mechanism in the calcification process. The ions were first bound to the wall and their ionic concentration increased. Then there was precipitation.

Böhm and Goreau (1973), from an analysis of their $^{45}Ca$ activity data, proposed a two-compartment exchange system, the seawater–alga system. They considered that at least two pools existed within the alga, making the whole at least a three-compartment catenary system of the

type seawater–polysaccharides–skeleton, with free space and organelles qualifying as additional compartments. The dynamics of the system include the uptake of calcium from the seawater and its release into the seawater. Some calcium is deposited and remobilized in the skeleton, with most if not all of the calcium that is returned to the seawater originating from the carbonate deposits. The water-soluble polysaccharides of the wall incorporate calcium 7–14 times more rapidly than the calcium carbonate deposits. Böhm and Goreau did not, however, obtain conclusive evidence for linking calcium binding of the wall and crystallization.

Many aspects of this work have been continued by Borowitzka and Larkum (1976a, b, c, 1977) working in Australia with the species *cylindracea*, *discoidea*, *macroloba* and *tuna* from the Great Barrier Reef. Lheir experiments with the living alga utilized branches of seven or more segments rather than entire thalli. Light intensities in photosynthesis experiments, measured at the water surface, were 2800 lux, while Halimedae which were planted but not yet used in experiments at the time received 1200 lux at the water surface over a 16-hour light period. Carbon-14 techniques were used for much of the photosynthetic work.

Their study included an investigation of the exchange of calcium between seawater and alga using $^{45}Ca$, of the sources of inorganic carbon for photosynthesis and calcification, and of the effects of metabolic inhibitors on these two processes. Part of the work included calculations of the effects on pH and on the concentration of carbonate ions in a closed seawater system such as the spaces of a *Halimeda* segment, when carbon dioxide and bicarbonate ions are removed by photosynthesis, and calcium carbonate precipitation occurs.

From their work and the results of others, they concluded that calcification in *Halimeda* is primarily a function of the anatomy of the alga and the uptake of carbon dioxide during photosynthesis, and that the calcium-binding polysaccharide of the wall plays little or no role in the process.

Since the spaces of the segment are enclosed, entry of ions into them must be by movement through the confluent walls of the peripheral utricles or through the filaments. Borowitzka and Larkum considered that the pathway of carbon and calcium to the spaces was mainly by diffusion through the shared peripheral utricle walls. In the light, carbon dioxide uptake for photosynthesis from the seawater of the spaces, which is supersaturated with calcium carbonate, results, according to their calculations, in an increase of pH and in the conrentration of carbonate ions within the spaces, thereby stimulating the cate of aragonite precipitation. When respiration only takes place, the

released carbon dioxide lowers the pH and concentration of carbonate ions in the spaces, inhibiting calcification.

Before light stimulation of calcification can occur the photosynthetic rate must exceed a certain threshold value (Borowitzka and Larkum, 1976b), and the rate of carbon dioxide removal by photosynthesis from the spaces must exceed, by a certain factor, the supply entering the spaces. A model of this scheme is shown in Fig. 60.

FIG. 60. A model of calcification in *Halimeda*, which takes place within the spaces of the segment. These spaces are separated, in most species, from the outer seawater environment by a fusing or adhering of the covering lamellae of adjacent peripheral utricles. The extent of the adhesion depends on the species and somewhat on the age of the material. The postulated movements and fluxes of ions during photosynthesis, which takes place within the peripheral utricles and to a lesser extent in the remainder of the filament system of the segment, are shown. These include a light-stimulated proton flux. The end result is the precipitation of calcium carbonate in the interutricular and interfilamental spaces of the segments. Black dots at the plasmalemma indicate fluxes postulated to be active. (Modified from Borowitzka, 1977.)

## 4. *Progress in calcification studies: a review*

Calcification, although not widespread among algae, occurs regularly in over 100 genera. The calcium carbonate crystals are deposited

as calcite or aragonite, but the two species forms are not mixed within plants. In the genus *Halimeda* aragonite is deposited, and the crystals are predominantly needle-shaped. Carbonate deposition seems to be an important function in the metabolism of *Halimeda.*

The deposition of aragonite in *Halimeda* occurs within the segment but outside the filaments that comprise it, that is, it takes place within the closed or essentially closed spaces of the *Halimeda* plant.

The first crystals form in the spaces between the peripheral utricles, at the filament wall surface (interutricular and not intercellular space), when the segments are about one to two days old. A distinct organic matrix has not been observed, and crystal orientation is random. The deposits increase rapidly with age until most of the space within a segment is filled. Secondary crystal formation occurs, the aragonite needles acting as nuclei.

The spaces within the segments are essentially closed since the peripheral utricles of most species adhere laterally at their outer edges. The seawater environment of the segment is not in free communication with the surrounding seawater except in the very youngest segments, and possibly the very oldest segments of some thalli. Such an environment could favour crystallization.

The mucilages of the filament walls contain a calcium-binding polysaccharide fraction. Its calcium complexing strength, however, is low, and conclusive evidence linking it with calcium carbonate deposition has not been obtained. The fibrous matting layer of the filament walls appears to be polysaccharide.

Two- and three- or more compartment systems have been proposed as representing the pathway of calcium from seawater to aragonite deposit. Other workers have concluded that calcification in *Halimeda* is primarily a function of the uptake of carbon dioxide during photosynthesis from the enclosed spaces of the segment. Theoretical calculations indicate a resultant increase in pH and in the concentration of carbonate ions within the spaces, which in turn stimulate the rate of aragonite precipitation.

These combined studies on calcification in *Halimeda* have added much in a relatively short time to our appreciation of calcification in this alga. They have also left unanswered questions which have interested more than one group of workers, such as the precise pH within the spaces of the segment at different metabolic phases and the importance of crystal nuclei in initiating aragonite deposition. We need more information on calcium within the filaments, and also some comparison between results of physiological experiments using intact

growing Halimedae, Halimedae recently collected from their reef habitats, and branches removed from these coenocytic plants.

The importance of calcification to the life of the plant is not understood. What is the energy cost? What are the benefits that pay for this cost? Is the process important to the cycle of senescence in *Halimeda*? Being conducted within the closed spaces of the plant, the process can scarcely be a passive consequence of manipulating carbonate ions. But we do not know why it is done.

*Halimeda* is an admirable plant to grow in culture and in which to study the control of chemistry outside a biological membrane. And in mastering the mechanism used by *Halimeda* to control the medium between its filaments we will learn something of how the whole organism maintains homeostasis without the benefit of cellular epithelium or, indeed, even an intact boundary layer.

## VII. Reproduction

Much of the reproduction of *Halimeda* may be by vegetative cloning, the details of which have now been followed in laboratory culture and are understood in outline. The complete sexual cycle, however, is still not known, with no observations of the development of a zygote into the familiar *Halimeda* thallus. A sexual episode appears to be an outpouring of the energy reserves of an entire thallus into the gametes, and involves the death of the parent plant. This is a breeding strategy reminiscent of an annual weed, though here it is followed by a plant that we now know can maintain itself for an indefinite number of generations between sexual episodes by vegetative means. The breeding strategy has much in common with that described by Williams (1975) as the "strawberry–coral model", though, as we shall see, the *Halimeda* version presents some unusual twists.

There was little information about reproduction in *Halimeda* when Fritsch (1935, 1948) wrote his treatise on the algae, or Dawson (1966) his book on marine botany. It was known, however, that plants were occasionally collected bearing tiny globules clustered on stalks along the margins of the segments or over their surfaces (Figs 61, 62). The clusters looked like miniature bunches of greenish to blackish grapes, and were sometimes sparse and restricted to one or a few segments; at other times they were dense and covered much of the thallus. The general form of these structures in a number of species had been

FIG. 61a. Figures 61a, b and 62a, b show stages of sexual reproduction in *Halimeda*. Above, early stage in production of gametangia in *H. cuneata* showing outgrowth of white filaments from segments. Scale bar is 1 mm. (Photograph courtesy of L. Böhm.)

FIG. 61b. Gametangia, 26–36 μm in diameter, have developed at the tips of many of the stalks (gametophores) on *H. cuneata*. Small cushion segments are particularly apparent between consecutive large segments. Scale bar is 1 mm. (Photograph courtesy of L. Böhm.)

FIG. 62a. *H. monile*, covered with clusters of greenish gametangia. Scale bar is 1 cm.

described by several workers, some of them having only preserved or dried material to work with, and the review of reproduction for the genus (Hillis, 1959) indicated that plants bearing these clusters were rarely collected and were known for only nine species.

The first workers to report these tiny globules, Derbès and Solier (1856) and later Schmitz (1880), worked with fresh *tuna* from the Mediterranean. They noted not only the structures but the release from them of biflagellated zooids. For some time thereafter, the contents of the globules were referred to, sometimes as zoospores, at other times as gametes, and there was little support for the choice of term other than

FIG. 62b. Same plant shown in Fig. 62a, in culture, five weeks later, showing complete disintegration of the thallus. In the reef the thallus would have collapsed sooner from currents and animal disturbances. Scale bar is 1 cm.

inference. That the flagellated zooids were evidence of a sexual cycle was not finally demonstrated until fusion was observed in remarkably recent times (Nasr, 1947; Chihara, 1956; Kamura, 1966; Merten, 1971; Meinesz, 1972b).

The demonstration of vegetative reproductive cycles in *Halimeda* has been even more recent. Field workers have long noticed that some sort of reproduction by creeping growth through sand must occur, but only recent culture work has shown the details and varieties of this process (Colinvaux *et al.*, 1965; Colinvaux, 1968b; Hillis-Colinvaux, 1973). This work shows that individual *Halimeda* thalli have a definite term to their existence, and that new thalli are cloned from creeping rhizoids of the parent thallus, or from broken portions partially buried by chance. There is no difficulty in recognizing generations in *Halimeda* (Fig. 63), whether these be sexual or asexual, and the life-cycle always seems to involve youth, a maturity measured in months, sometimes longer, senescence and death.

FIG. 63. Cloning of *incrassata*. The two large thalli have lived in the aquarium for approximately 14 weeks. The tallest of the five young thalli, produced by "runners" in the sand, is 23 days old. The others are less than 10 days old. Scale bar is 1 cm.

### A. *Sexual processes in* Halimeda

Feldmann (1951) provided the first modern description of the contents of the small globules or gametangia borne externally on a segment. His material was the large-segmented Mediterranean *tuna*, and he noted that mature gametangia were of two different colours, brown and green, which occurred on different thalli. The gametes released by the two were different also. Those from the brown gametangia were slightly larger (macrogametes), and usually contained three small chloroplasts and a posterior eyespot. Those from the green gametangia (microgametes) possessed the same number of chloroplasts but lacked an eyespot. He noted, too, that when the gametangia were first formed almost all the contents of the coenocytic filaments of the segment, especially the chloroplasts and amyloplasts, moved into the gametangia. The filaments of the segment, therefore, were essentially empty, and the thallus, as a result, appeared white.

These observations show that the sexual process involves:

(i) growth of gametangia on stalks or gametophores (Fig 64);

(ii) the transfer of the free organic matter of the thallus, including reserves, to the gametangia (holocarpy), a process that turns the parent thallus white;

(iii) release of gametes of different sizes;

(iv) fusion of gametes;

(v) death of parent thallus;

(vi) development of the zygote.

FIG. 64. Camera lucida drawings of gametangia on their gametophores (stalks), showing the three methods of origin of gametangia in *Halimeda*. Development from utricles is shown in Nos. 1, 6, 7 and 11; from medullary filaments of the segment in Nos. 2, 4 and 9; from medullary filaments at the node after fusion in Nos. 3, 5, 8, 10 and 12. Number 1, 3 and 4 are *favulosa*, Nos. 5–8 are *discoidea*, Nos. 2, 9 and 10 are *scabra* and Nos. 11 and 12 are *monile*. (From Hillis, 1959.)

The complete development of a zygote to a new thallus has not yet been observed and may possibly involve a different life-form.

1. *Development of gametangia*

Hillis (1959) described gametangia for *favulosa*, and listed the following species as those for which gametangia were known: ? *cuneata* (possibly misidentified), *discoidea*, *gracilis*, *incrassata*, *macroloba*, *monile*, *scabra*, *simulans* and *tuna*. Subsequently, gametangia have been described and drawn for *opuntia* (Kamura, 1966) and *cryptica* (Graham, 1975), and I have observed them on *copiosa*, *cuneata*,

*cylindracea*, *lacunalis* f. *lata*, *macroloba*, *macrophysa*, *micronesica* and *velasquezii*. Gametangia are therefore known for 60% of the species.

The stalks supporting the gametangia (gametophores) arise from the segment in three ways (Hillis, 1959):

(i) as continuations of the main medullary filaments subsequent to the nodal fusion characteristic of the species (Fig. 64, Nos. 3, 5, 8, 10, 12);

(ii) as lateral outgrowths without fusion from medullary filaments (Fig. 64, Nos. 2, 4, 9);

(iii) as extensions from peripheral or secondary utricles (Fig. 64, Nos. 1, 6, 7, 11).

Contents of the gametophore are continuous with those of the filaments of the supporting segment, and true plugs or septa such as noted by Howe for *scabra* (1905a) have not subsequently been reported for this or other species (Feldmann, 1951; Hillis, 1959; Colinvaux *et al.*, 1965; Graham, 1975).

Significant taxonomic differences among species may occur in the dimensions of gametophores particularly the length, the extent of branching of gametophores, and in the size, shape and number of mature gametangia. In *cryptica* the gametangia are borne predominantly on the shaded under surface, rarely on the margins or at the nodes, and not on the upper surface (Graham, 1975). Non-reproductive characteristics, however, are more consistently available, and therefore are considerably more useful for species identification.

In laboratory aquaria I have found that when a *Halimeda* becomes fertile, the thallus changes, often dramatically, from green to white overnight or during the "dark" phase of growth, and clusters of gametangia develop on the surface of the segments or along their margins, from white filaments protruding beyond the surface of the segment. At first the developing gametangial structures are white, but they soon become pale green, then darken further as they mature (Fig. 61; Hillis-Colinvaux, 1973).

Electron micrographs of young, pale green gametangia show numerous plastids with sizeable starch grains (Fig. 65), at least in the vicinity of the wall which has the familiar matting of fine fibrils over its outer boundary. Electron-dense bodies (Section I) and granules are common, and spherical bodies are also present. Gametes have not yet formed.

The development of gametangia was once thought to be a rare event since few herbarium specimens have them. This paucity of fertile material in herbaria, however, is certainly a function of the brief

FIG. 65. *H. incrassata*. Section through immature, green gametangium in early organizational stages of microgametes, showing scattered chloroplasts often with starch and oil globules, electron-dense bodies and granules. Fine fibrils on exterior of gametangial wall can be seen in upper left-hand corner. Stained with lead tartrate. Scale bar is 1 μm.

existence of plants in the fertile condition. In my cultures gametes are usually released about 36 hours after the white gametangial stalks appear, leaving behind a white, disintegrating thallus which would be unlikely to be taken by collectors. Fertile plants can often be found in the field by diligent examination of large populations, but this procedure only became practicable with the advent of scuba. It remains true, however, that only a small proportion of a population may be found to carry gametangia at any one time (Beth, 1962), and that several asexual generations may pass before gametangia are produced.

## 2. *Development and fusion of gametes*

Gametangia in a late stage of development are either brownish or a very dark green and have the often-remarked "bunch of grapes" appearance. Electron micrographs of the dark green gametangia at an estimated 12–16 hours before the gametes would be released (Figs 66, 67) show that cleavage into microgametes is well advanced, although not yet complete. The microgametes contain a large, somewhat posteriorly oriented chloroplast, often with one or more starch grains. The single nucleus is generally above the plastid, and there are often three mitochondria. Two whiplash flagella are inserted into an anterior cytoplasmic papilla. The flagella have the standard 9 + 2 arrangement of microtubules. Small vacuoles and occasionally a large lipid body are

FIG. 66. *H. incrassata.* Section through very dark green gametangium fixed about 12–16 hours before the estimated release time of gametes. Gametes have been differentiated, but separation is not entirely complete (Fig. 67). Gametes containing chloroplast with starch, nucleus and mitochondria are separated from the gametangial wall shown in the upper right-hand corner by a thick layer of unidentified material, electron-dense bodies and spherical bodies. Several oblique sections of flagella are included. The wall has an outer coating of fine fibrils. Stained with lead tartrate. Scale bar is 1 μm.

present in the gametes as well. Between the gametes and the wall there is commonly a layer of the electron-dense bodies, often two, three or more thick, and a layer as thick or thicker than the wall of an unknown material (Fig. 66). Some of these substances may provide the mucilage that is released with the gametes as described later. Spherical bodies and electron-dense granules also occur in the region between wall and developing gametes. The wall has the fine fibrillar coating found in the

FIG. 67. *H. incrassata*. Section through very dark green gametangium fixed about 12–16 hours before the estimated time of discharge of gametes, showing gametes with mitochondria, chloroplast with starch (only partly shown), apical papilla with flagellum (second flagellum not in plane of sectioning). Also shown are long and oblique sections of flagella. Cleavage has not been completed, and the two microgametes are attached by a narrow bridge. Gametes were also observed joined in threes. Stained with lead tartrate. Scale bar is 1 μm.

younger gametangia and the filaments of the segment. Not all the cytoplasm is incorporated into the gametes.

I have followed the discharge of gametes, which in my laboratory cultures have been predominantly microgametes. Release occurs about

36 hours after the first sign of gametangial development, and usually within about an hour after lights go on in the controlled environment room. The number discharged by even a single thallus has frequently made the water of an 11·5 l aquarium resemble thick pea soup, and observation becomes extremely difficult.

Gametes are released in a series of puffs, with the units of each puff often held together by mucilaginous material (Hillis-Colinvaux, 1973). Merten (1971) also reported a mucilaginous substance discharged from *macroloba* gametangia for 15 of the 25 releases she observed. For the remaining 10 a mucilaginous casing formed around the gametangia. Discharge is not from individual pores in gametangial walls, but from one, possibly two, central siphons within the gametangial cluster (Fig. 64) which represent the undifferentiated tip of the gametophore. It is through such a structure that the gametes rush in the related genus *Chlorodesmis* (Ducker, 1965). Discharged gametes are more distinctly pear-shaped than when enclosed in gametangia. Characteristics of macro- and microgametes of different species, as reported in the literature, are given in Table XVI.

Although I have observed fusion, I have not been able to induce the resulting zygote to develop after it settled, nor is it clear that any have done so when fertile plants have been left in my culture tanks. All fresh plants in my cultures may be best explained as being outgrowths from rhizoids in the sand, for which there is much direct evidence (see below). Meinesz (1972b, 1973), however, managed to follow the development of zygotes for about one year, though, even then, a recognizable thallus had not been produced.

Meinesz began his observations by bringing plants of both sexes of *tuna*, which he found fertile in the wild, into his laboratory. Thalli bearing the two kinds of gametangia were placed together in glass dishes containing Millepore-filtered seawater of field temperature and arranged in indirect sunlight. The bottoms of the dishes were covered with glass slides. Air and circulation were provided by bubbler and pump. After the gametes had discharged and fused, the glass slides were placed in Petri dishes containing von Stosch's artificial seawater prepared with filtered water. The Petri dishes were exposed to different conditions of temperature and light, but the most successful were those maintained at 20–23 °C in indirect sunlight. The seawater was changed every 15 days, and the glass slides were moved to another container if other algae or bacteria developed. When, after one year the resultant growth was 0·5–1 cm tall, the glass slides were placed in a closed-system seawater aquarium equipped with bubbler and filter (Meinesz, 1973).

TABLE XVI. CHARACTERISTICS OF MACRO- AND MICROGAMETES OF *Halimeda*

| *Species* | *Colour of gametangia at maturity* | *Macrogamete (+) or microgamete (−)* | *Length (L) × width (μm)* | *Eyespot* | *No. of chloroplasts* | *References* |
|---|---|---|---|---|---|---|
| *tuna* f. *platydisca* | Brown | + | 7–8 × 3–4 | Present | *c.* 3 | Feldmann (1951) |
| | Green | − | 5–6 (*L*) | Absent | *c.* 3 | |
| ? *cuneata* | | + | 6·3–7·5 × 2·5–3·4 | | | Chihara (1956) |
| | | − | 5·0–6·3 × 2·0–2·9 | | | |
| *incrassata* | Dark green | + | 12·4–22·5 × 7·0–13·5 | Present | 6–23 | Kamura (1966) |
| | Yellowish green to dark yellow-green | − | 3·5–11·0 × 2·5–6·0 | Absent | 1–3 | |
| *opuntia* f. *opuntia* | Dark green to dark yellow-green | + | 5·0–7·5 × 2·2–3·5 | Present | 1–3 | Kamura (1966) |
| | Dull to dark yellow-green | − | 4·8–7·0 × 2·0–3·0 | Absent | 1 | |
| *opuntia* f. *intermedia* | Dark green | + | 6·8–8·4 × 2·6–3·3 | Present | 1–3 | Kamura (1966) |
| | Dark yellow-green | − | 4·8–6·0 × 2·5–3·7 | Absent | 1 | |
| *macroloba* | | + | 6–10 × 3 | | | Merten (1971) |
| | | — | 1·5–2·1 (*L*) | | | |
| *cryptica* | | | 6–9 (*L*) + ? smaller ones | | | Graham (1975) |

Meinesz (1972b, 1973) reported that after one week of growth under these conditions, the zygotes had a diameter of 5 μm, and contained a single nucleus and four to five chloroplasts. In seven months they developed into spheres of 100–150 μm diameter containing a single large nucleus of 7–10 μm diameter and over 500 lenticular chloroplasts with one or two large grains of starch. Amyloplasts were absent. This stage he called a "protosphere", the term protonema being inappropriate.

Then a number of changes occurred, spread over about two weeks. The coenocytic condition was established by division of the large nucleus to form nuclei of 2–3 μm diameter. The chloroplasts lost their starch, and thereafter appeared like rice grains. Amyloplasts differentiated. A positively phototrophic filament of about 30 μm diameter grew out of the sphere, and a few days later a negatively phototrophic filament developed from the opposite end.

After about five additional months of culture there were a number of erect and creeping filaments. The erect ones were about 90–130 μm in diameter and 2 cm tall, and at the tips of some were slight dichotomous or trichotomous forkings. The creeping filaments proliferated in all directions, and sometimes produced additional erect filaments as well. The diameters of the creeping filaments, which were often constricted, were variable. A scheme of these changes is given in Fig. 68. Subsequent development was not observed.

Meinesz' observations thus end with the production of a filamentous mat, and the stages that must be passed between this structure and an adult thallus are still unknown. We have a similar ignorance of the sexual development of many taxa in the whole order Caulerpales, not just in *Halimeda*. It may be that a mature thallus can grow directly from one or more of the filaments of the mat. On the other hand, new structures might develop which could be precursal to the *Halimeda* structures with which we are familiar. Various workers have suggested that some of the more filamentous Caulerpales, such as species of *Chlorodesmis* and *Pseudochlorodesmis*, may be part of the cycle of genera such as *Halimeda* (Taylor *et al.*, 1953; Papenfuss, 1962; Ducker, 1965; Meinesz, 1972b).

In the laboratory, after the gametes have been released, the white thallus disintegrates, with segment after segment being shed until, within two or three weeks, little more than a heap of segments remains (Fig. 62). Merten (1971) observed that in the field the thallus collapsed in a day or two after the gametes were released. Occasionally only a few segments become fertile in laboratory cultures, and then only one or so branches are shed, but this pattern is uncommon. Usually most of the alga is involved.

One large nucleus approximately 7–10 μm in diameter; > 500 lenticular chloroplasts with starch grains; no amyloplasts; 100–150 μm in diameter.

Erect, positively phototrophic filamentous extension approximately 30 μm in diameter; nucleus divides forming regular-sized nuclei; chloroplasts lose starch and are the shape o a rice grain.

Negatively phototrophic filamentous extension developed at opposite end to other extension; first amyloplasts appear.

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Filaments approximately 2 cm tall and 90–130 μm in diameter in five months; some erect filaments have dichotomous or trichotomous branching at their tips; creeping filaments proliferate with some branches becoming erect.

FIG. 68. Scheme of development, in culture, of zygote of Mediterranean *tuna* over one year, indicating morphological and cytological characteristics of protosphere and juvenile filament stages. The mature *Halimeda* thallus has not yet been obtained from zygotes in culture. (Adapted from Meinesz, 1972b, 1973.)

### B. *Vegetative reproduction of* Halimeda

*Halimeda* plants that grow in sand reproduce by "runners" of filaments (Fig. 69). These filaments, or bundles of filaments, are at least 20 cm long (the limits of my aquaria) and spread laterally through the substrate from the main holdfast (Colinvaux *et al.*, 1965; Colinvaux, 1968a, b; Hillis-Colinvaux, 1972, 1973). They are non-photosynthetic,

FIG. 69. Vegetative reproduction in *Halimeda* by "runners". A fine, filamentous thread or collection of such threads connects the rhizoidal portions of four young Halimedae which developed in an aquarium. See also Fig. 46. (Photograph by The Ohio State University Department of Photography.)

and are individually fine and threadlike. The walls of the filaments are relatively thick, and in places pigmented yellow and regularly constricted, so that the thread sometimes appears like a string of beads, particularly in the immediate vicinity of the plant. Eventually they produce a tight clump or cone-like mass of filamentous material (Fig. 70) which pushes up out of the substrate and from which the *Halimeda* segment is organized (Section VI). More segments are produced, sometimes at the rate of at least one a day per growing tip (Colinvaux *et al.*, 1965). Eventually the physical connections between young and parent thallus are lost.

This same mechanism, the development of new thalli by independent and usually horizontal growth of rhizoidal filaments away from the holdfast, may exist for rock growers as well. Certainly holdfasts and filaments of many other algae grow across rock or penetrate it, with the

FIG. 70. Two young *Halimeda* plants (arrowed), not yet emergent from the substrate, developing from the larger thallus by rhizoidal runners. The white conelike masses at their tips are similar to ones that form the first segments in similar young plants. Development may be somewhat atypical because rhizoidal material, by being next to aquarium wall, has been exposed to light. The diameter of the white discs is 0·85 cm.

siphonaceous alga *Ostreobium*, which appears to grow exclusively in rock, being a notable example of the ability of some filaments to penetrate this substrate.

There are also other methods of vegetative reproduction. Prostrate-growing Halimedae, such as *micronesica*, *opuntia* and to some extent

*renschii*, sometimes produce medullary filaments which remain uncorticated. These filaments grow to a length of several segments and are frequently intertwined, forming coarse, orange-coloured ropes (Fig. 46) which I have sometimes referred to as "rope-like extensions" (Hillis, 1959; Section VI). Some thalli have a number of these extensions, produced on as many branches, which are frequently firmly fixed to rock at various points along their length. Sometimes noticeably younger thalli are attached to an older plant by these extensions, indicating that such filaments not only anchor a thallus, but initiate new ones (Fig. 46).

Another mechanism for vegetative reproduction lies in the production of rhizoidal filaments between segments. These filaments, at least initially, provide additional anchorage, but they also permit division of the alga into separate thalli as the older, more basal segments of the branch disintegrate. This method of growth and clone development (Fig. 71) appeared to be important in maintaining some of the large patches of *macrophysa* and *opuntia* at Enewetak.

On a few occasions I have observed how cloning might occur when a thallus is partially buried in shifting sand. Although half and sometimes more of the thalli observed were buried, and the buried portions had lost their green colour and started to disintegrate, extensive new growth occurred from the branch tips. The new segments had all the signs of vigour, possessed the muted green colour characteristic of many growing Halimedae and were unepiphytized. For these plants it seems likely that independent holdfasts would develop near the bases of the actively growing branches, perhaps as described above for *macrophysa*. A number of separate thalli would result.

In addition, vigorous branches of *Halimeda* which have been separated from the main thallus can develop holdfast systems, thereby functioning as reproductive structures (Hillis-Colinvaux, 1972, 1973). Such *Halimeda* "fragments" might be produced in the reef by waves, storms or animals, and they might be transported in currents. Under favourable conditions they could become established and develop into complete thalli.

Vegetative reproduction seems to be the way in which many individual *Halimeda* plants are produced. Many of the familiar aggregations of Halimedae, whether on rocks or in patches of sand, are probably clones (Figs 63, 72). And the commonest method of cloning is by the outgrowth of rhizoidal filaments, either from holdfasts or from the tips of segments. It is a matter of note, however, that the individual plants so produced have limited lives. The ageing thallus becomes coated with epiphytes whereas the segments of a young plant growing from the

FIG. 71. Early stages in the clonal development in *H. monile* by disintegration of older thallus, and eventual development of new holdfasts near the bases of actively growing branches. In this way several vegetative thalli are produced. Two of the actively growing erect branches have whitish to pale green apical segments which are less than 48 hours old. Scale bar is 1 cm.

parental filament is epiphyte-free. Cloning in *Halimeda* serves as a defence against epiphytes even as it increases the numbers of the plants.

### C. *Reproduction in other Caulerpales*

The genera *Penicillus*, *Rhipocephalus* and *Udotea* also produce new thalli by filamentous runners from holdfast filaments (Colinvaux *et al.*, 1965; Colinvaux, 1968b, c; Hillis-Colinvaux, 1973, includes earlier literature). In aquaria the filamentous connections have been of a single filament or several to many intertwined filaments. The connections observed have been considerably more delicate than the rhizome-like connections illustrated by Duchassaing (1850) for *Penicillus* ( = *Nesea*), and by Ernst (1904) for *Udotea*, and they do not appear to persist. New

FIG. 72. (Top) A stand of *H. cylindracea* in the lagoon of Enewetak Atoll, photographed from above. Clumped and linear arrangements of thalli suggest clonal development. Long dimension of large clump in lower left-hand corner is approximately 9 cm. (Bottom) Clonal development in *stuposa*, at the northern end of the lagoon of Enewetak Atoll. Excavation indicated that many of the *stuposa* clones were the result of lower portions of the thalli being buried in shifting sand. Note the different ages of thalli, the clumped or sometimes linear arrangement, and the overgrowth of some thalli by blue-green algae. Approximate width of the cylindrical segments is 2 mm.

generations of *Penicillus*, *Rhipocephalus* and *Udotea* have generally been produced in my culture systems more rapidly than those of *Halimeda* (Table XVII). For *Penicillus* the plants are also considerably shorter-lived, a *Penicillus* thallus living about two months.

Three types of thallus have developed from the *Penicillus capitatus* Lamarck plants in culture:

typical thallus with stalk and brush, which is the commonest;
thallus of a very few filaments about 1–4 cm tall which sometimes branch dichotomously (Fig. 73);
cluster of filaments similar to those of the preceding type.

The second and third types of thallus resemble the *espera* condition of the forma *mediterranea* of the genus (Huvé and Huvé, 1961; Meinesz, 1972a; Roth and Friedman, 1976). The *espera* phase was first described as a distinct genus, *Espera mediterranea* Decaisne, then transferred to the genus *Penicillus* as *P. mediterraneus* (Decaisne) Thuret. Huvé and Huvé (1961) demonstrated that it was a stage in the life-cycle of *Penicillus capitatus* f. *mediterranea* (Decaisne) Huvé and Huvé. Vigorous *Penicillus* thalli can also regenerate a new capitulum if the old one is removed (Kupfer, 1907; Hillis-Colinvaux, 1973).

Sexual stages appear to be infrequent, again partly because the thallus is destroyed in the process. They are known for *Udotea* (Nizamuddin, 1963; Meinesz, 1969, 1972c) and *Penicillus* (Colinvaux, 1969b; Hillis-Colinvaux, 1973; Meinesz, 1975). In *Udotea* the edge of the thallus becomes fringed with loose filaments (Nizamuddin, 1963; Meinesz, 1969) which appear to be short extensions of the filaments of the blade of the fan. Biflagellated gametes are released from the tips of the filaments (or gametangia) early in the morning, and thalli connected by stolons release their gametes at the same time (Meinesz, 1969).

The gametes are anisogamous and are borne on separate thalli for *U. petiolata* (Turra) Børgesen, with only the macrogametes possessing an eyespot (Meinesz, 1969) as in *Halimeda*.

The development of the zygote of *Udotea petiolata* has been followed (Meinesz, 1972c), using the same techniques as for *Halimeda*. An irregularly shaped, somewhat flattened protosphere was first produced which reached its maximum development in culture in five months, with a diameter of between 60 μm and 90 μm, a single nucleus of 6–9 μm diameter, 200–300 chloroplasts and no amyloplasts. The protosphere subsequently produced two filamentous outgrowths from which a mass of filaments developed, which were heteroplastic and coenocytic, and were of the same general form as the filaments produced by the *Halimeda* zygote. Meinesz considered the filamentous stage he obtained

TABLE XVII. INCIDENCE OF VEGETATIVE REPRODUCTION IN 4 GENERA OF CAULERPALES IN FIRST 5 WEEKS OF CULTURE, AND FOR *Halimeda* AFTER 16 WEEKS

| *Genus* | *No. planted* | *Total new plants in 5 weeks* | | *Total new plants in 16 weeks* | | *Total dead (including fertile plants)* | | *No. fertile* |
|---|---|---|---|---|---|---|---|---|
| | | No. | % | No. | % | No. | % | |
| *Penicillus*[a] | 53 | 36 | 68 | — | — | 5 | 9·4 | 0 |
| *Rhipocephalus* | 2 | 1 | 50 | — | — | 0 | 0 | 0 |
| *Udotea* | 21 | 7 | 33 | — | — | 0 | 0 | 0 |
| *Halimeda* | 377 | 4 | 1 | — | — | 4 | 1·0 | 3 |
| | 240 | — | — | 160+ | 67+ | — | — | — |

[a] Average number initially planted in an aquarium is 2 Penicilli, 1 *Udotea* and 10–12 Halimedae.

FIG. 73. Vegetative reproduction in *Penicillus* and *Udotea*. (Top) An aquarium showing a cluster of young Penicilli around an old *Penicillus* with white capitulum. Two other young Penicilli appear in the left foreground. A young *Udotea* is developing to the left of the large *Udotea*. All young plants are from rhizoidal runners, and the aquarium had been established five weeks when the photograph was taken. The diameter of the white discs is 0·85 cm. (Bottom) Filaments of the *espera* stage of *Penicillus capitatus* from the Caribbean, developed in culture from rhizoidal runners. Scale shown is 11 mm long. (Lower photograph by The Ohio State University Department of Photography.)

with *U. petiolata* to be identical with the vegetative thallus of *U. minima* Ernst.

The development of the zygote has not been observed for *Penicillus* but there are two reports of fertile plants with some variation in details. Hillis-Colinvaux (1973) observed the conspicuous white thalli of two individual Caribbean *P. capitatus* plants after gamete discharge in aquaria. The capituli of both thalli were surrounded by a halo of brown fuzz which microscopically appeared as soft, easily broken, non-calcareous extensions of the capitulum filaments (Fig. 74). They were

FIG. 74. Sexual reproduction in *Penicillus*. (Top) Mature *Penicillus capitatus* with brush (capitulum) covered with brownish, soft, uncalcified fuzz composed of extensions of the filaments of the capitulum. Scale bar is 1 cm. (Bottom) Filaments from the capitulum showing calcified (left) and uncalcified (right) portions. The uncalcified portion is the presumed gametangium, although release of gametes was not observed. Scale bar is 500 μm.

about the same diameter as the regular filaments, without obvious cross walls between calcified and uncalcified portions, and were sometimes dichotomously branched. The tube extensions and main filaments of the capitulum were essentially empty of contents, indicating discharge, and the apical ends of the soft filaments were open (Fig. 74). Meinesz (1975) observed discharge from thalli of *P. capitatus* f. *mediterranea*, and briefly described the gametangia, without figures, as spherical, and up to about 30 μm in diameter. The gametangia were located among the filaments of the capitulum and discharge was by rupture of their walls.

These few data from other Caulerpales suggest that similar breeding strategies prevail for much of the group. The principal method appears to be cloning by sending out "runners" of filaments. Sexual reproduction is infrequent and always leads to the death of the thallus. Development of zygotes seems to require many months, at least five, although the complete process of development has not been followed for any taxon of the group.

### D. *Reproductive strategy and the strawberry–coral model*

*Halimeda* populations appear to be clones which maintain themselves by vegetative means for numbers of generations that seem to be unlimited. Yet occasionally individuals, or, more rarely, parts of individuals, devote their entire resources to a sexual episode. Although the full course of the development of the zygote is still not known, there is reason to suggest that sexual reproduction is followed by either a resting stage or dispersal. The value of both vegetative cloning and sex to plants and animals with life-cycles like this has been explained by Williams (1975) with his strawberry–coral model.

#### 1. *The strawberry–coral model*

For an organism living in a habitat which remains unchanged for a time which is long in terms of the generation time, Williams (1975) argues that it is a better reproductive strategy to produce individuals identical to successful parents than it is to leave the next generation open to the risk of a great variety of competing genotypes. Individuals of a parental strawberry or coral clone will already have been selected during a series of competitive exclusions with neighbouring clones, and continued success requires that the winning formula be repeated. A sexual effort in such clones should only follow when the very high cost of producing many disastrously unsuitable experiments becomes less than the cost of making more copies of the parent. This cost of a sexual endeavour may well only be met when the cost of more vegetative reproduction is local extinction.

Sex, in Williams' view, should only be required when it is necessary to make individuals for competitive struggles in new and untried circumstances. Sex, therefore, should precede the making of resting stages that will survive a hostile environmental episode, since the circumstances in which the clones of the future will compete are likely to be different to those familiar to the parent clone. In a like manner, sex will also precede episodes of dispersion, since the propagules must

colonize habitats which will certainly be unlike that familiar to the parent clone. Finally, sex may well be the reproductive resort of individuals in the middle of the parent clone, even when the habitat remains unperturbed. These individuals will gain no advantage in fitness by producing copies of themselves since their surroundings are already full of their own copies. For these crowded ones in the middle of the clone the best hope of fitness will be to send out colonizing propagules (made various by sex), or to flood the old clonal habitat with new experimental genotypes, one of which just might be better than the parental strain.

It is important to notice that Williams' model is based on the postulate that fitness will be won in competition with other individuals or clones. Diversity through sex is demanded, in the first instance, not by the physical needs of new habitats but because a slight competitive advantage in new or changed habitats may go to a fresh genotype. It is on grounds of competitive advantage that sex should precede resting and dispersal, or be the resort of individuals in the middle of clones.

## 2. *The* Halimeda *reproductive strategy summarized*

The commonest means of reproduction appears to be by vegetative cloning. Most of this takes place by sending out "runners" of rhizoidal filaments. Sand-dwelling forms thrust the filaments through the sand so that each plant looks to be *de novo* and independent. Rock forms spread more obviously from epicentres. Secondary forms of vegetative reproduction are the sprouting of vegetative parts and the establishment of pieces broken off from thalli.

Sexual reproduction is sporadic and almost always involves the death of the entire thallus. The usual pattern is that a sexual episode is separated from the next by one or more vegetative generations. Sex involves the production of an extremely large number of flagellated gametes to the manufacture of which the entire resources of the parental protoplasm have been devoted. This gamete swarm is to be expected to yield a large swarm of zygotes.

The data on what happens to the zygotes are extremely scanty, but nonetheless suggestive. The zygote appears to develop very slowly, taking months for the initial growth. And the result of this growth is a filamentous mat in no way like the parental thallus. After 12 months in a laboratory container no more development is observed. The development time of a zygote, therefore, appears to be of the order of one to two vegetative generations. It is also of a length to serve as a resting stage to pass the adverse seasons of an annual cycle.

### 3. Halimeda *strategy as a variant of the strawberry–coral theme*

The correspondence of the *Halimeda* breeding strategy with the requirements of the strawberry–coral model is obvious and close. There are large populations established and maintained by cloning, and sex is an intermittent and unusual procedure. It becomes profitable to look at the life-history of *Halimeda* with the predictions of the model in mind.

(a) *Fluctuations in the habitat are small compared with the generation time.* Halimedae, in most environments, conform to this prediction in the same way that the corals discussed by Williams do. The habitat is unchanging on time-scales long enough to permit competitive exclusions between clones whose reproductive cycle is of the order of a calendar year. There is, however, the possibility of devastating grazing on clones. A number of browsing animals are known to eat *Halimeda*, raising the possibility that the almost pure stands produced by a clone could be systematically wiped out by a population or migration event among the herbivores. If *Halimeda* were to be regularly and drastically cropped, then it would be expected that competitive advantage would go to strains which are cropped least. The clonal habit would then be a disadvantage, the chances of fitness would be improved by variety, and the vegetative production of a clone should yield to sexual reproduction. There is at least reason to argue, therefore, that the unchanging environment demanded by the strawberry–coral model may not always exist for tropical Halimedae, even when the physical habitat remains constant.

Our data are not yet good enough to resolve this question. One way of looking at it is to note that it is a prediction of the strawberry–coral model that the environment be essentially constant, and to extrapolate from this the prediction that cropping of *Halimeda* must be slight. There are no data for a satisfactory test of this prediction, though there are lines of argument which suggest that the prediction may not be met. Opuntioid forms of *Halimeda* are grazed by urchins, and numerous taxa have been shown to eat the sand-dwelling forms (Randall, 1964, 1967; Mathieson *et al.*, 1971; Earle, 1972). Also there is much patchiness in the distribution of *Halimeda* clones which might be easy to understand if the patches represented a pattern of grazing.

(b) *Resting stages are produced by sexual reproduction.* The scant data on zygote development are in keeping with this prediction, in that the zygotes develop very slowly. It is also true, however, that the adult thallus can persist for a very long time in an apparently moribund

condition. Plants survive for at least 2 years in culture when covered with epiphytes. It may be that *Halimeda* has a dual system of providing resting stages, just as auxospores of diatoms may be sexually or asexually produced.

(c) *Dispersal stages are expected to be produced by sexual reproduction.* The evidence for how *Halimeda* disperses is extremely slender and, indeed, essentially no more than speculation. It is possible that the limited amount of transoceanic dispersal accomplished by members of the genus (Section VIII) may be accounted for entirely by the chance drifting of bits of broken thalli, and so do not require a sexual event. On the other hand, the zygotes are made after fusion of motile gametes and may result in producing something that would pass as part of the phytoplankton. It could also be that the filamentous mat which Meinesz (1972b) describes can float in the plankton and thus travel for months before settling. But there are no data. It would be worthwhile to test this prediction of the strawberry–coral model: that there may be in the tropical plankton zygotes or filamentous mats of *Halimeda*.

(d) *Sexual episodes will be triggered by environmental cues for changing conditions or will occur in groups of individuals at the centres of clones.* There are no convincing data that the production of gametangia is ever synchronous across a *Halimeda* clone or population. There have been some suggestions that chemical cues may be needed to bring on a sexual episode, a postulate which involves the prior postulate that sexual reproduction be synchronous. But observations of my cultures argue against this. Table XVIII describes the appearance of fertile individuals in my cultures over a six-month period following collection from Ocho

TABLE XVIII. INCIDENCE, OVER A SIX-MONTH PERIOD, OF FERTILE *incrassata* FROM JAMAICA, ESTABLISHED IN 44 AQUARIA IN COLUMBUS, OHIO, ON 2 JULY, 1969

| *Aquarium identification* | *No. of thalli fertile* | *Approximate dates thalli fertile* |
|---|---|---|
| 45 | 4 | 8.IX.69, 8.X.69 (2),[a] 13.X.69 |
| 55 | 2 | 11.VIII.69, 10.XI.69 |
| 64 | 2 | 11.XI.69 (2) |
| 69 | 2 | 18.IX.69 (2) |
| 77 | 3 | 16.IX.69, 30.IX.69, 20.X.69 |
| 11 separate aquaria | 1 each | 12.VIII.69 to 6.XI.69 |

[a] Numbers in parentheses represent number in aquaria.

Rios in Jamaica. The collections were planted in 44 aquaria, at densities of a dozen per tank on 2 July, 1969. In 11 tanks a single thallus became fertile and released gametes between 12 August and 6 November. In none of these 11 tanks did another plant become fertile, although all were bathed in an opaque green cloud of gametes for a number of hours. In five tanks more than one thallus developed gametangia and gametes, but individual plants waited up to a month after their neighbour's sexual episode before they too developed gametangia. These data suggest rather strongly that *Halimeda* thalli do not take sexual cues from one another. In addition, in 20 years of field work in three oceans, I have never seen any incidence of gametangia that would suggest that a synchronous reproductive effort was being made. This observation appears to be in keeping with the observations of other workers (Beth, 1962; Merten, 1971), and it is probably a safe, if tentative, conclusion that *Halimeda* populations do not produce gametangia synchronously.

It may be that Halimedae represent an extreme version of the strawberry–coral model which is an adaptation to some of the world's most constant physical environments. What changes there may be in the local physical circumstances of life in the tropical range of its growth are too small to be worth the expense of sexual reproduction, involving, as it does, the destruction of an entire thallus. Asexual cloning therefore, spans the seasons and persists from year to year. The only circumstance then left by the model, when sex will pay, is that of individuals in the centres of clones, for whom making carbon-copies of themselves is pointless. The sporadic sexuality of *Halimeda* may, in fact, represent the incidence with which individuals are surrounded by their own clonal descendants and thus forced into sex.

## VIII. Biogeography and Phylogeny

When identifying specimens of *Halimeda*, geographic distribution is often a helpful character with which to supplement morphological criteria. In spite of being an ancient pantropical genus, therefore, the evolutionary history of *Halimeda* is still recorded in its geography. There seem to be few species of very wide range but rather patterns of local parallel evolution. However constant is the distribution of warm equatorial waters the Halimedae of different parts of it are effectively isolated. They cross ocean gaps but poorly, as would be expected from our knowledge of their dispersal systems (Section VII). We may approach the study of biogeography and phylogeny of this genus, therefore, with the expectation that there is preserved the print of ancient episodes of

dispersion, perhaps even those resulting from very slow processes like the movements of ocean plates.

### A. *Present distribution*

Representatives of the genus *Halimeda* grow wherever there are warm seas, sufficient light and appropriate substrate. The band of sea known as tropical, and delimited by lines of latitude 23·5° north and south of the equator, therefore provides a rough model of its worldwide distribution. Warm waters, however, are only approximately delimited by a fixed number of degrees of latitude, since their extent is determined by ocean currents, which in turn are affected by the rotation and orbiting of the earth and the topography of intervening land masses. The tropical band of sea is asymmetric. It is broad on the western side of the oceans, thin on the eastern side, a pattern which is most marked for the Atlantic and Pacific Oceans. The shores of island groups such as Bermuda and southern Japan, as a result, are bathed by warm waters, although geographically they are north of the Tropic of Cancer. Both afford habitats for *Halimeda*. But Peru, located within the tropics, has cold waters along its coast and is without *Halimeda*. The precise latitudinal extent of tropical water shifts seasonally, generally moving to the north in the middle months of the calendar year, to the south at the end and beginning of the year. Halimedae at the northern and southern limits of the generic range, therefore, are exposed to a seasonally fluctuating environment. The usual temperature of the tropical water is in the neighbourhood of 25 °C.

All the species of *Halimeda* are restricted to this asymmetric tropical band except *tuna* and *cuneata* (Fig. 75), and their distribution within this band is summarized in Table XIX. *Halimeda tuna*, both the typical and large-segmented forms, also grows in the Mediterranean where it is the only *Halimeda* species. *Halimeda cuneata*, alone among the species, occurs in a band of cooler water, to about 20 °C, which corresponds to the subtropical zone. This particular taxon appears to be absent from the tropical region where the other *Halimeda* species occur, although our knowledge of its precise distribution is confused because other species, particularly *discoidea*, have commonly been identified as *cuneata* (Hillis, 1959). Initially it appeared to be restricted to the southern subtropics, where it is known from the tip and western shores of South Africa, southern Madasgascar, south-west Australia and south-east Australia (Fig. 75; Hillis, 1959), but during the International Indian Ocean Expedition it was collected in the northern hemisphere near Okah, at the mouth of the Gulf of Cutch on the north-western

FIG. 75. Subdivision of ocean basins as used in the text, and distribution of *H. cuneata* based on verified specimens. (1) Western and central Indian Ocean; (2) eastern Indian Ocean and western Pacific; (3) eastern Pacific; (4) western Atlantic; (5) eastern Atlantic; (6) Mediterranean.

coast of India (Section IV). It is commonly reported from Japan, but the material I have seen has been *discoidea*.

TABLE XIX. GEOGRAPHIC DISTRIBUTION OF THE SPECIES OF *Halimeda*

| | *Map region (Fig. 75)* | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *1* | *2* | | *3* | | *4* | | *5* | | *6* |
| *Species* | *w.central I.O.* | *e.I.O.* | *w.P.O.* | *e.P.O.* | | *w.A.* | | *e.A.* | | *Med.* |
| | | N. | S. | N. | S. | N. | S. | N. | S. | |
| [a] *incrassata* | + | + | + | | | + | + | | | |
| *favulosa* | | | | | | + | | | | |
| *monile* | | | | | | + | | | | |
| *cylindracea* | + | + | + | | | | | | | |
| *stuposa* | + | + | | | | | | | | |
| ? [a] *simulans* | | + | | | | + | + | | | |
| *borneensis* | | | + | | | | | | | |
| *macroloba* | + | + | + | | | | | | | |
| [a] *opuntia* | + | + | + | + | | + | ?+ | | | |
| *goreauii* | | | | | | + | | | | |
| *minima* | | + | | | | | | | | |
| *renschii* | + | + | + | | + | | | | | |
| *velasquezii* | + | + | + | | | | | | | |
| [a] *copiosa* | + | + | + | ? + | | + | | | | |
| *distorta* | | + | + | | | | | | | |
| [a] *tuna* | + | + | | | | + | + | + | + | + |
| *scabra* | | | | | | + | | | | |
| *cuneata* | + | | + | | | | | | | |
| *lacunalis* | + | + | | | | | | | | |
| *gigas* | | + | | | | | | | | |
| *macrophysa* | + | + | + | | | | | | | |
| [a] *discoidea* | + | + | + | + | | + | + | + | | |
| *taenicola* | | + | + | | | | | | | |
| *lacrimosa* | | | | | | + | | | | |
| [a] *gracilis* | + | + | + | | | + | + | | | |
| *bikinensis* | + | + | | | | | | | | |
| *micronesica* | + | + | + | | | | | | | |
| *fragilis* | + | + | | | | | | | | |
| *melanesica* | | | + | | | | | | | |
| *cryptica* | | | | | | + | | | | |
| Total No. species | 17 | 21 | 16 | 2–3 | 1 | 13 | 5–6 | 2 | 1 | 1 |
| Total excluding pantropical species | 11 | 14 | 11 | 0 | 1 | 6 | 0 | 0 | 0 | 0 |

[a] Present in Regions 2 and 4; considered pantropical.

1. *The ocean groups*

Table XIX groups the *Halimeda* species by region of the oceans in which they have been found. Only seven of the modern species are pantropical and are known at least for the western Atlantic, western Pacific and eastern Indian Oceans. Only one of the pantropical species has entered the Mediterranean Sea. Undoubtedly the lists for the Indian, Pacific and Atlantic Oceans will increase with more collecting, but definite patterns do emerge. Most striking of these is that characteristic species swarms of Halimedae have evolved for the Atlantic and Indo-Pacific regions, even though the environments of each are sufficiently alike for seven species to be established throughout. The youngest basin of warm water, the Mediterranean, has no endemic species and only one of those found worldwide. This pattern seems to speak of an ancient lineage in which local speciation proceeds but slowly.

Changes since the earlier revision of the genus (Hillis, 1959) include the addition of new species and the extension of known distributions, both of which are likely to occur in the future as well. It is particularly likely that some of the species now known only for the Pacific may be found in the Indian Ocean, where even less collecting has been done than in other oceans. It would also be interesting to know if species restricted to the Indian Ocean exist.

Further collecting will also be needed to determine the true extent of endemism within the genus, for it seems likely that the known ranges of some very "local" species like *cryptica*, *favulosa*, *gigas*, *goreauii*, *lacrimosa*, *melanesica*, *scabra* and *velasquezii* will be extended.

Table XIX also shows that of the four regions with more than ten *Halimeda* species, the greatest number is found in the Pacific, the least in the Atlantic. This pattern is exhibited by other tropical organisms, and may be a function both of area and of palaeohistory. This table also indicates that more species occur in the western portions of the Pacific and Atlantic Oceans. One might be tempted to conclude that the Marshall Islands, Jamaica and the Bahamas, with their peak numbers of *Halimeda* species for the Pacific and Atlantic Oceans respectively, represent centres of speciation or, alternatively, that larger areas or islands support more species of *Halimeda*. These conclusions, however, are premature, for these and other high numbers mostly represent regions of relatively intense collection and study. As many or possibly more species of *Halimeda* may eventually be known for other sites when their floras are adequately sampled and studied. The species list from Honduras, for example, has increased from six to nine as a result of

relatively recent scuba collections. In reality, it may be longer, and some increase in numbers of species for neighbouring Central American countries is also likely, although the eventual total from these areas may never be as high. In the south-western Pacific, New Caledonia and other island groups probably have a more diverse *Halimeda* flora than is now recorded.

## 2. Halimeda *and coral distributions compared in outline*

Wells (1969) suggests that only two reef coral provinces are clearly recognizable, the Indo-Pacific and the Atlantic, and that subprovinces can be identified only "with misgivings". The preliminary data for *Halimeda* (Table XIX) suggest greater local differentiation than this, though the same major separation between Atlantic and Pacific is evident. It may be that when the *Halimeda* and other algal populations of reefs have been studied with the taxonomic intensity of the corals, their separation into provinces will be no more precise. Yet other explanations for the more local distributions are possible.

It seems likely that corals disperse much better than do Halimedae, since a dispersal phase is a normal part of the life-cycle of coral species whereas in most *Halimeda* reproduction is vegetative. *Halimeda* populations of a remote shoreline, therefore, are more insular than coral populations and likely to exhibit more local endemism. It may also be that plant habitats are less restricted than those of reef corals, because *Halimeda* grows not only on reefs, but also in sand, on dead reefs and at depths well below the lower limits for reef-building corals. There may thus be more opportunities for local speciation for *Halimeda*, perhaps particularly in sites which might not be reached so easily by propagules transported across oceans.

When the distribution of *Halimeda* species is better known it will be an interesting exercise to compare species distributions between corals and *Halimeda* species in some detail.

## 3. Halimeda *distributions in species-poor areas*

Since relatively few areas have been extensively worked for *Halimeda*, we cannot, at present, realistically ask some of the more interesting questions pertaining to the geographical distribution of the genus. Within this framework of caution some additional comments, nonetheless, are possible. A few areas with a low number of *Halimeda* species such as the Hawaiian Islands (four), Costa Rica (one), Easter Island (one), Galapagos Islands (none), Bermudan Islands (four),

Mediterranean region (one) and the Red Sea (three to five) have been rather carefully worked, at least in the shallower parts of their reefs. It therefore seems to be established that these sites do indeed support very few *Halimeda* species. And there can be very little doubt that the Galapagos Islands are without *Halimeda*, even though the related siphonaceous genus *Caulerpa* is present. It is necessary to ask why the *Halimeda* flora of these places is so poor.

These sites combine two characteristics that might be expected to restrict the opportunities for *Halimeda*:

the sites are remote, insular or isolated;

the sites have either patchy or variable environments which may frequently be outside the physical tolerance of the genus.

The remoteness of the sites should be expected to restrict the rate of immigration or recruitment. This must work particularly strongly for an organism which seems to have very poor powers of dispersal. The variable environments might be expected not only to restrict the rate of establishment, but to increase the rate of local extinction. The paucity of Halimedae in these places, therefore, may be explained in the classic manner of MacArthur and Wilson (1967): we have equilibrium numbers of species set low by a high extinction rate and a low recruitment rate.

What we know of the reproductive strategy of Halimedae (Section VII) suggests that dispersal must indeed be slow. To reach a site as remote as Easter Island or the Galapagos with a piece of broken thallus drifting the seas seems an unlikely process, and we have no reason to believe that zygotes could survive such a voyage. And establishment of propagules of these kinds is probably very unlikely. The evidence of our cultures supports this. Other *Halimeda* relatives such as *Batophora* and *Acetabularia* frequently appear in culture tanks, even though pains have been taken to clean sand, water and cultivars. But no *Halimeda* has appeared which cannot be shown to be a vegetative outgrowth of another plant. The *Halimeda* reliance on vegetative cloning is an excellent tactic for spreading from a place of establishment, but it is not accompanied by an effective mechanism for making the first invasion.

It may be that the variable environments of these sites with few species operate more as further obstacles to immigration than as agents of extinction. All the sites have something unusual about their oceanic regimen: the periodic extremes of *El Niño* at the Galapagos (Wyrtki, 1973); the winter in Bermuda and the Mediterranean. These events must narrow the window of opportunities for colonizations. In short, the

low numbers of Halimedae in these places may not be so much the result of a MacArthur and Wilson equilibrium as an almost infinitely prolonged early colonization stage.

### B. *Palaeobiogeography and prehistory*

*Halimeda* lived and contributed its segments to ancient reefs much as it does today. The known fossil Halimedae have been found in limestone facies of the Tethyan (Mediterranean and Persian Gulf) region (Elliott, 1960), Mexico and Texas (Johnson, 1969). The genus itself is first recorded from the Cretaceous (Elliott, 1960; Johnson, 1969), but would date from the Middle Jurassic if the two genera, *Boueina* and *Arabicodium*, which are similar to it, are included in the genus as recommended by Elliott (1965) and Johnson (1969). The epithet *Halimeda* has priority. These early Halimedae are small-segmented, and are considered to have developed from hybridizations between the species groups *Arabicodium* and *Bouenia* (Elliott, 1965). The existence of such a long historical record, uncommon among macroalgae, has the potential of providing considerable information about the evolutionary history of the taxon as well as contributing to the understanding of present-day distribution. However, the data for *Halimeda* are few at present.

The known distribution of fossil material as indicated above is along part of the borders of the Tethys Sea and the western North Atlantic. It also seems likely that halimediform algae grew in shallow-water sites over a wider range of these particular shores as well as extending westward into the Indo-Pacific, along the eastern "Pacific" shores of the existing land masses, and by Miocene times possibly along the northern shores of Australia. Examination of new sites may prove that this is so. The faunas for the Caribbean and Mediterranean regions of the time appear to have much in common (Valentine, 1973; Berggren and Hollister, 1974a; Hallam, 1975), which is possibly the outcome of a current system common to much of the palaeoequatorial region, and to the low variability of climate. Perhaps the *Halimeda* flora also was fairly similar for much of the region.

Within the Tethyan area itself, five fossil species of *Halimeda*, *H. nana* Pia, *H. praemonilis* Morellet and Morellet, *H. eocaenica* Morellet and Morellet, *H. praeopuntia* Morellet and Morellet and an unnamed *Halimeda* species, have been reported for the Tertiary preceding the Messinian crisis (Morellet and Morellet, 1922, 1941; Elliott, 1960). One species of *Boueina* also occurred. There was, therefore, considerably more species diversity of *Halimeda* in this

region than is shown by the taxon today for the Mediterranean, where only two forms of *H. tuna* are known.

Events in the history of the area during the intervening millions of years, as presently interpreted by plate tectonics and continental drift, may provide insights into the cause of this dramatic decrease in diversity. They include the closing of the eastern end, then the western end of the Tethys Sea during the first half of the Cenozoic. The effect was to isolate the Tethys from the marine biota of both east and west. These events were followed by extreme evaporation in the region, with a sea-level drop of several thousand feet in the western Tethys during the Miocene (Berggren and Hollister, 1974a, b; Hsü *et al.*, 1977). This Messinian crisis was accompanied by massive extinction of marine life. It seems likely that the *Halimeda* flora did not survive, or at most existed in a relict flora to the immediate west.

Following this mass extinction of the Tethyan flora, the present *Halimeda* of the Mediterranean must have been the result of a recolonization event, probably from the Atlantic Ocean. This would be a plausible event following the Messinian crisis because there was then a more northerly extension of warm water in the Atlantic Ocean than now (Berggren and Hollister, 1974a, b). This warm water allowed penetration of the new Mediterranean basin by the panoceanic species, *tuna*.

This reconstruction of the history of the Mediterranean *Halimeda* flora is of special interest because it gives us a clue to the slow pace of evolutionary events within the genus. The events of the Pliocene and Pleistocene combined have left the Mediterranean with but a single species in circumstances which suggest that the initial colonization was at the beginning of this period. If this is true, then the panoceanic species *H. tuna* is ancient and conservative.

It is true, of course, that the above conclusions on longevity of species drawn from the Mediterranean reconstruction are vulnerable to arguments that *tuna* is a recent immigrant, but with the Suez Isthmus having been closed and the cool waters now prevailing in the adjacent Atlantic this seems unlikely. It may also be that a more complicated history of speciation in the Mediterranean is hidden from us by extinctions in the Pleistocene. It would be very useful indeed to recover a fossil history of the genus from the Mediterranean covering the last five million years.

This view of the paucity of species in the Mediterranean adds an extra dimension to the discussion of places with impoverished *Halimeda* floras that is given above. It is concluded there that the very low recruitment rate of Halimedae may be the principal factor in producing

low diversity, so much so that it is not necessary to resort to processes of extinction required by an equilibrium model. If recruitment is not only difficult and slow, but is actually confined to brief geologic periods, when current patterns are favourable, then the slow-recruitment model is amplified. It is argued above that the Mediterranean may have collected its ancestral *tuna* population during a brief favourable period after the Messinian crisis. A similar argument can be applied to the flora of the Canary and Cape Verde Islands, which may been have acquired during the same limited opportunity.

Other historical events may explain the present low species diversity of *Halimeda* elsewhere. The eastern Pacific, for example, would have become isolated from any eastern centre of distribution after the uplift of the Isthmus of Panama during the Neogene. In addition, its biota then as now was separated from western Pacific centres of distribution by a distance which *Halimeda* propagules appear unable to bridge.

For the southern Atlantic, a change in the pattern of surface currents, possibly accompanied by increasing separation from the Tethyan centre of distribution and succeeded by a slow rate of speciation, could explain much of the present-day low *Halimeda* species diversity. Berggren and Hollister (1974a) postulated current systems which could have introduced Tethyan elements along the entire Brazilian coast as late as the early Palaeogene. Present-day current patterns isolate both northern and south-eastern coasts of Brazil from the modern centre of distribution of *Halimeda* in the Atlantic which is the Caribbean. Additional collecting in the southern Atlantic may increase the species list somewhat, but the Brazilian flora has been worked extensively by Joly and his students.

These available studies of the fossil record of *Halimeda* seem to hold the clear inference that the genus tends towards conservative species, that dispersal is indeed slow, and that present distributions may well reflect past geological events as well as contemporary ecological processes.

### C. *Rates of speciation within the genus*

Once evolved, *Halimeda* relatively quickly seems to have replaced *Arabicodium* and *Bouenia* which are not known after the Cretaceous (Elliott, 1965). Elliott suggests, too, that the genus diversified rather rapidly during its early history into a number of species, some fossil, such as *H. nana* (Pia, 1932), *H. praeopuntia* (Morellet and Morellet, 1922), *H. praemonilis* and *H. eocaenica* (Morellet and Morellet, 1941),

and some modern. There was also an increase in the size of segments and possibly in the size of the entire thallus. Three of the species, *praeopuntia*, *eocaenica* and *praemonilis*, are described by their authors as resembling the modern species *opuntia*, *opuntia* f. *minor* (=*goreauii*) and *incrassata* f. *monilis* (=*monile*) respectively (Morellet and Morellet, 1941), with similarities such that Morellet and Morellet questioned the assignment of separate names to them.

For the remaining taxa, *H. nana* and the undescribed species, the literature data are too sparse to associate them definitely with Recent species. Even so, two of the five types of nodal filament pattern delimited in Section III, those present in the Opuntia and Rhipsalis sections, and representing the sprawling and sand-binding habitats respectively, are represented in the species *praeopuntia*, *eocaenica* and *praemonilis*. It seems likely that one or more tunoid species (section Halimeda) also had differentiated before the Messinian crisis. If so, then three of the five types of nodal filament structure would have existed. These would correspond to the only patterns of nodal filaments present in modern species of pantropical distribution (Table XIX), plants which also represent the major habitat types of sprawling, sand-binding and rock-growing. And interestingly, only pantropical species are present in modern reef communities of the Hawaiian Islands, the American shores and nearby islands of the eastern Pacific (with the exception of Easter Island), the Mediterranean, the Canary and Cape Verde Islands and Brazil (Table XIX, bottom line), while three of the four species growing in the Bermudan Islands are pantropical also.

*Halimeda* has been an important sediment-producer throughout its history (Wray, 1977), which implies that overall conditions for its growth have been favourable, and that there have been substantial populations during much of this time regardless of alterations in oceans and currents. Some of these changes would have led to extinction, others to isolation sometimes followed by speciation. With the development of various barriers such as the Isthmus of Panama, or the land mass at the eastern end of Tethys, separate Indo-Pacific, western Pacific and Atlantic groups would have been created out of the pantropical stock. Subsequent speciation within them would lead to the development of taxa unique to these particular regions. Figure 76 illustrates possible lineages among Recent *Halimeda* species, and the directions in which development from pantropical stock may have occurred in different ocean regions as suggested by known distribution and similarities of habit and morphology. Some pantropical species, particularly *tuna* and *incrassata*, occur infrequently in many of the collections from the Pacific Ocean, and it is possible that satellite

FIG. 76. Hypothetical lineages of *Halimeda* species from the pantropical modern and fossil species named in the boxes. (a) Species erect or pendant from rock except *gracilis*; holdfast usually $\leqslant 1$ cm long. (b) Sand-"rooted" species; holdfast usually $> 1$ cm long. (c) Species that sprawl or creep; often more than one point of attachment on a thallus. IP = Indo-Pacific; P = Pacific; A = Atlantic distributions as currently known.

species such as *lacunalis*, *macrophysa*, *macroloba* or *borneensis* may be successfully replacing them. An alternative explanation is that their low numbers may be an artifact of the collections available.

The time-scale for the first events in the history of *Halimeda* has been ascertained by the location of fossils in the appropriate strata, and by inference from our understanding of subsequent historical events. Some modern species, however, may have existed earlier than hitherto implied. The reason for questioning the time-scale lies in the present disjunct distribution of *H. cuneata*. One explanation for its modern occurrence in the southern subtropical regions, delimited by the south-eastern tip of South Africa, southern tip of Madagascar, south-western and south-eastern coasts of Australia, and in the northern subtropical region of the Gulf of Cutch in north-west India (Fig. 75) is that this species had evolved at least by the time the regions represented were located in the same latitude, that is, before India had joined with continental Asia. The latest that they were in close proximity was in the Late Cretaceous (Smith and Briden, 1977). If *cuneata* existed then, it seems likely that other modern pantropical species had also evolved, and therefore would have coexisted with the fossil species which, as already indicated, have been described for a later epoch. An alternative explanation is that *cuneata* formerly occurred along much of the east coast of Africa and the western shores of India, that it eventually extended into subtropical waters and was displaced, or essentially so, from tropical regions. This line of reasoning does not require such an early differentiation of the taxon. Information from fossils may provide the decisive support for one of these hypotheses.

In conclusion it may be said that there is much direct evidence in the fossil record for *Halimeda* species being both conservative and ancient. The data allow the working hypothesis that many of the present panoceanic stocks can be identified as early as the beginning of the Tertiary. Local speciation has occurred only where isolation has been very prolonged. The possibility that diversity is a function of very poor and spasmodic opportunities for recruitment, rather than due to the establishment of species equilibria, is encouraged.

### *D. A biogeographical approach to the phylogeny of the Caulerpales*

Morphological characteristics have provided most of the information for placing *Halimeda* in phylogenetic schemes (Gepp and Gepp, 1911; Gilmartin, 1966; Parker, 1970), but again biogeographical data can contribute useful support or indicate weaknesses.

The Gepps (1911) suggested a common calcified ancestor for the calcareous genera, and devised a separate evolutionary scheme for the non-calcareous members of the group (Section III). This could be part of the scheme proposed below as well, with *Udotea*, *Halimeda*, *Arabicodium*, *Boueina* and the other calcareous genera developing from such an ancestor. However, even the limited data we have do not support the rigorous development of calcified and uncalcified taxa from calcified and uncalcified stock respectively. Calcified groups within the marine algae have arisen independently, *Padina* in the Phaeophyta for

FIG. 77. Phylogenetic scheme for the Codiaceae proposed by Gilmartin (1966). The genera *Udotea* and *Avrainvillea* were considered to be in the Udoteaceae following Nizamuddin (1963), and hence were not included in the scheme.

example, and calcified and uncalcified phases alternate in the life-cycle of *Pedobesia* (MacRaild and Womersley, 1974; Section III), and possibly even in *Halimeda*. Whether or not the juvenile filaments of *Halimeda* (Section VII) are calcified is not indicated by Meinesz (1972b).

A more elaborate scheme is presented by Gilmartin (1966) (Fig. 77). He considered *Tydemania*, with its uniaxial construction, to be a primitive member of the Codiaceae and a connecting link between *Rhipocephalus*, *Halimeda* and *Penicillus*. Recent data have indicated some weaknesses in this scheme, however. It is not supported by wall chemistry, the wall of *Codium* containing mannan while that of *Halimeda* contains xylan (Parker, 1970). However, in spite of the helpful study of Parker, the data on wall chemistry within the group are scant, and the character may prove not to be a valid one for phylogenetic purposes. The scheme is also not supported by plastid structure, with both homoplasty and heteroplasty, and their associated differences, occurring in a single evolutionary line (*Codium* and *Halimeda* respectively); nor is it vindicated on ecological grounds. Gilmartin suggested that

*Tydemania*, as a putative primitive Codiacean, may have survived in abundance only in deep-water habitats. Although it grows well in this environment, it also occurs in sizeable populations at some sites of 3–5 m depth in Enewetak Lagoon, the same lagoon in which Gilmartin worked (Hillis-Colinvaux, 1977), and I have observed well-developed stands of it in water of −1 m to −4 m in the Indian Ocean near the small islands of Banyak, Batu, Siburu and Stupai off the west coast of Sumatra.

The distributional data for the genera of the Caulerpales (Table XX) provide the basis for a new scheme (Fig. 78). It is suggested that the

FIG. 78. New phylogenetic scheme of Caulerpales, excluding the monogeneric Caulerpaceae, based on biogeographic data.

five pantropical genera *Halimeda*, *Udotea*, *Avrainvillea*, *Caulerpa* and *Pseudocodium* are the oldest, and had differentiated before free east–west exchange of tropical marine biota was brought to an end by the closing of the Tethys Sea. The other genera may have coexisted with them and subsequently have become extinct over part of the range, or they may have evolved later. Considering the present distribution of these genera, at least as known, the latter seems the more likely interpretation for the taxa of all but the last column which are not included in the scheme because the distributional patterns shown for them are interpreted as reflecting incomplete data. One or more of the genera in

TABLE XX. GEOGRAPHIC DISTRIBUTION OF THE GENERA OF CAULERPALES

| *Pantropical* | *Indo-Pacific* | *Pacific* | *Atlantic* | *Other* |
|---|---|---|---|---|
| *Halimeda*[a, b] | *Tydemania*[a] | | *Penicillus*[a, b] | ? *Penicillus*[a, c] (? w.P., e.A., Med.) |
| *Udotea*[a, b] | | | *Rhipocephalus*[a] | |
| *Avrainvillea* | *Chlorodesmis* | *Callipsygma* | | *Boodleopsis* (w.P., e.A.) |
| | | | | *Rhipilia* (w.P., e.A.) |
| *Caulerpa*[b] | *Geppella* | | | *Pseudochlorodesmis* (w.P., e.A., Med.) |
| *Pseudocodium* | *Rhipiliopsis* | | | *Cladocephalus* (I., w.A.) |

[a] Calcareous genera.
[b] Present in the Mediterranean also.
[c] This distribution is derived from Siboga and earlier expedition reports of the genus around Australia. This material needs re-examination.

this column eventually may be shown to be pantropical. If the remaining taxa evolved later, then the calcareous genera *Tydemania*, *Penicillus* and *Rhipocephalus*, which are the ones of interest herein, would be more recent than *Halimeda* and *Udotea*. More detailed lineages have not been shown but *Tydemania* and *Penicillus* appear more closely related to *Halimeda* than to *Udotea*. *Caulerpa*, as the only genus of the Caulerpaceae, has not been included in the scheme which consequently is restricted to the Udoteaceae.

The uniaxial construction of *Tydemania* has an interesting parallel with that of *H. cryptica*, a species known only from −25 m and deeper in the eastern Atlantic. It seems likely, however, that this morphological feature evolved independently in the two taxa, and is an adaptation of these two algae to a particular niche, rather than a primitive characteristic, as suggested by Gilmartin (1966). This niche may well involve successful growth under conditions of low light intensity and low energy reserves, leading to economy of form. In addition to the reduced numbers of medullary filaments that both taxa possess, the economy would extend, in *H. cryptica*, to the secondary utricles which are less fully developed on the shaded surface. So far a similar *Halimeda* species has not been found outside the Caribbean and the niche may be occupied by *Tydemania* or other taxa elsewhere, or perhaps, as with other *Halimeda* species, appropriate regions have not yet been explored adequately.

These phylogenetic schemes, both past and present, remain largely speculative. Some advances in understanding the relationships of the genera have been made, however, and there is an increased appreciation of avenues in which subsequent research would be particularly profitable. The long geological record of *Halimeda* and the widespread recent distribution of this genus indicate some of the impact the genus may have had, and is continuing to have, on tropical reefs. This contribution will be examined in more detail in the final sections.

## IX. Productivity

All Halimedae are plants of shallow coasts or of coral atolls and as such they are members of some of the very few highly productive communities of the oceans (Ryther, 1969; Koblentz-Mishke *et al.*, 1970; Colinvaux, P. A., 1973, 1974, 1978; Bunt, 1975). The record of their own high productivity is preserved in many a coral reef, as in those at Funafuti where a significant part of the reef structure was found to be made of *Halimeda* segments (Section II). Understanding the productive

capabilities of Halimedae, therefore, is necessary both for studies of energy flux through tropical reef communities, and for studies of the building of reefs themselves.

The productivity of atolls, on which so many Halimedae grow, is a particularly interesting subject since atolls are typically set in the unproductive blue waters of the main ocean deserts. Atolls are without the nutrients supplied by run-off from the land to coastal sites, nor are they typically supplied with the nutrients of upwellings. This has made their high productivity difficult to explain, and even now it is not understood in detail, though the outlines are becoming clear.

That the atoll marine system is not dependent on the nitrogen, phosphorus and zooplankton transported into it from the impoverished surrounding waters was demonstrated first by Sargent and Austin (1949, 1954) for Rongelap Atoll in the northern Marshall Islands. They established that this atoll was inwardly sustaining, using the technique of flow-respirometry, a method subsequently employed by Odum and Odum (1955) for their work on Enewetak Atoll which is also in the Marshall Islands. This atoll too they found to be self-supporting, and their figure for the gross productivity of a coral reef community, together with a subsequent one obtained by Kohn and Helfrich (1957), is a useful base-line calculation of the productivity of tropical reefs since the technique measures community productivity for the transect of measurement. These studies do not tell us, however, how this high productivity is achieved, or the contribution of individual reef components, like the populations of large algae.

Answers to both these questions are essential to an understanding of productivity of the whole reef and energy flow in the reef system, as well as to reef modelling. Some appreciation of the first question, how the high productivity is achieved, is provided by the realization that nitrogen and possibly phosphorus are recycled within the system (Johannes *et al.*, 1972), the presence of some such pattern being expressed earlier in the review of coral reefs by Yonge (1963). The 1972 report is part of the recent work of the SYMBIOS team that studied essentially the same part of the Enewetak reef as did the Odums, as well as a more northerly transect. Some details of the results of this team effort are still being published, but what is available adds strongly to the evidence that atolls may be nearly closed systems. They fix their own energy and cycle their own nutrients, are fertile islands in an infertile sea. In this respect coral atolls have to the ecologist something of the impact of lowland tropical rain forest, because this too supports itself on nutrient-poor substrate through very efficient nutrient retrieval systems. For the rain forests we have a fairly clear idea how nutrient

retrieval and cycling work, but we know much less about the parallel systems in a coral atoll. It seems not unreasonable to expect that nutrient retrieval and cycling is sponsored by the primary producers, suggesting that the productivity of the various plant components of the reef ecosystem is a necessary subject for research.

Figures 79 and 80 are photographs of the section of the Enewetak reef studied by the Odums and the SYMBIOS group. This section was

FIG. 79. The inter-island study site of Odum and Odum (1955) is 0·4 km north (right) of this islet, Japtan, on Enewetak Atoll, and north of the ship hulk, a relict of the Second World War. The Odum transect extended from the algal ridge, where the waves are breaking, towards the lagoon for approximately 300 m. The reef in this region is approximately 455 m wide. (Data from Odum and Odum, 1955.)

chosen for its suitability to the flow-respiratory method of productivity measurement and does not include all parts of the atoll system. In particular, it does not include most of the macrophytes. Plants included in the transect were principally the algae of mats together with the symbiotic and boring algae associated with the corals, as well as some encrusting algae. In a careful search of much of this section of reef in 1975 I was unable to find a single *Halimeda* plant. This observation is perhaps brought into perspective by noting that borings from Enewetak show that *Halimeda* segments are a principal ingredient of the Enewetak reef matrix, just as they are at Funafuti (Couch *et al.*, 1975).

FIG. 80. Two of six zones of the Japtan transect described by Odum and Odum (1955) in their inter-island transect: the encrusting zone (top), and zone of smaller coral heads (bottom). Halimedae were not found in either zone during our December 1975 visit. Breaking waves show at the top of these underwater pictures. Depth is *c.* 1·5 m.

The Halimedae of an atoll live in the deep water of the outer slopes, in the shallows of the lagoonal coasts of the islets, in the reef passages, on pinnacles and on the lagoon floor. It is at these sites that much of the productivity of the reef system, both of carbon and of carbonate, must occur, and at these sites we have very few measurements indeed. Halimedae and other large algae occupy rather similar sites in fringing and barrier reefs, and there again the measurements are few.

Apart from work on coralline red algae like those of the reef front (Marsh, 1970; Littler, 1973; Smith and Marsh, 1973; Connor and Adey, 1977), our measurements of the productivity of macrophytes of reefs seem to be confined to a few on sea grasses (Odum, 1957; Westlake, 1963; Qasim and Bhattathiri, 1971; Patriquin, 1973, and a few on *Halimeda* and other Caulerpales (Gessner and Hammer, 1960; Drew, 1966; Drew and Larkum, 1968; Johnston and Cook, 1968; Johnston, 1969; Hillis-Colinvaux, 1974). Yet it obviously is necessary that we master the contribution of the calcareous green plants to both the energy and carbonate fluxes of reef systems.

### A. *Production of organic carbon*

Primary productivity in aquatic communities is measured by a number of methods of which two of the principal ones are the light : dark bottle technique and the *in situ* $^{14}C$ uptake method (Steemann Nielsen, 1952; Strickland, 1960, 1966; Strickland and Parsons, 1968; National Research Council, 1969; Vollenweider, 1969). Their use has led to numerous papers on primary productivity, and the topic may appear at times to be well worked. For macrophytes, however, this is deceptive. These two techniques were developed for phytoplankton, and are hard to apply directly to macrophytes, although Drew and Larkum (1968) chose $^{14}C$ methodology for *Udotea* in the field, and Borowitzka and Larkum (1977) used it in a laboratory measure of photosynthesis with detached branches of *Halimeda*. The coenocytic nature of the algae involved could present special problems which are not discussed in these papers. The technique of flow-respirometry, which is also used, as mentioned earlier, generally provides a measure of community rather than population productivity, and is restricted to regions where there is significant water flow in one direction for a meaningful length of time. It is of limited use for most macrophytes except for calcareous Rhodophyta of the reef algal ridge.

A few attempts have been made to apply gas exchange techniques to individual plants, or to bits of reef or sand surface, by enclosing these in plastic bags, jars or acrylic hemispheres (Sargent and Austin,

1954; Odum and Odum, 1955; Odum, 1957; Wells, 1977), the most elaborate being that of Wells. But none of these attempts have been directed to *Halimeda* or, indeed, to other large tropical macrophytes. They have measured gas exchange in encrusting or micro-communities of sand only. Johnston (1969) cut fresh discs from the non-calcareous siphonaceous alga *Caulerpa* in the field and measured the productivity of these discs by the standard light and dark bottle technique. Both

FIG. 81. Apparatus for measuring productivity of macrophytes growing in laboratory aquaria, by monitoring changes in oxygen production occurring within the aquarium over 36 hours or more. The aquarium with established, growing, clean plants is filled with water, and sealed with a thick plexiglass lid machined to fit, which in addition is held firmly in place by an O-ring seal and turnbuckles. The lid is designed with a number of entrance ports. A peristaltic pump, left front, maintains a water flow of approximately 0·3 m $s^{-1}$ past the oxygen probe. Other equipment items of the system are an oxygen meter (top right) and recorder (top left). The aquarium in the photograph contains 40 *Penicillus capitatus* thalli, but production in *Halimeda* was measured in the same way.

Marsh (1970) and Hillis-Colinvaux (1974) established populations in aquaria which could then be converted into closed circulating-water systems (Fig. 81), with exchanges in oxygen production being monitored for a number of hours. Both authors manipulated environmental parameters to measure effects on photosynthesis, Marsh for calcareous red algae, and Hillis-Colinvaux for *Halimeda* and other calcareous

green algae. The extent of the measurements for the productivity of *Halimeda* and the other calcareous green macrophytes is therefore small.

### 1. *Productivity of* Halimeda *in laboratory culture*

Figure 81 illustrates the apparatus used for measuring the productivity of separate populations of *Halimeda*, *Thalassia* and *Penicillus* by gas exchange. Details of the method are given in Hillis-Colinvaux (1974), but essentially the procedure is to select tanks of healthy-looking plants that have been maintained in the laboratory for a period of one or more months, to attach the fitted lid and apparatus to their aquarium tank, to record oxygen tensions for the cycle of 12 hours light and 12 hours dark to which they have been accustomed, and to calibrate the oxygen probe with Winkler titrations at the beginning and end of each run. Halimedae used were all the sand-dwelling *incrassata* in populations of about a dozen individuals, each approximately 7 cm tall (excluding the holdfast). This population density of about 220 plants $m^{-2}$ is within the natural range for the species. Natural populations of 100 $m^{-2}$ are common, and densities of nearly 500 $m^{-2}$ are found in parts of the Glory Be reef (Section X). Energy provided was white light at intensities between 320 and 600 ft-c.

Under these conditions *H. incrassata* produced at the following rates:

| | |
|---|---|
| net production | 2·5 mg C per thallus per day, or 0·56 g C $m^{-2}$ $d^{-1}$ |
| gross production | 4·5 mg C per thallus per day, or 1·0 g C $m^{-2}$ $d^{-1}$. |

Several of the conditions of the laboratory measurements, however, suggest these estimates are conservative. The thalli, at 7 cm, were small, since many wild plants grow to 20 cm above the sand. This difference may, however, be somewhat offset by the fact that the lower portions of tall wild plants tend to be covered with epiphytes, or to have segments which are losing their green colour. Light intensities at noon in the shallow areas where this species attains high populations are much higher than those in our laboratory, and the plants are supplied with flowing tidal water instead of recirculating water.

Finally, it must be noted that laboratory measurements have not been applied to the Halimedae that attain the highest cover on reefs, the sprawling, rock-anchored forms like *opuntia*. On the Glory Be reef *opuntia* populations may attain a cover of 90%, more than four times

the cover of sand-dwelling forms like *incrassata*. The highest estimate for productivity of *Halimeda* populations given by Hillis-Colinvaux (1974) is arrived at by extrapolating the *incrassata* measurements to populations growing at the density of *opuntia* populations. By this procedure maximum productivities of 4·1 g C $m^{-2}$ $d^{-1}$ (gross) and 2·3 g C $m^{-2}$ $d^{-1}$ (net) are attained. These estimates for *opuntia* populations cannot as yet be confirmed in the laboratory because of the difficulty of maintaining the rock-attached forms of *Halimeda* in culture.

### 2. *Contribution of* Halimeda *to carbon production in reefs*

A rough estimate of the contribution of *Halimeda* to the carbon flux of an entire reef can be obtained by applying the above laboratory results on the productivity of individual *Halimeda* thalli to population data of the only reef for which we have a *Halimeda* census, the Glory Be reef on the north shore of Jamaica. Glory Be is the name given to a short section of the Jamaican fringing reef occupying a well-defined bay separated by headlands (Hillis-Colinvaux, 1972, 1974). The reef is described in Section X.A and illustrated in Figs 89–96. Percentage cover of *Halimeda*, by species, was estimated for each section of the reef from the shoreline to the region of the *Acropora palmata* corals and the buttresses. By using the cover data (Table XXI) and assuming that all species of *Halimeda* produce equally well regardless of depth or microhabitat, we can compute the contributions of the *Halimeda* populations to the total carbon flux of the reef.

Table XXI gives the results of applying the laboratory productivity data to the census of Glory Be reef. The total daily net production, from the region of the shallowest-growing Halimedae to the outer channel, an area of 9840 $m^2$, which supports 1 110 300 *Halimeda* plants (calculated from Tables XXI and XXXIII) is

$$2779 \text{ g C d}^{-1} \quad \text{or} \quad 1014 \text{ kg C yr}^{-1}$$

yielding a range of net productivities for the reef, where estimated *Halimeda* cover was 10% or higher, of

$$0{\cdot}31\text{–}2{\cdot}25 \text{ g C m}^{-2} \text{ d}^{-1} \quad \text{or} \quad 113\text{–}821 \text{ g C m}^{-2} \text{ yr}^{-1} \quad \text{(Table XXI).}$$

The lower figures of this range were at sites where plants other than *Halimeda* predominated, or where there was grazing by urchins or fish, with one of the lowest figures in dense stands of *Thalassia*. Total macrophyte productivity in these stands is, of course, very large. The vertical sides of coral rocks are excluded from the range given, because

TABLE XXI. CALCULATED PRIMARY PRODUCTIVITIES FOR THE GLORY BE REEF, NEAR OCHO RIOS, JAMAICA[a]

| *Region* | *Ecological notes* | *Approximate area* ($m^2$) | *Halimeda cover in June* (%) | *Halimeda productivity* ($gC\ m^{-2}\ d^{-1}$) *Gross* | *Net* | *Halimeda productivity estimated for region* ($gC\ d^{-1}$) *Gross* | *Net* |
|---|---|---|---|---|---|---|---|
| Tidal sandy beach | — | — | 0 | 0 | 0 | 0 | 0 |
| *opuntia* rocks | | | | | | | |
| 3–6 m out | Population appears physically limited | 22 | 5 | 0·23 | 0·13 | 5 | 3 |
| 6–8 m out | — | 15 | 90 | 4·05 | 2·25 | 61 | 34 |
| *Thalassia* beds in shore reef | — | 58·3 | 15 | 0·68 | 0·38 | 40 | 22 |
| Inshore reef flat | — | 555 | 35 | 1·58 | 0·88 | 877 | 488 |
| rock sides and outcrops of lagoon | Urchin density 12 $m^{-2}$ | 733 | 1 | 0·05 | 0·03 | 37 | 22 |
| Lagoon sands | — | 2290 | 5 | 0·23 | 0·13 | 528 | 298 |
| Reef flat: *Zoanthus* zone | Urchin density 12 $m^{-2}$ | 6167 | 12·5 | 0·56 | 0·31 | 3454 | 1912 |
| Moat | Urchin density 6–20 $m^{-2}$ | — | 2·5 | 0·11 | 0·06 | — | — |
| Total to outer channel | | 9840 | | | | 5002 | 2779 |

[a]Modified from Hillis-Colinvaux (1974).

the Halimedae were essentially absent, probably because of grazing pressures. Outcrops of the back-reef and the moat of the reef crest (which contained much wave-stirred sand) are also excluded.

In Table XXII these results are compared with data for phytoplankton productivity supplied by Ryther (1969). The highest figure Ryther cites, that for upwellings, is about one-third of the performance of dense stands of *Halimeda* in a coral reef. Even where *Halimeda* plants are thinly spaced in *Thalassia* beds their contribution to productivity is still better than that of phytoplankton of typical coastal waters. Even the average productivity of the Halimedae of the Glory Be reef is equal

TABLE XXII. COMPARISON OF NET PRODUCTIVITY OF *Halimeda* POPULATIONS WITH PHYTOPLANKTON PRODUCTION

| *Population* | $gC\ m^{-2}\ yr^{-1}$ |
|---|---|
| Phytoplankton[a] | |
| Coastal | 100 |
| Upwellings | 300 |
| Mean ocean | 50 |
| *Halimeda* populations[b] | |
| Low density in *Thalassia* beds | 139 |
| Low density in algal communities | 321 |
| High density | 821 |
| Mean of Glory Be reef | 190 |

[a] Data from Ryther (1969).
[b] Data from Table XXI.

to phytoplankton production in coastal waters, in spite of the fact that large areas of reef are denied to *Halimeda* by grazing animals, living corals and the surf.

The contribution of fixed carbon to a reef by *Halimeda*, therefore, may be very high, and the primary productivity of a tropical area or coral reef, taken as a mosaic of fleshy algae, calcareous algae, sea grasses and photosynthetic corals, may be of the same approximate order of magnitude as the most productive of Mann's (1972) *Laminaria* forests in Nova Scotia. Accounts of the productivity of tropical waters should include the high values encountered in these latitudes, as well as the proverbial low ones, a point well made in the comparative study of productivities of Antarctic and tropical–subtropical regions by El-Sayed and Turner (1977), and the significant contribution of benthic algae should not be ignored as is done so frequently. Coral reefs occupy about

0·2% of the unproductive world ocean (calculation based on reef area information in Smith (1978)), or about twice the space Ryther (1969) assigned to regions of upwelling. Since Ryther was able to show that upwelled areas produce about half the world's fish supply (he did not specifically include coral reefs in his calculations), the primary productivity of tropical reefs, to which *Halimeda* contributes significantly, is an important world resource.

### 3. Halimeda *productivity compared with other reef production*

In Table XXIII the *Halimeda* estimates are compared with other reef productivity data. *Halimeda* productivity appears to be of the same order of magnitude as that of *Thalassia* and species of intertidal Cyanophyta. The discrepancy with *Caulerpa* may be accounted for, at least partly, by differences in technique, particularly the cutting of discs from the siphonaceous *Caulerpa* thallus which would inevitably produce some loss and disruption of filament contents. More extensive comparisons must be made with caution since the data have been obtained by a variety of procedures, including different light intensities, and the impact of light intensity has not been fully evaluated. They have not been extrapolated to an annual basis because the pertinent standing crop data are sparse.

Except where there are extensive beds of *Thalassia*, *Halimeda* is usually one of the most obvious plants in a coral reef or atoll. In spite of the roughness of the data in Table XXIII, if seems apparent that *Halimeda* may well be as productive as other primary producers in the reef. Some of the estimates for whole-reef metabolism of parts of the reef where there are few to no *Halimeda*, like those of Odum and Odum (1955), appear larger than the estimate for *Halimeda* based on laboratory culture, but there seems good reason to believe that the *Halimeda* estimates are conservative. It must be of interest to obtain direct measures of the productivity of Halimedae as they grow on reefs.

It remains true that the Glory Be reef is the only reef for which we have a *Halimeda* census, and that on a solitary occasion. For no reef have we recurrent census descriptions of the standing crops of *Halimeda* at different times of the year. And there are apparently no measurements at all on the production of wild populations of *Halimeda* by gas exchange, cropping or incremental harvest. Until these measurements are made it will not be possible to state accurately the contribution of *Halimeda* to the remarkably high productivity of coral reefs. If the productivity of *Halimeda* in the wild is as high as these provisional data suggest, however, there must be interesting questions to be asked about

TABLE XXIII. PRIMARY PRODUCTIVITIES OF TROPICAL REEF ORGANISMS AND COMMUNITIES[a]

| *Organism or community* | *Productivity* ($gC\ m^{-2}\ d^{-1}$) *Gross* | *Net* | *Reference* |
|---|---|---|---|
| *Thalassia* populations | 10·6 | — | Odum (1957) |
| | — | 3·8 | Westlake (1963) |
| | — | 5·8 | Qasim and Bhattathiri (1971) |
| Algal ridge, *Porolithon* | 1·5 | 0·66 | Marsh (1970) |
| Cyanophyta, intertidal | — | 0·65–2·15 | Bakus (1967) |
| Caulerpales | | | |
| *Caulerpa* | — | 0·07 | Johnston (1969) |
| *Udotea petiolata* | — | 0·1 | Drew and Larkum (1968) |
| *Halimeda, opuntia* rock with *c.* 90% cover | 4·1 | 2·3 | Hillis-Colinvaux (1974) |
| *Halimeda, c.* 15% cover in *Thalassia* beds | 0·68 | 0·38 | Hillis-Colinvaux (1974) |
| Reef corals | | | |
| Gorgonacea, four genera | 3·7–6·8 | — | Kanwisher and Wainwright (1967) |
| Scleractinia, ten genera | 2·7–10·2 | — | Kanwisher and Wainwright (1967) |
| Coral reef community | 4·1 | — | Sargent and Austin (1954) |
| | 9·6 | — | Odum and Odum (1955) |
| | 8·0 | — | Kohn and Helfrich (1957) |
| Microflora, tropical sediments | — | 0·02–0·22 | Bunt *et al.* (1972) |
| Plankton, tropical oceanic | 0·18 | 0·11 | Beers *et al.* (1968) |

[a] Modified from Hillis-Colinvaux (1974).

its nutrient supplies and its role in maintaining the nutrient cycles of a reef system.

### B. *Carbonate production*

*Halimeda* is a producer, not only of reduced carbon, but also of loose carbonate sediment, and it has become clear that unconsolidated sediments are more important to the building of a reef than the carbonate incorporated into the reef framework (Milliman, 1974). Stoddart (1969) estimates that four to five times more loose sediment is produced than is incorporated as reef framework. This loose sediment is produced by Foraminifera, by the large benthic animals of the reef system like molluscs and some echinoderms, as accretionary deposits on the blades of sea grasses, and by the green calcareous algae, the most abundant and widespread of which are Halimedae.

There seems some uncertainty in the minds of students of coral reefs over the relative importance of *Halimeda* segments to the total flux of loose sediments into a reef. The subject is naturally approached from the point of view that coral reefs are just what they are called, "reefs made of coral", which is to say that they are animal creations. Furthermore, a visit to a reef reveals corals in abundance but, unless you dive and hunt, no obvious green plants. As we noted earlier, the transect at Enewetak studied by the Odums and the SYMBIOS group (Johannes *et al.*, 1972) contains few to no Halimedae or other large green algae. Apart from the borers and the symbionts, the main evidence of plant life is given by the encrusting red algae of the fore-reef where the waves break. But these red algae are properly regarded as part of that reef framework that contributes only a quarter of the reef mass (Stoddart, 1969).

#### 1. Halimeda *as one of the principal contributors to atoll mass*

The classic borings at Funafuti (Hinde, 1904; Judd, 1904) provided the first evidence that the actual mass of a coral atoll (and hence perhaps of all coral reefs) might not be made of the visible corals and red algae of the reef ridge itself, and these borings implicated *Halimeda*. In the boring through the floor of the lagoon the first 20 m of sediment was between 80% and 95% recognizable *Halimeda* segments (Fig. 82). Similar conclusions were reached for the unconsolidated lagoon deposits at Bikini, Enewetak and other atolls of the Marshall Islands by Emery *et al.* (1954) (Fig. 83). Table XXIV shows similar results from a number of lagoons collected by Milliman (1974). It seems clear that *Halimeda* segments are a major constituent of many lagoon deposits. Table XXV

FIG. 82. Cross-section of Funafuti Atoll, Ellice Islands, showing some of the results of the cores raised by the Coral Reef Committee of the Royal Society (1904). *Halimeda* segments were the chief constituent for the first 60 feet below the lagoon floor. They also were the predominant component of the main boring between 652–660 feet, but this depth is not included. (From Ginsburg *et al.* (1963), original data from Judd (1904) and Hinde (1904); reproduced with permission.)

extends the data to various forms of peripheral reef, where *Halimeda* segments can collect in channels, lagoons and behind sills.

At Funafuti the *Halimeda*-rich stratum of unconsolidated sediment ended with an unconformity which was almost certainly the subaerial exposure surface which had been weathered during the last eustatic lowering of sea-level. In the lower parts of this boring, under the unconformity, only one-third of the recognizable parts were *Halimeda*, the other two-thirds being foraminiferans (Fig. 82).

If we accept the Funafuti, Bikini and Enewetak results as correct in suggesting that lagoonal accretions of sediment are likely to be very largely *Halimeda* segments, then it is reasonable to postulate that the ultimate origin of the mass of an atoll depends on the relative rates of accretion on the lagoon floor and along the reef ridges. We may write:

$$A_m = (H_s L + R_v R_h)\, t$$

where $A_m$ is the atoll mass, $H_s$ is the deposition of *Halimeda* segments

FIG. 83. The distribution of *Halimeda* sediments, compared to other major sediments, in the lagoon of Enewetak. Lines of equal abundance are drawn through the 25, 50 and 75% values. The lower two figures give the cumulative percentages of the six categories of sediments recognized along the transect $AA'$, and a profile of the lagoon bottom from $A$ to $A'$ showing some of pinnacles. (From Emery *et al.* (1954), reproduced with permission.)

per unit area, $L$ is the area of lagoon, $R_v$ and $R_h$ are the vertical and horizontal components of the growth of the reef ridge, $t$ is the time.

Both the lagoonal and reef-ridge contributions to the atoll mass must be functions of the history of sea-level and perhaps of other

TABLE XXIV. AVERAGE SKELETAL COMPOSITION OF SAND-SIZE COMPONENTS OF SOME LAGOONAL SEDIMENTS[a]

| *Source of lagoonal sediment* | Halimeda | *Calcareous red algae* | *Coral* | *Mollusca* | *Foraminifera* | *Other* |
|---|---|---|---|---|---|---|
| Caribbean Reefs | | | | | | |
| Florida | 38 | 3 | 7 | 18 | 7 | 7 |
| Alacran | 23 | 5 | 15 | 7 | 7 | 2 |
| Hogsty | 1 | 1 | 4 | 10 | 4 | 1 |
| Courtown Cays | 28 | 21 | 28 | 12 | 6 | 1 |
| Albuquerque Cays | 31 | 14 | 20 | 12 | 6 | 3 |
| Roncador Bank | 37 | 12 | 22 | 12 | 5 | — |
| Serrana Bank, east | 61 | 4 | 9 | 7 | 5 | 1 |
| Serrana Bank, west | 13 | 1 | 8 | 10 | 3 | 1 |
| Pacific Reefs | | | | | | |
| Funafuti | 77 | Tr. | Tr. | Tr. | 21 | Tr. |
| Bikini | 57 | — | 17 | 9 | 15 | 1 |
| Enewetak | 35 | — | 42 | 8 | 14 | — |
| Johnson Island | 1 | 61 | 24 | 12 | 2 | — |
| Cocos (Guam) | 17 | 18 | 45 | 18 | 2 | — |
| Raroia | Tr. | Tr. | 43 | Tr. | 28 | — |
| Ifaluk | 32 | 6 | 15 | — | 29 | 15 |
| Midway | 7 | 31 | 18 | 15 | 19 | 10 |
| Kure | 4 | 42 | 18 | 10 | 18 | 8 |
| Pearl and Hermes | ←48→ | | 17 | 18 | 6 | — |

[a] Adapted from Milliman (1974). Figures are percentage skeletal components in total sediment.
Tr., trace.

processes in the growth of reefs of which we may not be fully aware. Each lowering of sea-level by eustacy would be expected to eliminate the lagoonal (largely *Halimeda*) contribution to the atoll mass in circumstances where at least the horizontal component of reef growth may continue, even if attenuated. Each eustatic lowering also affords an opportunity for the exposed reef ridge to be weathered and deposited on the *Halimeda* matrix of the old lagoon floors. Thus a history of eustacy will alternately favour the deposition of *Halimeda* and non-*Halimeda* sediments into the atoll mass. Added to this time-variant function must be the effects of different rates in the growth of the reef ridges themselves.

Coral matrix is formed by the vertical growth of the reef ridge which accompanies changes in relative sea-level associated with both eustacy and isostacy, by the horizontal growth of the reef ridge and by the

TABLE XXV. AVERAGE SKELETAL COMPOSITION OF SAND-SIZE COMPONENTS OF SOME PERIPHERAL REEF SEDIMENTS

| *Source of peripheral sediment* | Halimeda | *Calcareous red algae* | *Coral* | *Mollusca* | *Foraminifera* | *Other* |
|---|---|---|---|---|---|---|
| Caribbean Reefs | | | | | | |
| Florida | 30 | 10 | 20 | 12 | 6 | 7 |
| Alacran | 40 | 11 | 26 | 7 | 8 | 1 |
| Andros | 17 | 33 | 24 | 6 | 12 | 6 |
| Hogsty | 2 | 19 | 27 | 22 | 5 | 1 |
| Courtown Cays | 28 | 21 | 35 | 10 | 3 | — |
| Albuquerque Cays | 32 | 21 | 30 | 9 | 2 | 1 |
| Pacific Reefs | | | | | | |
| Ifaluk | 10 | 23 | 36 | — | 23 | 9 |
| Midway | 6 | 35 | 25 | 12 | 14 | 8 |
| Kure | 2 | 52 | 15 | 12 | 10 | 9 |
| Great Barrier | 10–30 | 17–40 | 20–40 | 4–15 | 8–20 | 5 |
| Inter-reef | 5–10 | 0–15 | 5–65 | 15–40 | 20–35 | 5–30 |

[a] Adapted from Milliman (1974) and Orme (1977). Figures are percentage skeletal components in total sediments.

growth of coral pinnacles from the lagoon floor. A scheme describing the mutual influences of these accretion processes on the final composition of the atoll mass is given in Fig. 84.

The mutual dependency among these various processes is clear. Low sea-level will be a time of very low contribution of *Halimeda* to the atoll mass because of the extinction of the lagoon. It will also be a time of relatively low coral contribution because the pinnacles will be extinguished. In times when there is little eustatic fluctuation the contribution of *Halimeda* segments into the lagoon may be relatively large, perhaps being the dominant process. But the increase of atoll mass by the *Halimeda* segments must have an isostatic effect, thus increasing the possibilities for growth of the reef ridge and the pinnacles.

The history of the atoll fabric may be investigated by drilling, and the fabric revealed by drill cores from any part of the structure must reflect recurrent local changes, as the site may have fluctuated from pinnacle to lagoon and the sea-level may have been high or low. There is likely to be a bias, however, in the record since most borings are from on the reef ridges or near them. And there may be a difficulty in reconstructing the actual origin of the reef fabric being examined due to the changes which have taken place during diagenesis, cementation or

FIG. 84. Scheme showing influences of accretion processes on the final composition of atoll mass.

consolidation. In particular, it is worth noting that most of the Foraminifera contributing to reef structures have calcite skeletons which may well survive diagenetic processes better than the aragonite of *Halimeda* or corals.

Table XXVI describes some of the results from 3 of the 42 drill cores from the Enewetak Atoll recently raised by Couch *et al.* (1975). The core from Cactus Crater was chosen from this suite because it was near the outer edge of the reef, taken under 10 m of water in the crater left by an atom bomb exploded on the outer reef flat. The second core from the same island (Runit) was chosen as being the longest core from the middle of the island. The general sites of both these cores are shown in Figs 85 and 97. The core from Engebi was chosen merely on the basis of length. No examination of the matrices of the 42 cores was made in choosing these three data sets.

In Table XXVI the Enewetak core log data are abstracted at arbitrary intervals of 5 m. The data are estimates by eye of the percentage composition of the various constituents of the core sections by volume. Names are given, therefore, only to what is well and clearly preserved. Both *Halimeda* and coral fragments are common, and fluctuate up and down the cores. Foraminifera occasionally predominate, but are usually of less importance than both *Halimeda* segments and coral fragments. As would be expected from the method of analysis,

TABLE XXVI. LOG DATA FROM THREE BOREHOLES AT ENEWETAK[a]

| *Depth (m)* | Halimeda | *Coral* | *Foraminifera* | *Red algae* | *Echinoderms* | *Mollusca* | *Unidentified* |
|---|---|---|---|---|---|---|---|
| HOLE XC-1. RUNIT IN CACTUS CRATER | | | | | | | |
| 15 | 5 | 20 | 10 | Tr. | Tr. | — | 60 |
| 20 | 10 | 20 | 5 | Tr. | Tr. | Tr. | 60 |
| 25 | 10 | 20 | 5 | Tr. | Tr. | Tr. | 60 |
| 30 | 5 | 20 | Tr. | Tr. | Tr. | Tr. | 60 |
| 35 | 10 | 10 | Tr. | Tr. | Tr. | — | 85 |
| 40 | 5 | 10 | Tr. | Tr. | — | — | 80 |
| 45 | Tr. | 15 | Tr. | — | — | — | 60 |
| HOLE XRU-2a. RUNIT ON LAND | | | | | | | |
| 5 | Tr. | 15 | 5 | 10 | — | Tr. | 70 |
| 10 | 5 | 50 | Tr. | Tr. | Tr. | Tr. | 30 |
| 15 | 5 | 5 | 5 | 20 | Tr. | Tr. | 55 |
| 20 | 15 | 10 | 5 | 10 | Tr. | Tr. | 55 |
| 25 | 40 | 5 | Tr. | 5 | Tr. | Tr. | 40 |
| 30 | Tr. | 5 | 10 | Tr. | — | Tr. | 80 |
| 35 | Tr. | Tr. | Tr. | Tr. | — | Tr. | 90 |
| 40 | 15 | 50 | 15 | Tr. | — | Tr. | 15 |
| 45 | 15 | 50 | 15 | Tr. | — | Tr. | 15 |
| HOLE XEN-G. ENGEBI ON LAND | | | | | | | |
| 10 | 5 | 20 | 55 | — | — | — | 15 |
| 15 | 10 | 20 | 20 | — | — | Tr. | 30 |
| 20 | 50 | 20 | 10 | 5 | Tr. | Tr. | 15 |
| 25 | 40 | 30 | 10 | 10 | — | Tr. | 10 |
| 30 | 30 | 30 | 10 | 5 | Tr. | 5 | 15 |
| 35 | 30 | 30 | 10 | 5 | Tr. | 5 | 15 |
| 40 | Tr. | 50 | — | — | — | 5 | 40 |
| 45 | — | 95 | — | — | — | — | 5 |
| 50 | 30 | 50 | — | 5 | — | — | 15 |
| 55 | 5 | 40 | 5 | — | Tr. | Tr. | 40 |
| 60 | 10 | 40 | 20 | — | — | Tr. | 30 |
| 65 | 10 | 50 | — | — | Tr. | Tr. | 40 |

[a] Data are culled from the drill logs given by Couch *et al.* (1975), and have been taken at arbitrary intervals of 5 m. The original data are estimates by eye of the percentage of each constituent by volume (the percentages are approximate and have not been rounded to add up to 100). For location of Islets see Fig. 97.
Tr., trace.

the largest constituent consists of unidentified fragments. It may be that there is enough information in the complete data-set of the 42 cores to assign some part of the unidentified fraction to one of the other

FIG. 85. (Top) Air photograph of Runit Islet showing two atom bomb craters in the reef, with LACROSSE in foreground (approximately 115 m horizontal diameter) and CACTUS behind it. The lagoon is in the background. (Bottom) A grove of *H. incrassata* thalli in the centre of CACTUS crater, at − 11 m. Diameter of broader segments is approximately 7 mm.

classes, but the data in their present state are sufficient to suggest strongly that *Halimeda* contributes to the mass of a coral atoll to a significant extent compared with the coral contribution. And this observation comes from cores taken on islets or the reef ridge, not in the lagoon where the contribution of *Halimeda* would be largest.

The evidence of drill cores, therefore, is that a significant part of the mass of coral atolls is made of the segments of this one green alga, *Halimeda*. Much of the work of maintaining the atoll habitat is done by these plant populations, and the solar energy flux they transduce not only fuels food chains but also contributes to the structure of the ecosystem in a way that may be necessary to the system's homeostasis.

### 2. *The shedding of segments and the segment fates*

The aged, white, yellowish or greyish segments commonly are shed from the apical portions of a *Halimeda* thallus by a natural separation from the node, rather like a tree leaf being shed in the autumn. In sprawlers such as *macrophysa* and *opuntia* they also may be lost basally (Hillis-Colinvaux, 1977; Section VI).

Segments are also lost basally and deposited *in situ* when lower portions of a thallus are buried.

Initially much of the material contributed to the reef environment may be entire segments, but the segments of a few species such as *macrophysa* and *favulosa* are delicate, and sometimes may not be shed intact. It is noteworthy that these two species have the largest utricles (Hillis, 1959; Section III, IV), that in *macrophysa* the utricles do not adhere laterally, and in *favulosa* they are attached only lightly.

Segments of some of the rock growers-sprawlers, when shed, may shift deeper into the rock crevices in which the living thallus is cloistered. The species *macrophysa* is a good example, *opuntia* somewhat less so. Most commonly, however, the segments floor some surface in the immediate vicinity, from whence they may be transported by the currents to other sites, or they may be transported directly. The pattern of movement will depend both on their weight (branches may be involved initially as well as segments) and on the strength of the currents. Their transport out of the region may be slowed by the growth of blue-green algal mats over them (Figs 102, 103), or by various gelatinous materials within the sediments (Moore *et al.*, 1976).

At Enewetak (Fig. 83) some of the lagoonal sediments may have originated on the fore-reef, and some lagoonally derived *Halimeda* material may be transported through the passes in the reef to outer areas. Such movements may be somewhat seasonally controlled, since

both the amounts of *Halimeda* segments shed and the types of currents may have seasonal components. At the Enewetak sites I visited, the commonest species were *macrophysa*, *opuntia*, *cylindracea*, *gigas*, *distorta*, *copiosa* and *lacunalis* f. *lata*. These, then, are the species, about half the total number found on the atoll reef, which would contribute most of the *Halimeda* sediments (Hillis-Colinvaux, 1977), but it is likely that two or three from this short list produce the bulk of the Enewetak sediments. *Tydemania expeditionis*, the only other calcareous green alga present at Enewetak in sizeable populations (Gilmartin, 1960, 1966;

FIG. 86. Composition of sand-sized sediment from the fore-reef slope (−15 m to −55 m) and island slope (−123 m to −308 m) of Discovery Bay, Jamaica. Graph bars from top to bottom represent *Halimeda*, calcareous red algae, corals, molluscs, foraminifera and "other". (Data from Moore *et al.*, 1976.)

Hillis-Colinvaux, 1977), also contributes to the sediments but not in an easily recognizable form.

In Jamaica most of the *Halimeda* sediments derived from the shallower parts of the reef, that is, from the back-reef, reef crest and fore-reef to about −55 m, are dammed by sill reefs at the base of the fore-reef slope (Goreau and Goreau, 1973; Goreau and Land, 1974; Moore *et al.*, 1976). The contribution of the genus to identifiable sediments of the island slope (depth approximately −122 m to −305 m) is at least as great (Fig. 86). In the suite of samples available for analysis

from the island slope approximately 50% of the *Halimeda* material was identified as *cryptica*, 34% as *goreauii*, 7% as *copiosa* and 5% as *gracilis*. The deep fore-reef is a likely source for most of the *cryptica* (Moore *et al.*, 1976) which is the most prominent species of this part of the reef (Fig. 86), but some may have been derived from the fore-reef, as *goreauii* and *gracilis* would appear to be, since *cryptica* grows in this region also (Colinvaux and Graham, 1964).

The fate of segments in the sediments varies. That many of them remain essentially entire or in sizeable pieces for some time is demonstrated in numerous samples of loose sediments, or in the whole segments that frequently floor the immediate vicinity of a grove of Halimedae. Eventually, by processes of disintegration, cementation and recrystallization, they may be bound, together with other reef organisms, into carbonate rock such as that described from the Marshall Islands (Emery *et al.*, 1954) or the *Halimeda*-rich packstones and grainstones surrounding the Discovery Bay Canyon of Jamaica (Moore *et al.*, 1976). They also may be weathered into carbonate muds early in their history, as on some of the Bahaman Banks where Neumann and Land (1975) report that calcareous green algae have produced 1·5–3 times the mass of aragonitic mud and *Halimeda* sand now in the 7 m deep Bight of Abaco.

A significant portion of the disintegration of *Halimeda* segments may result from the activities of sediment-feeders such as holothurians and echinoids, while living segments may be processed *in situ* by grazers. Grazing activity will decrease the quantity of recognizable sediments and affect the qualitative results of sediment determinations.

### 3. *Comparative calcium uptake by* Halimeda *and other reef organisms*

Goreau (1963) estimated rates of calcium uptake attained by many reef organisms over short periods. His methods were to place fresh and healthy terminal growing portions in light and dark bottles, to inoculate the bottles with $^{45}Ca$, and to leave them on the reef in 1–2 m of water for $1\frac{1}{2}$–$2\frac{1}{2}$ hours, ending in the full sunlight of noon. To be able to compare rates of calcium uptake between animals and plants of very different form he expressed all results in terms of nitrogen, determined on the same samples. When considering Goreau's results it must be remembered that the disturbance to the organism represented by the incubation procedure was very different from taxon to taxon, the light intensity being appropriate to the usual ambient conditions for some species but not for others, and so on. The data are of great interest,

TABLE XXVII. CALCIUM UPTAKE BY *Halimeda* IN LIGHT AND DARK[a]

| | *Light* | | *Dark* | | *Light : dark ratio of means* | |
|---|---|---|---|---|---|---|
| *Species* | *Calcium uptake* ($\mu gCa\ mgN^{-1}\ h^{-1}$) | *Skeletal growth* (% *increment* $h^{-1}$) | *Calcium uptake* ($\mu gCa\ mgN^{-1}\ h^{-1}$) | *Skeletal growth* (% increment $h^{-1}$) | *Calcium uptake* | *Skeletal growth* |
| *incrassata* | 870 ± 119·6 (5) | 3·7 ± 0·412 (5) | 1197 ± 153·7 (5) | 5·19 ± 0·620 (5) | 0·73 | 0·71 |
| *monile* | 431 ± 307·8 (5) | 1·37 ± 0·244 (5) | 281 ± 263·9 (5) | 1·01 ± 0·600 (5) | 1·53 | 1·36 |
| *opuntia* | 365 ± 58·4 (5) | 0·89 ± 0·223 (5) | 517 ± 562·6 (8) | 0·64 ± 0·424 (8) | 0·71 | 1·35 |
| *tuna* | 310 ± 234·4 (10) | 1·36 ± 1·26 (10) | 359 ± 467·8 (7) | 1·9 ± 2·55 (7) | 0·86 | 0·71 |
| *goreauii* | 277 ± 40·4 | 0·33 ± 0·055 (4) | 151 ± 39·8 (5) | 0·20 ± 0·055 (5) | 1·83 | 1·64 |
| *discoidea* v. *platyloba* | 183 ± 121·8 (4) | 0·83 ± 0·374 (4) | 154·4 ± 37·10 (4) | 0·50 ± 0·100 (4) | 1·19 | 1·66 |
| *gracilis* v. *opuntioides* | 130 ± 15·6 (3) | 0·28 ± 0·141 (3) | 158·0 ± 82·1 (3) | 0·18 ± 0·032 (3) | 0·82 | 1·53 |
| *simulans* | 108 ± 23·5 (4) | 0·37 ± 0·141 (4) | 72·1 ± 14·63 (5) | 0·13 ± 0·045 (5) | 1·50 | 2·84 |

[a] From Goreau (1963). Rates are means ± standard deviation. Numbers of experiments are in parentheses.

however, for the revelation that rates are remarkably similar throughout generic taxa, and for suggesting that rates of deposition in algae and in corals are greater in the light, and therefore may be associated with photosynthesis.

Table XXVII gives Goreau's results for the species of Halimedae he used and Table XXVIII for some hermatypic corals. The difference in the light : dark ratios of calcium uptake between the two groups is very

TABLE XXVIII. RATES OF CALCIUM UPTAKE AND ACCRETION IN HERMATYPIC CORALS[a]

| | *Light* | | *Dark* | | *L : D Ratios* | |
|---|---|---|---|---|---|---|
| *Coral sample* | *Uptake* | *Accretion* | *Uptake* | *Accretion* | *Uptake* | *Accretion* |
| *Acropora cervicornis*; | 118·48 | 0·280 | 47·9 | 0·060 | 2·47 | 4·67 |
| apical corallites; | 134·34 | 0·330 | 19·43 | 0·039 | 6·91 | 8·7 |
| (pooled samples) | 63·6 | 0·140 | 20·6 | 0·029 | 3·10 | 4·8 |
| | 106·2 | 0·272 | 18·4 | 0·04 | 5·8 | 6·8 |
| lateral corallites; | 77·26 | 0·102 | 13·03 | 0·019 | 4·9 | 5·4 |
| (pooled samples) | 78·42 | 0·089 | 10·16 | 0·011 | 7·7 | 8·1 |
| | 34·01 | 0·059 | 9·48 | 0·010 | 3·6 | 5·9 |
| | 64·3 | 0·102 | 4·90 | 0·017 | 13·1 | 6·0 |
| | 60·7 | 0·091 | — | — | — | — |
| | 42·2 | 0·066 | — | — | — | — |
| *Millepora complanata*; | 86·6 | 0·026 | 65·2 | 0·014 | 1·3 | 1·9 |
| terminal cm only; | 77·3 | — | 34·4 | — | 2·3 | — |
| (pooled samples) | 60·3 | — | 15·2 | — | 4·0 | — |
| *Porites furcata*; terminal cm only; (pooled samples) | 26·7 | 0·028 | 5·6 | 0·008 | 4·8 | 3·5 |

[a]From Goreau (1963). Uptake in $\mu gCa\ mgN^{-1}\ h^{-1}$, accretion in percentage increment $h^{-1}$.

apparent. Figure 87 illustrates Goreau's conclusion that there is a close affinity between the members of a plant taxon in the calcium uptake rate.

Calcium is present within the *Halimeda* segment not only as aragonite, but also in the cytoplasm, filament wall and spaces of the segment. Measurement of calcium uptake, therefore, is more than a measure of rate of calcification, and the variations obtained in calcium uptake rates with different labelling and washing times (Table XXIX) are partly a consequence of these different locations within the plant. Rate of calcium uptake also would be expected to vary with the environmental conditions of the experiment, and the physiological condition of the segment and plant.

TABLE XXIX. INFLUENCE OF LENGTH OF LABELLING AND WASHING PROCEDURES ON THE UPTAKE OF CALCIUM – 45 BY *Halimeda*[a]

| *Species* | *Calcium uptake (nmol min⁻¹ g⁻¹ dry wt)* *Light* | *Dark* | *Labelling time (h)* | *Washing time (min)* | *Reference* |
|---|---|---|---|---|---|
| *discoidea* | 55·8 ± 37·1 (4) | 57·1 ± 11·3 (4) | 1·5–2·5 | 120 | Goreau (1963) |
| *discoidea* | 178 | 145 | 12 | "Brief" | Stark *et al.* (1969) |
| *opuntia* | 111·3 ± 17·8 (5) | 157·6 ± 171·5 (8) | 1·5–2·5 | 120 | Goreau (1963) |
| *opuntia* | 347 | 145 | 12 | "Brief" | Stark *et al.* (1969) |
| *tuna* | 94·5 ± 71·4 (10) | 109·4 ± 142·6 (10) | 1·5–2·5 | 120 | Goreau (1963) |
| *tuna* | | | | | |
| (mean) | 459·9 ± 26·7 (59) | 241·9 ± 9·6 (48) | 2 | 1–2 | Borowitzka and Larkum (1976a) |
| (range) | (336·4–735·5) | (240·2–336·4) | — | — | Borowitzka and Larkum (1976a) |

[a] Data recalculation and compilation from Borowitzka and Larkum (1976a). Numbers of experiments are in parentheses.

FIG. 87. Linear relationship of calcium uptake within members of a taxon. The Chlorophyta are represented by 18 taxa, the Rhodophyta by 16. The overall linear relationship between the two functions is somewhat different in the two divisions of algae, as shown by the slopes of the regression lines. The curves were fitted by the least squares method. As the carbon accretion is related to tissue growth and the calcium accretion to skeletal growth, the slopes of the lines indicate that tissue growth rates in the Chlorophyta are proportional to the 0·3 power of the skeletal growth rate, whereas in the Rhodophyta the tissue growth rate is proportional to the 0·5 power of skeletogenesis. (From Goreau, 1963.)

It is probably unwise to attempt to convert Goreau's figures into carbonate productivities per segment, thallus or unit area. The nitrogen basis of the measurements is excellent for comparing rates of uptake at the apex in vigorously growing specimens over short time intervals, but it does not follow that estimates of nitrogen in whole plants will let these data yield carbonate fluxes from senile plants. It is noted in Table XXX that segments are at their heaviest at senescence. Calcium uptake may not be a linear function of segment age.

### 4. *Rate of segment production and the accumulation at Glory Be reef*

The contribution of *Halimeda* populations to the carbonate mass of a reef is a function of the rate at which segments are lost, the carbonate content of the segments at loss and the destruction of carbonate between loss from the *Halimeda* and incorporation into the sediment. Losses of carbonate from shed segments are by such processes as destruction by detritus-feeding animals (in which event the net carbonate accumulation may not be altered) and solution. These carbonate

TABLE XXX. ARAGONITE CONTENT OF *Halimeda*, BY AGE AND SPECIES[a]

| *Species* | *Description of material* | *Sample size (No. of segments)* | *$CaCO_3$ per segment (mg)* | *% $CaCO_3$ dry wt per sample* |
|---|---|---|---|---|
| *incrassata* | Eight small young thalli; pale olive colour | 1051 | 2·2 | 57·5 |
| *incrassata* | (a) Apical[b] and subapical segments ( = segments 1 and 2); dark yellow-green | 110 | 1·4 | 66·3 |
| | (b) Segments 3–5 from apex; dark yellow-green | 83 | 2·3 | 71·0 |
| | (c) Segments 6–10 from apex; yellow-green | 43 | 3·6 | 70·1 |
| | (d) Basal segment; pale red-green, average length × width × thickness = 1 × 0·5 × 0·2 cm | 5 | 13·3 | 59·2 |
| | (e) Entire thallus | 241 | 2·3 | 67·9 |
| *incrassata* | Basal segment; light yellow-green, 0·5 × 0·7 × 0·15 cm | 1 | 3·0 | 69·4 |
| *incrassata* | (a) Segments 1 and 2; light yellow-green | 96 | 1·7 | 60·6 |
| | (b) Segments 3–5; light yellow green | 61 | 2·3 | 61·6 |
| | (c) Segments 6–10; pale yellow | 19 | 2·9 | 56·1 |
| | (d) Entire thallus | 176 | 2·1 | 59·0 |
| *incrassata* | Light yellow-green plant | 98 | 1·4 | 56·1 |
| *incrassata* | Dark yellow-green plant | 45 | 3·1 | 58·5 |
| *incrassata* | Light yellow-green plant | 98 | 1·8 | 47·3 |
| *incrassata* | Light yellow-green plant | 102 | 1·7 | 56·2 |
| *incrassata* | Light yellow-green plant | 148 | 2·4 | 52·2 |
| *incrassata* | Plant recently fertile and segments white | 210 | 2·3 | 55·6 |
| *incrassata* | Plant recently fertile and segments white | 112 | 4·2 | 64·3 |
| *incrassata* | Plant recently fertile and segments white | 98 | 2·5 | 67·1 |
| *incrassata* | *Segments white and loose*, would readily be removed from plant by currents; not basal | 763 | 2·5 | 77·8 |
| *incrassata* | Segments white and *fallen* from plant | 299 | 4·0 | 83·0 |
| *discoidea* | (a) Segments 1 and 2; light yellow-green | 22 | 9·2 | 57·6 |
| | (b) Third segment from apex; light yellow-green | 10 | 18·2 | 70·7 |
| | (c) Fourth segment from apex; light yellow-green | 14 | 14·0 | 74·1 |
| | (d) Basal segments; pale olive, 1·5 × 1·0 × 0·1 cm | 2 | 7·8 | 65·4 |
| | (e) Entire thallus; collected at 16 m depth | 48 | 15·4 | 66·5 |
| *discoidea* | (a) Apical segments; light yellow-green | 57 | 2·2 | 57·5 |
| | (b) Second segment; light yellow-green | 35 | 4·2 | 67·0 |

TABLE XXX (*cont.*)

| *Species* | *Description of material* | *Sample size (No. of segments)* | *$CaCO_3$ per segment (mg)* | *% $CaCO_3$ dry wt per sample* |
|---|---|---|---|---|
| | (c) Segments 3 and 4, light yellow-green | 27 | 6·2 | 64·8 |
| | (d) Segments 5, 6 and 7; light yellow-green | 15 | 10·4 | 68·2 |
| | (e) Basal segments; light yellow-green, 0·4 × 0·5 × 0·2 cm | 9 | 17·1 | 57·2 |
| | (f) Entire thallus; collected at 16 m depth | 143 | 5·2 | 62·8 |
| *discoidea*[c] | — | — | — | 47·8 ± 3·6 |
| *discoidea*[d] | — | — | — | 47·4 |
| *goreauii* | Pale yellow | 175 | 1·1 | 65·3 |
| *goreauii* | Pale yellow | 102 | 1·6 | 65·5 |
| *goreauii* | Pale yellow | 168 | 1·3 | 72·8 |
| *goreauii* | Pale yellow | 151 | 1·4 | 68·5 |
| *goreauii* | Pale yellow | 96 | 1·5 | 69·6 |
| *opuntia* | Reef top; outer green segments | 152 | 9·0 | 72·0 |
| *opuntia* | Reef top; lower whitish segments | 474 | 6·5 | 61·0 |
| *opuntia*[c] | — | — | — | 84·7 ± 2·05 |
| *opuntia*[d] | Basal | — | — | 80·7–89·6 |
| | Midway | — | — | 55·5–67·4 |
| | Apical segment | — | — | 27·6–46·4 |
| *cuneata*[d] | Basal[e] | — | — | 22·5 |
| | Midway[e] | — | — | 31·8 |
| | Apical[e] | — | — | 32·3 |
| *cuneata*[d] | Basal[e] | — | — | 21·8 |
| | Midway | — | — | 34·0 |
| | Apical | — | — | 33·0 |
| *gracilis*[d] | — | — | — | 74·3 |
| *macroloba*[f] | Mature thalli | 44 thalli | — | 74·3–80·7 |
| | Juvenile thalli | 28 thalli | — | 70·7–73·3 |
| *monile*[d] | — | — | — | 71·9 |
| *tuna*[g] | — | — | — | 59·7 |

[a] All data Hillis-Colinvaux (unpublished), except as below.
[b] All apical segments are older than 48 hours and hence are calcified (Section VI).
[c] Stark *et al.* (1969).
[d] Böhm (1973a).
[e] Analysed by X-ray diffraction.
[f] Merten (1971).
[g] Prat and Hamackova (1946).

losses to shed segments are hard to estimate and may not be significant in the initial stages of forming loose sediment. The production of shed segments can be estimated if we know the carbonate content of typical segments, the rate at which a single thallus sheds segments, and standing crop data. In this subsection the production of carbonate by the *Halimeda*

populations of the Glory Be reef is estimated from these three components of carbonate production.

(a) *Carbonate contents of* Halimeda *thalli.* Figures for the amount of calcium carbonate in *Halimeda* thalli are given in Table XXX, and for comparison information is provided for other Caulerpales in Table XXXI. The data from our laboratory were obtained using the Hutchinson–MacLennan method (Barnes, 1959). Dried and cleaned young field specimens which I collected in Jamaica provided most of the material, but the fertile *incrassata* and the last two *incrassata* samples listed of "about to fall" and "fallen" segments were collected in a laboratory environment though much of the calcification occurred in the reefs of Jamaica. Although no uncalcified one- to two-day-old segments were included in the study, or any old white sub-basal and basal segments, the data show some of the range encountered within a species, as provided by segments of different ages and with different rates of metabolism. The variation among species, if the subtropical *cuneata* is excluded, is not as great, and might be even less if younger and older *incrassata* were better represented in the samples.

These data show, with the possible exception of *cuneata*, that the carbonate content of a segment is a function of segment age, which is a reasonable conclusion. Older segments generally have more carbonate than young segments, and this is particularly true of the final death and loss of segment stages, as is shown clearly in the data for *incrassata*, where the segments with most carbonate were those collected after death (the very heavy basal segments are specialized structures not typical of the segment flux). In interpreting the data for *cuneata* two factors must be considered: that apical segments older than about 48 hours generally are as physiologically mature as most other segments on the thallus (Section VI) and hence the separation into "apical" and "midway" segments is not necessarily meaningful, and that *cuneata* has, in addition to the regular segments, stalk and collar segments (Section IV). The stalk region is uncalcified; the extent of the aragonite deposits in collar segments has not been critically examined.

These conclusions are in agreement with results from an earlier calcification study by Wilbur *et al.* (1969). There must be further variations in carbonate content with local circumstance and with time of year. Thalli of some species, for example, appear to be more heavily calcified in deeper water (Fig. 88; Böhm, 1973a). But in spite of these caveats it seems reasonable to proceed to compute a carbonate flux using the estimate for a typical dead *incrassata* segment as given in Table XXX.

TABLE XXXI. ARAGONITE CONTENT OF CALCAREOUS CAULERPALES OTHER THAN *Halimeda*[a]

| *Species* | *Description of material* | *$CaCO_3$ in plant (g)* | *% $CaCO_3$ dry wt per sample* |
|---|---|---|---|
| *Penicillus capitatus* | Plant almost exposed at low tide; 3 cm tall, excl. holdfast, 1·7 cm broad; young; pale olive | 0·0565 | 34·4 |
| *P. capitatus* | Small young plant, capitulum 0·4 cm broad; dark greenish-grey | 0·0028 | 7·5 |
| *P. capitatus* | Small young plant, capitulum 0·4 cm broad; dark greenish-grey | 0·007 | 10·9 |
| *P. capitatus* | Mature plant, capitulum 3·7 cm broad; light olive-grey | 0·3778 | 42·0 |
| *P. capitatus* | Mature; capitulum 2·4 cm broad; light olive-grey | 0·1995 | 29·3 |
| *P. capitatus* | Mature; capitulum 1·7 cm broad | 0·1715 | 42·9 |
| *P. capitatus* | Mature; capitulum 1·8 cm broad; light grey | 0·2333 | 46·7 |
| *P. capitatus* | Mature; capitulum 2·3 cm broad; light grey | 0·2070 | 41·4 |
| *P. capitatus*[b] | — | — | 55·9 |
| *P. ad lamourouxii* | Mature; capitulum 3·5 cm broad; light grey | 0·2604 | 34·6 |
| *P. lamourouxii*[b] | — | — | 45·9 |
| *P. pyriformis*[b] | — | — | 58·9 |
| *Rhipocephalus phoenix*[b] | — | — | 46·2 |
| *R. sp.*[b] | — | — | 54·4 |
| *Udotea flabellum* | Plant almost exposed at low tide; light yellow-green | 0·0553 | 33·3 |
| *U. flabellum* | Light yellow-green | 0·0708 | 42·6 |
| *U. flabellum* | Light yellow-green; holdfast shared with preceding plant | 0·1416 | 47·2 |
| *U. flabellum*[b] | — | — | 37·9 |
| *U. conglutinata*[b] | — | — | 31·5 |
| *U. cyathiformis*[b] | — | — | 35·5 |
| *U. ad spinulosa* | Light yellow-green | 0·0422 | 38·1 |
| *U. wilsonii*[b] | — | — | 37·9 |

[a] All data Hillis-Colinvaux (unpublished), except as below.
[b] Böhm (1973a).

(b) *Yield of carbonate as dead segments from* H. incrassata *thalli.* The mean carbonate content of 299 fallen *incrassata* segments is 4·0 mg (Table XXX). We now need to know how many such segments an *incrassata* plant produces in a year, and for this the data are very

FIG. 88. Calcium carbonate content of some Jamaican Halimedae in relation to depth. The number of collections analysed is given in each box of the graph. (From Böhm, 1973a.)

scanty. There are no field data beyond the general observation that white moribund segments are observed on wild plants, that plants do die as entire thalli and that death of the entire thallus always follows the release of gametes. None of these observations of wild plants allows estimates of either the frequency of death or the frequency at which single segments are shed. For the best approximations it is necessary to use data from our laboratory cultures.

In the aquaria cultures individual plants of *incrassata* have lived for as long as two years, though the latter part of such a life seems to be spent covered in epiphytes, or under attack from epiphytes which have to be removed at frequent intervals. Plants in that condition have been seen in the field, but they are not usual and it is hard to believe that they can persist. On the other hand, there is no evidence for rapid turnover of populations as occurs in culture with *Penicillus* of which there may be four or six laboratory generations per year. For want of better data it is, perhaps, conservative and best to assume that a typical wild *incrassata* would live out the more vigorous part of its laboratory term of months, which allows us to assume that it contributes its total stock of segments in the white senile condition in a year.

The mean number of segments on 15 *incrassata* thalli sacrificed for other purposes in the laboratory was 131. These were field-grown *incrassata* that had been in the laboratory only a few weeks, though some were in one sense "mature" since they became fertile. However, the field collections were always of smaller plants, because these were best suited to the aquaria, and the figure of 131 segments per plant is biased towards the small side. It seems reasonable to assume that the typical *incrassata* thallus in the wild has 200 segments when full grown.

The flux of carbonate to reef sediments from an *incrassata* population, therefore, is $200 \times 4$ mg $= 0{\cdot}8$ g per thallus per year. This and other conversion factors for computing productivities from *Halimeda* census data are given in Table XXXII.

(c) *Carbonate flux from Halimedae at Glory Be reef.* The *Halimeda* census data for Glory Be reef that were used when calculating the flux of reduced carbon can be used for calculating the carbonate flux also, if we accept some simplifying assumptions. All Halimedae of the reef are considered to be equivalent to *incrassata* thalli, and the rate of loss of senile segments is considered to be constant at all parts of the reef. The more dangerous assumption is that all of the Halimedae are equivalent to *incrassata*, though the errors introduced may not be great in the light of the other uncertainties. Table XXX shows that of the two common rock-growing Halimedae of cushion life-form in the

TABLE XXXII. CONVERSION FACTORS COMPUTING PRODUCTIVITIES FROM *Halimeda* CENSUS DATA

| | |
|---|---|
| Carbonate production | = 0·8 g carbonate thallus$^{-1}$ yr$^{-1}$ |
| Productivity (net) | = 2·5 mg C thallus$^{-1}$ d$^{-1}$ |
| 1% cover (*incrassata*) | = 10 thalli m$^{-2}$ |
| Turnover time is $\frac{1}{2}$–3 generations yr$^{-1}$ | |

area, *opuntia* segments are heavier (mean weight of $CaCO_3$ 7·75 mg) than *incrassata* segments, and *goreauii* segments are lighter (mean 1·38 mg). A single specimen of *goreauii* in the laboratory collection had 175 segments and a single specimen of *opuntia* 626. An *opuntia* plant, however, covers more space than an *incrassata* plant. With these great uncertainties, it seems reasonable to base a rough estimate on converting cover data to *incrassata* thalli and proceeding on the assumption that each thallus contributes the computed 0·8 g $CaCO_3$ yr$^{-1}$ to the reef.

The estimated reef population of 1 110 300 *Halimeda* plants then contributes 888 kg of carbonate per year, or approximately 90 g m$^{-2}$ yr$^{-1}$ (area 9840 m$^2$, Table XXI). The equivalent rate of sedimentation, assuming 60% porosity as did Stockman *et at.* (1967), is 4066 mm yr$^{-1}$. This was on a reef where the average *Halimeda* cover was 10%, although *opuntia* populations of shallow rocks reached local densities of 90% cover.

(d) *Comparison with other calculations and possibilities of error.* Neumann and Land (1975) made similar calculations for the whole Bight of Abaco in the Bahamas, a shallow basin of 2750 km$^2$. With an average density of *Halimeda* plants of 25 m$^{-2}$ they estimated the standing crop of the whole Bight of Abaco to produce $25{\cdot}47 \times 10^9$ g carbonate. If we assume one crop a year, as was done above, this gives a carbonate flux of 9·26 g m$^{-2}$ yr$^{-1}$, or one-tenth of the estimate for the Glory Be reef. The discrepancy is undoubtedly due to the different *Halimeda* densities. A density of *Halimeda* of only 25 plants m$^{-2}$ is low unless it is a species like *macroloba*. Sand-dwellers may grow at densities 20 times this, and higher densities still are represented by the sprawling thalli of *opuntia* plants growing on rocks at densities of 90% cover. The figures actually used for the Bight of Abaco work are in fact several times larger than the 9·26 g m$^{-2}$ yr$^{-1}$ calculated from the Abaco data here because it was assumed that there would be 6–12 crops of *Halimeda* per year. As is argued above, there is no evidence for such rapid turnover in *Halimeda*.

Stockman *et al.* (1967) made a similar budget for the production of lime muds in Florida by *Penicillus*, concluding that *Penicillus* contributed between 3 g and 25 g carbonate $m^{-2} yr^{-1}$. These results depended on very low population densities of between two and eight plants per square metre, but the passage of six generations a year. This generation time is in accord with my experience of growing *Penicillus* in laboratory culture, it having a shorter life-cycle than *Halimeda*. But it is possible for *Penicillus* to exist at much higher densities than were found in the Florida study, when the total *Penicillus* carbonate production could equal that of the Halimedae of Glory Be reef.

It is evident that calculation of the carbonate flux produced by calcareous green algae is sensitive both to population density and turnover times. Population densities vary by two orders of magnitude, with commensurate effects on calculated carbon flux. Errors in estimating turnover time ought to be reduced by the realization that *Halimeda* is predominantly a long-lived alga. We need field data for the typical length of life of the various species, but it seems likely that more than one to three generations a year, depending somewhat on species, will be found to be unusual. Some additional data are provided by the observations of R. Spies, P. Lamberson and myself on an experimental plot of *cylindraceae* in Enewatak Lagoon, in which over 70% of the original thalli were present at the end of 4 months. Granted the errors that can be introduced by population densities and length of life, the agreement of the calculations of Chave *et al.* (100 g carbonate $m^{-2} yr^{-1}$) with the results from Glory Be is possibly fortuitous.

(e) *Carbonate production in whole reefs: contribution of* Halimeda. In the analysis of the mass of an atoll given above and in Fig. 84, it was suggested that the growth of a reef should be considered in two parts: the reef ridges and the lagoonal areas. In the former there is very active growth of the coral assemblage and encrusting algae, in the latter there is a large contribution of *Halimeda* and other green macrophytes. Smith and Kinsey (1976) likewise divided reef systems into two components, and further suggest that each has a characteristic modal rate of carbonate production.

Smith and Kinsey (1976) give calculations of carbonate production for the Enewetak reef ridge based on measures of the changing alkalinity of the waters flowing over the reef. Their measures are thus comparable to the measures of carbon fixation by flow-respirometry, and give a direct measure of carbonate accumulation on the section of the reef accessible to the technique. Accumulation on the reef ridge is given as 4 kg $m^{-2} yr^{-1}$. This is contrasted with estimates for lagoons

and other still-water sites of 0·8 kg $m^{-2}$ $yr^{-1}$. Where the lagoon is of considerable size, as in many atolls and barrier reefs, this bimodal division of production rates indicates that the lagoonal environments probably contribute most to the mass of the reef, since the area of the lagoon only has to be four to five times that of the reef ridges for its total contribution to be the larger.

Production of carbonate in lagoonal and still-water areas is principally divided between coral pinnacles, Foraminifera, chemical precipitation of calcite and the calcareous green algae. It is, therefore, of interest to see what densities of *Halimeda* are required to yield a significant part of the carbonate production of 0·8 kg $m^{-2}$ $yr^{-1}$ found by Smith and Kinsey (1976) for the lagoon as a whole.

The *incrassata* production rate was calculated above to be 0·8 g per thallus per year. For the total production of a lagoon to be provided by sand-dwelling Halimedae growing on horizontal surfaces would require a population density of 1000 plants $m^{-2}$. Apparently the highest densities so far recorded are 500 plants $m^{-2}$ in a few "clearings" among the *Thalassia* beds of the Glory Be reef. Dense populations in shallow water at Glory Be, Enewetak and elsewhere of an *incrassata–cylindracea* type of thallus have about 100 plants $m^{-2}$. A clearly visible growth of *Halimeda* over the floor of a whole lagoon, therefore, would produce about one-tenth of the total estimate of Smith and Kinsey. This is by no means impossible and there are reports in the literature of lagoon floors having what seem, from a ship-board collecting station, to be dense covers of *Halimeda* (Emery *et al.*, 1954). On two dives to the floor of the Enewetak Lagoon in 1975, however, I found that much of the visible terrain was almost devoid of Halimedae. Shallower lagoons (Enewetak is from 40 m to 70 m deep), however, may have denser stands. But there are also other factors to be taken into account.

The above calculations neglect two sources of *Halimeda* segments that may well constitute the major part of the total *Halimeda* contribution: the rock-growing *opuntia*-type Halimedae of the pinnacles and of the deep fore-reef. *Halimeda opuntia* at Glory Be attained local cover densities of 90%, which is roughly equivalent to an *incrassata* population of 900 plants $m^{-2}$, and, since the sprawling life-form of these plants always tends to produce high cover, like the tillering patterns of grasses, local populations always tend to be dense. Some of the pinnacles at Enewetak support considerable populations of Opuntioid forms, and the total vertical faces of the pinnacles must be very large. With over 2000 pinnacles in the lagoon, if the lagoon were drained the aspect would be rather like the teeth of a rubber hair-brush. Without direct data on segment production by these rock-growing forms (not so far

available because of the difficulty of maintaining them in culture) it is not possible to calculate their contribution, but there is clearly the possibility for a large component of total production to be included.

And to the pinnacle Halimedae must be added those of the deep fore-reef. In Jamaica, at depths of −61·5 m to −91 m, there are very dense populations of *cryptica* and lesser populations of *copiosa* (an Opuntioid form) which locally attain 60% cover (Moore *et al.*, 1976). It seems likely that similar growths are prevalent outside the fore-reef of atolls, though no census data are available because of the difficulties of diving operations at these sites. Some considerable part of the production of the deep fore-reef, which contributes heavily to the sediments of the island slope of Jamaica (Fig. 86), may be swept up in the vigorous onshore currents of these atolls, to be deposited later in the still waters of lagoons.

In conclusion it may be said that the bimodal production suggested by Smith and Kinsey (1976) seems to accord with the drill-core data and the scanty *Halimeda* production figures. It is necessary to look at the older literature describing very high production figures for the whole reef, like those collected by Chave *et al.* (1971), with the realization that they do not imply actual growth of coral reef ridge itself, but the carbonate accumulations of the whole reef system. The largest part of this accumulation is probably in the large areas of the quiet lagoons. *Halimeda* is a very significant contributor to this accumulation both from the production of sand-dwelling plants in shallow water, and from the rock-hanging forms of the pinnacles and possibly of the deep fore-reef.

## X. *Halimeda* Distribution in two Reef Systems

This chapter describes two reef systems from the point of view of *Halimeda*, or at least from the point of view of an investigator asking questions about reefs as the habitat of *Halimeda*. As with all reef studies there are constantly in the background questions of how the reefs were built, but these questions are again likely to be phrased from the point of view of *Halimeda*: "In what way have the *Halimeda* populations contributed to the structure and mass of the reef?" It is suggested that this might be a timely bias, since the great majority of studies on coral reef systems have been designed on the unspoken assumption that the essential process in reef-building is the construction of the coral framework. It has already been mentioned (Section IX) that the classic studies on reef productivity, like those of Sargent and Austin (1954) and Odum and Odum (1955), are of small sections

of inter-island reefs in which *Halimeda* is entirely absent or a minor component. And yet *Halimeda* is one of the principal contributors to reef structure, sometimes perhaps the most important one (Section, IX).

Two reef systems have been examined with *Halimeda* principally in mind. They are a section of the fringing reef on the north shore of Jamaica where a *Halimeda* census was made (Hillis-Colinvaux, 1972), and Enewetak Atoll where two *Halimeda* investigators have dived.

### A. *The Glory Be reef, Ocho Rios, Jamaica*

"Glory Be" is the name of a house near the village of Ocho Rios, sited roughly in the centre of the north shore of Jamaica. The patch of reef approached from the house was chosen for this study because two headlands marked off a convenient length of reef (Fig. 89), and because the high cliff of fossil limestone gave a vantage point which greatly aided mapping of the various regions of the reef. The approximate coordinates of the reef section are 77°0′ W, 18°24′ N.

The reef at Ocho Rios is part of the Jamaican fringing reef which has been extensively studied and described by Goreau and members of his laboratory working from the nearby Discovery Bay (Goreau, 1959; Goreau and Goreau, 1973), and I first became interested in the north-shore reef system when conducted over it by T. F. Goreau in 1962. I made a preliminary survey of the Glory Be reef in September 1968 (when the water was somewhat disturbed from the passage of a hurricane), and carried out the main part of the census in three weeks in June 1969. The census extends out only to the beginning of the outer channel or moat zone (7 in Fig. 89), being extended beyond this down to a depth of 20 m (moat, buttress and fore-reef) only by qualitative observation, supplemented by observations at our other work site of Runaway Bay. Qualitative descriptions of *Halimeda* populations down to about 70 m are given in Goreau and Goreau (1973). Seasonal assays of *Halimeda* populations at these greater depths are urgently needed.

A profile through the Glory Be reef is given in Fig. 90, the numbered parts of which are included on Fig. 89 and in Table XXXIII. These reef zones need to be understood in the context of the reef nomenclature established by Goreau and his laboratory, the usages of which have changed slightly over the years. In Table XXXIII the Goreau equivalents are given as they appear in Goreau and Goreau (1973). The comparison of the Glory Be nomenclature with Goreau's reveals not only a finer classification of the near-shore zones at Glory Be, but also some added features of the Glory Be reef system not present in Goreau's generalized model.

TABLE XXXIII. DISTRIBUTION OF *Halimeda* SPECIES, ZONAL DENSITIES, NET PRODUCTIVITY AND CARBONATE PRODUCTION FOR SECTIONS OF GLORY BE REEF SHOREWARD OF MIXED CORAL ZONE

| *Goreau equivalent zone* | | *Glory Be zone* | *Width (m)* | *Depth (m)* | Halimeda *cover* $m^{-2}$ (%) | Halimeda *thalli* $m^{-2}$ (incrassata *equivalents, Table XXXII*) | Halimeda *species* |
|---|---|---|---|---|---|---|---|
| Inshore | 1. | Tidal sandy beach | — | — | 0 | 0 | — |
| | 2a. | *Opuntia* rocks | 3 | ≤0·3 | 5 | 50 | *opuntia and goreauii* |
| | 2b. | *Opuntia* rocks | 2 | ≤0·3 | 90 | 900 | *opuntia and goreauii* |
| | 3. | *Thalassia* beds inshore reef | 5 | ≤0·3 | 15 | 150 | *monile, incrassata* |
| | 4a. | Inshore reef flat | 7 | ≤0·3 | 35 | 350 | *monile, incrassata, opuntia* |
| Lagoon | 4b. | Rock sides | — | <0·3–2·5 | 1 | 10 | *opuntia, goreauii* |
| | 5a. | Lagoon sand | 10 | Av. 2·5 | 5 | 50 | *incrassata, simulans* |
| | 5b. | Rock outcrops | — | Av. 2·5 | Incl. in 4b | Incl. in 4b | *opuntia, goreauii, tuna* |
| Reef flat or *Zoanthus* | 6. | Reef flat : *Zoanthus* | 20 | ≤0·3 | 10–15 | 125 | *opuntia, goreauii, tuna, opuntia* |
| Moat | 7. | Moat | 50 | Av. 4 | 1–5 | 25 | *incrassata* |

| *Section* | *Mean* Halimeda *density (thalli* $m^{-2}$) | *Mean* Halimeda *net productivity (gC* $m^{-2}$ $d^{-1}$) | *Mean* Halimeda *carbonate production (g carbonate* $m^{-2}$ $yr^{-1}$) |
|---|---|---|---|
| Typical reef section, 1 m. wide, Zones 1–6 | 164 | 0·4 | 131 |
| Section across inshore reef, 1 m wide, Zones 1–4 | 262 | 0·7 | 210 |

FIG. 89. Panorama of Glory Be reef, east of Ocho Rios, on the north shore of Jamaica. The regions shown are: (1) tidal sandy beach, (2) sand with emergent flat rocks, (3) sea-grass beds in about 0·3 m of water or less, (4) shore reef, (5) lagoon, (6) reef flat : *Zoanthus* zone, (7) moat. The distance from the pipe railing at right to the centre of the number five is 15·4 m.

FIG. 90. Profile of the Glory Be reef. The regions shown are: (1) tidal sandy beach, (2) sand with emergent flat rocks, (3) sea-grass beds in about 0·3 m of water or less, (4) shore-reef, (5) lagoon, (6) reef flat: *Zoanthus* zone, (7) moat, (8) mixed zone, (9) buttresses, (10) fore-reef terrace, (11) fore-reef escarpment, (12) fore-reef slope, (13) deep fore-reef. Regions 1–4 are subdivisions of Goreau's inshore zone (Table XXXIII), with each zone representing a very different habitat for *Halimeda*. The *palmata* or breaker zone as described by Goreau and Goreau (1973) is poorly developed at Glory Be, and the waves were observed breaking at the leading edge of the reef flat (6) as shown in Fig. 89. Only regions 1–9 of Glory Be could be included in the survey. Deeper regions have been added to the profile using our unpublished observations from Runaway Bay, and data from the Discovery Bay region (Goreau and Goreau, 1973). Below the profile the depth ranges of the ten *Halimeda* species known for Jamaica are given. Data are from Hillis-Colinvaux (1972, 1974), Colinvaux and Graham (1964) and Goreau and Goreau (1973). The symbols for the species are: i = *incrassata*, s = *simulans*, m = *monile*, o = *opuntia*, g = *goreauii*, co = *copiosa*, c = *cryptica*, t = *tuna*, d = *discoidea*, gr = *gracilis*. Regions of greatest abundance for *monile*, *opuntia*, *goreauii*, *copiosa* and *cryptica* are shown by the thicker lines.

FIG. 91. Central section of panorama of Glory Be reef, with specimen areas of *Thalassia* and *opuntia* rocks outlined. Textural changes in panorama outside the reef flat : *Zoanthus* zone do not demarcate the bottom features accurately. The position of the *Acropora*, north of the moat, is sketched in.

Zones 1–4 of the Glory Be classification are all subdivisions of what Goreau calls the *inshore zone*. These subdivisions each represent a very different habitat, and it is suspected that the four zones together are important to the total carbonate, carbon and *Halimeda*-segment flux of the reef. The combined *inshore zone* at Glory Be is separated from the shore side of a *reef flat: Zoanthus zone* (6) by a *lagoon* (5) as in the Goreau typical reef. During the two periods of work at the reef, waves did not break at the *palmata zone*, even though in Goreau's general model they do, and he regards the *palmata zone* and the *breaker zone* as one and the same. At Glory Be the waves broke at the leading edge of the reef flat (Fig. 89), after crossing the inundated *Acropora cervicornis* and *palmata* corals or *mixed zone* (8) and the *moat* (7). For this reason we originally called the Glory Be zone (7) "the breaker zone", and it is so described

in Hillis-Colinvaux (1974). Goreau's (1973) *palmata* zone has a more restricted interpretation than in the 1959 description of the reefs, where it is applied to the entire region between reef flat and buttresses, which in turn are followed by a *cervicornis* zone. The *palmata* zone, as delimited by Goreau and Goreau (1973) (their region 5), is poorly developed at Glory Be.

There is no need for concern that the obvious divisions of the Glory Be reef do not match precisely with Goreau's generalized model because every section of reef can be expected to be modified to local circumstances of tide, current and coastal morphology. And yet there is, perhaps, a question concerning the line at which the waves break; is the pattern at Glory Be an aberration because of the sheltered character of the bay?

1. *Methods of census*

The zonal boundaries in this system are distinct and can easily be identified both in the water and on the panorama (Fig. 89) made from the top of the cliff. The lengths and widths of the principal features of Fig. 89 were measured by identifying salient features such as individual rocks from the top of the cliff and on copies of the panorama, then taping the distances directly with a nylon line. Twenty-four lengths measured in this way were sufficient to compute the surface area occupied by each zone. Rough estimates for the mean width of each zone can also be made from a copy of the panorama on which the measured distances are superimposed, allowing the calculation of the relative areas of each zone along a metre-wide transect from the cliff to the outer channel. These estimates (Table XXXIII) are obviously crude, but the errors are probably not important for extrapolation purposes since reef-to-reef fluctuations in relative zone areas must be very large.

Estimates of densities of *Halimeda* and other algae were made by quadrat sampling, sets of nearest-neighbour samples and subjective estimates of percentage cover. A convenient quadrat for dense populations of *Halimeda* is a rectangle of plexiglass placed on top of the *Halimeda* population, when it is easy to count the plants underneath it. Nearest-neighbour samples were most convenient in sandy areas where *Halimeda* populations were sparse and where the swell made it hard for a diver to keep station. The diver chose one plant as it drifted into view, placed one edge of a steel rule against it, and pivoted to find the other plant of the pair. Estimates of percentage cover were found to be the only practicable way of assessing densities of the sprawling

plants of *opuntia* and *goreauii*. The census occupied about 30 hours of bottom time.

In order to compute carbon and carbonate fluxes for the various portions of the reef it was necessary to convert our laboratory measurements on *incrassata* populations from fluxes per thallus to fluxes per unit of cover. To arrive at a conversion factor we estimated the percentage cover of *incrassata* populations of known density. A density of 500 *incrassata* $m^{-2}$ covers 50%, so 100% cover is taken as the equivalent of 1000 thalli $m^{-2}$. The crudeness of this conversion for *opuntia* is self-evident, and it may be that the close-packed branches of a 90% cover stand of *opuntia* produce considerably more than would 900 *incrassata plants*. Without direct measures of the productivities of sprawling forms, however, there seems to be no way of making a more accurate estimate.

2. *Productivities at Glory Be*

The productivity of the parts of this reef has been discussed in Section IX, and the principal data are given in Tables XXI and XXXIII, with some of the results of the census being included in the latter. Conversion factors for computing productivities from *Halimeda* census data were derived from the Glory Be survey and the associated laboratory work and are given in Table XXXII.

3. *Narrative description of Glory Be reef*

At least ten species of *Halimeda* live in the reefs of the north shore of Jamaica, six of which (*opuntia, goreauii, gracilis, tuna, incrassata* and *simulans*) grow with varying success over much of the depth range of approximately −0·3 m to −60 m (Fig. 90; Section IV), or to the start of the deep fore-reef. None is regularly exposed at low tide. Of the remaining species, *monile* appears to be restricted to shallow water, and *discoidea* is limited essentially to the fore-reef and fore-reef slope (although it grows in shallow water elsewhere in the Caribbean). The thalli of *discoidea* sometimes appear to be growing in sand, but on closer examination they are invariably attached to some rock outcrop concealed by a thinnish veneer of sand. The species *copiosa* and *cryptica* are restricted mostly to the fore-reef slope and upper part of the deep fore-reef, that is, to depths of approximately 25–100 m. *Halimeda copiosa*, however, does occur in shallower water in the Pacific (see below and Section IV). These two species are the only ones to establish sizeable populations on the deep fore-reef (Goreau and Goreau, 1973), with *cryptica* being the more abundant.

(a) *Hard substrates.* Proceeding seaward onto the reef from the shore, the first *Halimeda* species to appear, whether it be a member of the Rhipsalis, Opuntia or Halimeda sections, is determined to a large extent by the substrate available. On the Glory Be reef it is rock, and sprawling over it are large, dense patches of *opuntia*, sometimes just covered by most low tides, with holdfast filaments developing frequently from between segments where the thallus makes contact with the substrate. When the mapping-transect study was carried out, this species occupied much of the surface of the very shallow inshore rock (regions 2, 4 and 6; Figs 89–91, and Fig. 92) as well as the rock sides of region 2, and rock sides together with coral outcrops of region 5. The total *Halimeda* cover of the very shallow inshore rocks (region 2), given in Table XXXIII, was the highest encountered in the parts of the reef

FIG. 92. Clumps of *opuntia* providing, at the site shown, about 50–60% three-dimensional cover on rocks of the inshore reef of Glory Be, in about 1 m of water. The breadth of most of the segments shown is 5–8 mm.

surveyed. Beyond the very shallowest regions *goreauii* sometimes accompanied *opuntia*, but seemed to be restricted to certain exposures on the coral rocks in shallow water. Past the reef flat (6), *goreauii* was more conspicuous and tended to replace *opuntia* in the deeper regions of the reef (Fig. 90).

(i) *Regions of low* Halimeda *density on hard substrate.* The seaward edge of the inshore reef flat (region 4) was conspicuously barren of *Halimeda*, appearing as a whitish border which can be seen on the panorama (Figs 89, 91) running across Fig. 89 from the dock at the right. Instead of supporting the heavy *opuntia* cover of the adjacent regions, this band of about 0·66 m width had a partial cover of grey-green algal fuzz, tiny *opuntia* and isolated *opuntia* cushions which showed signs of being grazed, with curved bites out of the segments, while the region was floored with similar segments. In addition, the few *opuntia* plants growing in the fringe had a conspicuously rounded cushion or cropped habit, and lacked the straggly projecting branches which result from active growth (Fig. 51). The coral rock itself was pitted, with numerous scattered hollows containing urchins at a daytime density of 12 $m^{-2}$. The densest *opuntia* cover on this urchin border reached 5%, with overall cover not greater than 1%. The upper portion of the adjoining vertical wall also was relatively barren of macroalgae; lower on the wall Halimedae were present, although their distribution was patchy and sparse. A 1% cover was estimated for the coral rock sides and rock outcrops of the lagoon. *Halimeda tuna* appeared on some of the latter, sometimes pendant and in shaded sites.

About two-thirds of the surface of the reef flat : *Zoanthus* zone (Fig. 91; region 6) also lacked *Halimeda* cover, and was urchin-barren like the one described for the seaward edge of the shore reef. The remaining third had an almost-closed cover similar to that of the inshore reef. *Halimeda opuntia* was the most prominent siphonaceous alga, and the thalli appeared to be grazed. Here also the seaward vertical face of the reef lacked conspicuous vegetation, including calcareous green algae. The *Halimeda* population was sparse throughout.

The buttress zone (Fig. 93; region 9), a region of hard substrate, might also seem a likely site for non-sand-growing Halimedae, including *opuntia*. Our census did not extend to this region at Glory Be, but at Runaway Bay (between Glory Be and Discovery Bay) *Halimeda* won little space on this wall of living coral, although scattered thalli of *opuntia* and *goreauii* occurred here and there. The absence of this genus from the north-shore buttresses was noted by Goreau and Goreau (1973).

FIG. 93. Part of a buttress. Halimedae are rare in this region of Jamaican reefs. They are also absent from the sand at the bases of the buttresses.

On the hard surfaces provided by the fore-reef slope and deep fore-reef, the genus is more successful, and at depths of −61·5 m to −91 m on the deep fore-reef of Discovery Bay cover by *Halimeda* was estimated as 10%, with *cryptica* occupying up to 60% of the available space on parts of promontories (Moore *et al.*, 1976).

(b) *Unconsolidated substrates.* The Halimedae of sands and muds are principally members of the Rhipsalis section, although *opuntia* and *gracilis*, in their sprawling growth, are sometimes associated with such substrates. The greatest cover achieved by these Halimedae for the parts of the Glory Be reef surveyed was in the shallow sandy flats of regions 3 and 4. These flats, although sometimes barren of macro-vegetation, generally supported large populations of sea grasses, the *Halimeda* species *monile* and *incrassata*, and the related calcareous green algae *Penicillus* (often *capitatus*) and *Udotea flabellum*. The resultant cover was essentially closed, and although the sea grass *Thalassia testudinum* König was a clear areal dominant, about 40% cover was provided by the above three genera of calcareous green algae, with the two *Halimeda* species accounting for about 15%. A fairly closed plant cover also existed in the sandy patches of the inshore reef flat (4), but much of it was provided by a spongy turf of about 16 cm

thickness, composed of red and brown algae. Amidst this carpet grew compressed thalli of *H. monile* and *H. incrassata*, their buried basal portions white. In some places, about 300 of these *Halimeda* thalli occurred in a square metre of turf, compressed amidst the fleshy algae.

(i) *Regions of low density of Rhipsalian Halimedae.* Much of the lagoon (5) is sandy, and one might expect extensive stands of *Halimeda*, the other calcareous Caulerpales, which are predominantly sand growers, and sea grasses. Such stands did occur (Fig. 94). In these shallow sandy areas, I found Lilliputian forests of *Thalassia testudinum*, and the densest population of *H. incrassata*, 441 thallim$^{-2}$, encountered on this particular reef. But the vegetation was patchy, and there were extensive barren areas along the edges of the reef rock and in the main part of the channel. Where vegetation occurred the sea grasses were usually the commonest, although the Caulerpalean genera *Halimeda*, *Penicillus*, *Udotea* and to a lesser extent *Rhipocephalus* were prominent too. These algae usually grew in parts of the channel which were some distance from the bases of reef walls, although a conspicuous exception was *Udotea ad spinulosa* which pushed up in tight clumps of about 40 clonal thalli under reef overhangs. The commonest Rhipsalian species in the inner channel was *incrassata*, but *simulans* mingled with it, particularly near the periphery of dense stands. *Halimeda* cover of the lagoon sands was about 5%.

Extensive patches of Rhipsalian Halimedae were anticipated in the wide moat (7) where the next unconsolidated substrate occurred proceeding seaward from the shore. There were, however, few obvious calcareous greens when the study was made. Seaward of the reef flat (6), with its few *Acropora palmata* and *Millepora* colonies, was first a channel of ripple-marked sand, some of it halimedoid, with dune-like waves being continually moved by the surge. Neither plants nor urchins were obvious, but worm cones occurred at intervals of a metre or so. The rippled area ended in a pebbled or cobbled region, also part of the moat (7). The rounded cobbles, typically 5 cm or so across but many larger, seemed to lie on *Halimeda* sand and occupied half the area. Patches of coral rock occurred throughout the cobble region. This part of the moat contained a *Diadema* population averaging about 6 m$^{-2}$, in places reaching a density of 20 m$^{-2}$. So large a population indicates heavy production, but sizeable algae such as *Halimeda* occupied only a tiny fraction of the grazed surface. Instead, over much of the pebble–cobble floor a fuzz of filamentous green algae grew, and this population seemed to be maintained by urchin grazing (Fig. 95). About 20% of the moat also contained reasonably dense stands, about 300 m$^{-2}$, of

FIG. 94. A grove of *H. incrassata* with the occasional *H. simulans* in about 1·6 m of water in the lagoon of Glory Be. Cover by *Halimeda* is about 30%, the proportion of young : mature : old *Halimeda* thali in the region of which this photograph is a part was 1 : 2 : 1 in September 1968. The commonest associated alga in this photograph is *Penicillus capitatus*.

FIG. 95. The cobble–urchin–fuzz system of the moat. The density of *Diadema* for the region averaged 6 $m^{-2}$, in places reaching 20 $m^{-2}$.

*Thalassia*, together with white urchins *Tripneustes esculentus* Leske and heart urchins *Clypeaster rosaceus* Linnaeus. The density of each of the two urchin taxa was estimated as 1 $m^{-2}$. Among the sea grasses were occasional small thalli of *incrassata*, of density about 4 $m^{-2}$. The *Thalassia* stands, alternating with the grassless, ostensibly barren areas, gave the impression of advancing and retreating, while the heart urchins and fuzz remained.

Where there are appropriate substrates, Rhipsalian species also grow in the deeper portions of the reef (Section IV; Fig. 90) such as the upper fore-reef slope. However, these deep-water Rhipsalian populations are never dense, as they are in the shallows. This is, to some extent, remarkable, for rock-growing pendant species like *copiosa* and *cryptica* do achieve very dense populations in deep water. The disturbance of suitable substrates by silting, or by slumping of reef, perhaps accounts for these smaller Rhipsalian populations at depth.

4. *Summary: factors affecting* Halimeda *distributions at Glory Be*

(a) *Association with sea grasses.* One of the best places to find a dense (*c.* 450 $m^{-2}$) population of Rhipsalian Halimedae is in the region of dense patches of *Thalassia*. The *Thalassia* stands constitute well-defined communities, the sand consolidated by a network of *Thalassia*

rhizomes (Fig. 96), and some of the less dense may contain very sizeable populations of *Halimeda*, or the dense *Halimeda* patches may be in adjacent areas. These especially thick *Thalassia* stands are restricted to shallow water between −0·5 m and −3 m. Even in apparently optimum sites the distribution of the *Thalassia* stands is patchy, and there is evidence that the patches themselves are unstable. Most patches terminate in what could well be called a blow-out: there is an

FIG. 96. Edge of a dense stand of *Thalassia testudinum*, partly fringed by other sea grasses such as *Diplanthera wrightii*. Here the calcareous alga *Penicillus capitatus*, with some *Udotea*, is prominent towards the edge of the bed, and extends into the sand of the lower left. There is a suggestion of a rotational process of colonizing sand, consolidation of the sand by sea-grass rhizomes, development of the dense *Halimeda* and other populations, and physical destruction of the community.

abrupt edge, with barren sand adjacent, and the discontinuity between the *Thalassia* community and the bare sand reveals a vertical section of the sand consolidated by the *Thalassia* rhizomes which in places is about 10 cm high. These observations suggest very strongly that there is a rotational process of colonizing sand, consolidation of the sand by sea grass rhizomes, development of the dense *Halimeda* and other alga or sea grass populations, and then physical destruction of the community. The dynamics of this process are of immense importance to the total *Halimeda* productivity of the reef.

(b) *Grazing and the Opuntioid forms.* Straggling growth-forms of *opuntia* on rocks form the densest *Halimeda* stands, reaching covers of about 90%, which is probably more than the equivalent of 900 Rhipsalian Halimedae per square metre. There seems to be good reason for thinking that the sites where densities like these can be attained are limited by grazers for many *opuntia* patches show direct signs of having been grazed, and apparently suitable sites are both barren of *opuntia* and are the habitat or territory of some urchins or fishes. It is possible that there are seasonal or periodic fluctuations in grazer populations, in which event total *Halimeda* densities may fluctuate very widely from time to time.

(c) *Factors restricting* Halimeda *on bare bottoms.* *Halimeda* populations are low on the sandy bottom of the moat and on the fore-reef terrace. For the sandy, duned parts of the moat that lacked vegetation, the explanation may be that the sands are kept too mobile by the wave surge, and that only exceptionally well-anchored plants survive. On the barrens of the moat floor urchin grazing is a possibility, because high densities of urchins were found, and the vegetation which was there, a short soft algal fuzz, is a life-form that might result from heavy grazing.

## B. *Enewetak Atoll*

There are more data from Bikini and Enewetak (the spelling preferred by the Marshallese) than from any other atoll, a consequence of their use for bomb tests. Thirty-five atomic devices have been exploded at Enewetak, and the bomb craters themselves are sometimes interesting sites for marine botany. As always, research has been concentrated on processes leading to the construction, maintenance, productivity and geology of the reef framework, with processes in the lagoon and among the macrophyte populations examined to a lesser extent. Geology and the structure of the reefs are described in Emery *et al.* (1954) and Ladd (1973), with Ladd also providing a list of the chapters of *U.S. Geological Survey Professional Paper 260* which reports on the Marshall Islands. Some of the results of core drilling of the reef are reviewed in Section IX. The classic studies of production on reef ridges by Odum and Odum (1955), as well as the more recent studies of the SYMBIOS group (Johannes *et al.*, 1972; Pomeroy *et al.*, 1974; Webb *et al.*, 1975; Wiebe *et al.*, 1975), also described Enewetak systems, with the earlier work of Sargent and Austin (1954) carried out in another atoll of the same group of islands.

Marine botany began with Taylor's (1950) survey as part of the preparations for Operation Crossroads. Taylor's monograph is essentially the results of many dredge hauls made as the requirements of military logistics allowed. Dawson (1957) added to the algal collections by diving, but the main effort at ecological marine botany by diving was the work of Gilmartin (1960, 1966). In the first paper Gilmartin described the lagoon bottom, and collections of algae at 21 stations, comprising a complete east–west transect of the lagoon and reaching to the maximum depth at about 65 m. It should be noted that the sand-dwelling *Halimeda* found most commonly by Gilmartin and described as *monile* is now properly known as *cylindracea*. The only report on algae at Enewetak since Gilmartin appears to be that of Hillis-Colinvaux (1977).

1. *Enewetak Atoll and the reef profile*

Enewetak Atoll consists of approximately 40 low islets on a broadly elliptical reef surrounding a large and deep lagoon (Fig. 97). Prevailing winds are important in shaping a reef (Yonge, 1951), and Ladd (1973) describes Enewetak as a typical "rough-water reef" since it lies in the belt of the north-east trade winds. Its windward side is consequently subjected to steady wave attack for about 9 months of the year. Its southern reefs are protected from the trade winds, but are periodically damaged by powerful long-period swells from the southern hemisphere, whereas the reefs of the west and north-west are exposed to relatively calm seas. These differences in the physical environment of the portions of reef bordering the small islets create an initial series of varied macrohabitats, to which are added the different conditions presented by the channels between the islets, and a lagoon of approximately 39 km in diameter, about 65 m at its deepest, with more than 2000 coral knolls or pinnacles (Fig. 83, bottom) and its own circulation system (von Arx, 1948).

Basic regions and features of the reef of this atoll are shown in profile in Fig. 98. Weather, accessibility of sites and work facilities severely limit the number of studies that can be made on the seaward portions of such reefs, so that we have few data of structure or communities to windward of the reef ridge.

The reef profile of Fig. 98 begins, therefore, just below the approximate depth (range *c.* −14·5 m to −25 m) at which a pronounced change of slope is known to occur. The region preceding it has been frequently called the "ten-fathom terrace". But since the slope break occurs over a range of many metres (Stoddart, 1969; Orme, 1977; Smith

FIG. 97. Map of Enewetak Atoll showing stations visited for *Halimeda* project, 1975, and their *Halimeda* and *Tydemania* species. *Halimeda* species: A1 = *incrassata*, A2 = *cylindracea*, A3 = *stuposa*; B1 = *opuntia*, B2 = *copiosa*, B3 = *distorta*, B4 = *minima*; C2 = *gigas*, C3 = *gracilis*, C4 = *lacunalis* f. *lata*, C5 = *macrophysa*, C6 = *taenicola*; D1 = *micronesica*, D2 = *fragilis*. *Tydemania* species: T = *expeditionis*. (Modified from Hillis-Colinvaux, 1977.)

and Harrison, 1977), it is better called the fore-reef terrace. Proceeding shoreward a spur and groove region is encountered, and breaking the surface at low tide is the algal ridge. Development of spur–groove and algal ridges vary considerably, however, and they may be absent. The spur–groove system is best developed on the windward sides of atolls; on the lee side smooth margins are the pattern (Tracy *et al.*, 1948).

The algal ridge has traditionally been called the "*Lithothamnion* ridge", and the component algae referred to as Lithothamneae or "nullipores". The name is a misleading one, however, brought about in

| | LAGOON REEF | | | ISLET or INTER-ISLAND CHANNEL | SEAWARD REEF | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Lagoon Basin Pinnacle ( 2000 + ) | Lagoon slope | Lagoon Terrace | | Beach | Back Reef | Algal Ridge | Reef-Crest Spur and Groove | Fore-Reef Terrace and Slope |
| Characteristics *Halimeda* population | Populations may be very dense close to shore and on tops of pinnacles | | | Approx.100% Cover, Some Sites | 0 | Probably Low | 0 | 15% Cover on 1 Site Leeward-Transitional Reef | ? |

FIG. 98. Profile of Enewetak Atoll, through windward reef to deepest part of lagoon, showing major features of reef. (Modified from Tracy *et al.*, 1955; Yonge, 1963; Orme, 1977.)

part by the tediousness, in the early stages of the taxonomy of the group, of identifying the calcareous algae involved, for *Lithothamnion* is a minor component, if present at all. The commonest members of the ridge are species of *Neogoniolithon*, *Porolithon* and *Lithophyllum*, and up to ten genera commonly may be present (Adey and MacIntyre, 1973). This ridge, showing various degrees of development, also occurs in the Caribbean (Adey, 1975; Adey and Burke, 1976; Adey *et al.*, 1976), and it therefore does not represent a difference between the reefs of Atlantic and Pacific as formerly believed (Stoddart, 1969; Milliman, 1974). To the region of shallow waters shoreward of the ridge I have applied the general term back-reef (or reef flat). I have not subdivided it according to predominant coral type as is commonly done, since these divisions are not meaningful to our present understanding of *Halimeda* distribution at Enewetak.

Water flowing across this back-reef may continue directly into the lagoon, or its passage may be interrupted by low, carbonate islets built on the reef structure. Various vertical divisions of the lagoon reef have been described, again based on types of coral, but for *Halimeda* there is at present little reason for stressing them. Different environments among lagoon reefs are encountered in regions adjacent to inter-island channels, on the lagoon side of the passage between islets and bordering the islets themselves. The many pinnacles of the lagoon are active, tall coral heads of immense significance to the productivity and carbonate budget of the atoll.

### 2. *The distribution and diversity of* Halimeda *at Enewetak*

Fourteen species of *Halimeda* are known for Enewetak (Table XXXIV), and although the number may be higher when some of the problems of nomenclature are resolved, it is, even so, the greatest number yet reported from any specific area in the world, and is about the same as the total number of species of *Halimeda* known for the Atlantic Ocean. The within-habitat diversity, *sensu* MacArthur (1965), at any place in the atoll, however, is low (Hillis-Colinvaux, 1977). Twenty-one sites were examined during a 3-week visit to Enewetak, and at no station were as many as half the species found (Fig. 97). At only 10% of the stations were there six species, and at 40% of the stations there were three or fewer. At two stations, including the site of the Odum transect, no Halimedae were found. A station represented about 1–2 h of diving time. A striking observation first made by Gilmartin (1960) is that both sand- and rock-adapted species are found at all depths of the lagoon, from the shallows to the bottom,

though relative abundance and diversity appear to decrease with depth.

Rock habitats for the species with this habitat strategy are available on the reef crest, much of the back-reef, in the inter-island channels, at

TABLE XXXIV. SPECIES AND ABUNDANCES OF *Halimeda* AND *Tydemania* AT ENEWETAK ATOLL, DECEMBER 1975[a]

| *Map code (Fig. 97)* | *Species* | *Total No. stations where present* (%) | *Total No.* Halimeda *stations where present* (%) | *Relative in-site abundance*[b] |
|---|---|---|---|---|
| | *Halimeda* | | | |
| A1 | *incrassata* | 8 | 12 | 3 |
| A2 | *cylindracea* | 37 | 54 | 3 |
| A3 | *stuposa* | 11 | 16 | 3 |
| B1 | *opuntia* | 58 | 85 | 3 |
| B2 | *copiosa* | 24 | 35 | 2 |
| B3 | *distorta* | 29 | 43 | 2 |
| B4 | *minima* | 19 | 28 | 2 |
| C2 | *gigas* | 32 | 47 | 3 |
| C3 | *gracilis* | 16 | 24 | 1 |
| C4 | *lacunalis* f. *lata* | 24 | 35 | 3 |
| C5 | *macrophysa* | 68 | 100 | 3 |
| C6 | *taenicola* | 5 | 7 | 1 |
| D1 | *micronesica* | 5 | 7 | 1 |
| D2 | *fragilis* | 11 | 16 | 1 |
| T | *Tydemania* *expeditionis* | 16 | 24 | 2 |
| | *Udotea* Various species | — | — | 1 |

[a] From Hillis-Colinvaux (1977).
[b] 1 = a few species found by diligent searching; 2 = common, but a minor part of *Halimeda* community; 3 = abundant, a major part of the *Halimeda* cover.

the lagoon borders, and on the pinnacles and mounds of the lagoon floor. Unconsolidated material floors most of the lagoon, but there is little sand habitat elsewhere except for patches in the reef and its channels. Significantly for the distribution of the Rhipsalis group of *Halimeda*, the windward back-reef lacks the extensive sand terrain so important for *Halimeda* production in the Caribbean. It may be that the absence of an extensive sand flat along the back-reef is a characteristic of atolls, which makes the basis of their carbonate budgets

somewhat different from fringing reefs. An especially fine-grained unconsolidated substrate for Halimedae at Enewetak is provided by atom bomb craters.

(a) Halimedae *on the fore-reef and the spur and groove zones.* We have no data on *Halimeda* distributions on the fore-reef or at the greater depths below, but Jamaican experience suggests that there may well be dense populations or new species waiting to be found there. If these populations exist, they could be important to the carbonate budget of the lagoon because the strong onshore currents might be expected to carry shed segments over the reef. Species to be expected there include *copiosa*, *opuntia*, *gracilis*, *macrophysa* and *gigas*, with *Tydemania expeditionis*. This region is yet part of the "Mare Incognitum" (Ladd, 1961; Smith and Harrison, 1977) for plants as well as for corals.

There is no published account of *Halimeda* on the spur and groove region, but I was able to make one collection in a transitional spur and groove region in 1975. This was on the seaward side of the islet of Mut at the south-western corner of the atoll (Fig. 97) in about −10 m to −15 m of water. Four species of *Halimeda* were found on the spurs: *opuntia*, *distorta*, *gracilis* and *macrophysa*, with *opuntia* being much less common than the others. The species *distorta* and *gracilis* sprawled over, through and around the uneven reef surface, and together with *macrophysa*, which has a discrete rather than spreading habit (Fig. 99), filled many of the crevices between living coral heads. *Halimeda macrophysa*, in addition, hung somewhat more openly on the sides of the spur.

At the time of the visit, which was mid-December, some of the branches of *distorta* bore rows of several flabby, relatively uncalcified segments at their growing tips, which I interpreted as indicating very rapid growth. There were also many *Halimeda* segments in the sand in the immediate vicinity of the spur, which could indicate an equally rapid death and separation of older segments. Blue-green algae with unbranched trichomes were associated with the Halimedae. Cover of the spurs by *Halimeda* was estimated as approximately 15%, and the relative conspicuousness of *Halimeda* on them presents a marked contrast to the buttresses of Jamaica where Halimedae were rare. No Rhipsalian species were noted in the vicinity of the spurs, but this observation is not necessarily significant because a search could not be made in the time available.

(b) *Algal ridge and back-reef.* At the seaward edge of this region, where much of the force of the breaking waves is spent, especially on

FIG. 99. Clumps of *H. macrophysa* on a transition buttress on the Islet of Mut, Enewetak Atoll, at depths of 10–15 m.

the windward side, is the *Porolithon* ridge, almost a pure stand of encrusting red algae. The growth form of *Halimeda* is not adapted to the shock of waves as are those of calcareous reds, but the genus does grow, to some extent at least, in the passages and caverns of the surge channels. These are hung with lush green skeins which include the siphonaceous genus *Bryopsis* (Fig. 100). Taylor (1950) reports the *Halimeda* species *opuntia*, *micronesica* and *taenicola* from this approximate region on other Marshall Islands atolls, and they might well grow on some of the seaward reefs at Enewetak. Somewhat landward from the ridge Taylor also reports *opuntia*, *taenicola*, *micronesica* and *tridens* (=*incrassata*), and from the inner reef flat *stuposa*, *opuntia*, *bikinensis* and *lacunalis*, the last two in deep holes.

The part of the seaward reef I could explore most readily was that of the southern tip of Enewetak Islet (south-eastern part of the atoll). Stearns (1945) published on the decadent condition of this particular

FIG. 100. Surge channel behind the algal ridge on the seaward reef of Enewetak Islet, Enewetak Atoll. *Halimeda* grows, to some extent at least, in the passages and caverns of these channels, although it is not shown here. The algal growth on the rock surface includes blue-greens, ulotrichean filaments and lush green skeins of *Bryopsis*.

reef, and Ladd in his visits of 1950 and 1952 found this and some of the other reefs of the windward shores drab (Emery *et al.*, 1954), a condition which has been attributed both to rate of reef growth, and to the effects of bombardment and release of fuel oil during the Second World War. At the time of my visit to the area in 1975 the macroflora was sparse. There was, however, a good growth of smaller algae with much associated fauna. Many of the algae grew in short spongy turfs, and as green and blackish slimy rock coatings. The only *Halimeda* found was *macrophysa*, living in crevices behind the algal ridge, in water several centimetres deep at low tide.

In the abandoned limestone quarry of the inner back-reef of Enewetak Islet sizeable populations of the sprawlers *distorta* and *gracilis* grew, as well as *macrophysa*, and a bushy form of *minima*. The water depth is 1–1·3 m at low tide. This setting is more protected than the open reef flat.

(c) *Inter-island channels.* In the passes between the islets the flow of water across the algal ridge and back-reef continues into the lagoon uninterrupted by land. Most of the passes are shallow, and the current usually moves strongly in only one direction. Odum and Odum (1955), working in one of these channels on the windward side of Enewetak, obtained a maximum current of 1·44 m $sec^{-1}$ during high-water neap tide, and suggested that currents were probably twice this velocity during incoming springs.

The lushest growth of *opuntia* I encountered at Enewetak was towards the lagoon end of one of these channels, the pass between Lojwa and Alembel on the windward side of the atoll (Fig. 97). In its shallow (−2 m to −5 m), well-lighted, fast-moving waters almost every crevice, especially those exposed to full sunlight, seemed filled with this species. Segment shape was particularly variable, and sometimes the segments were tiny, but the characteristics were unmistakably "*opuntia*". Such thalli, presented separately to the taxonomist, could well provoke at least a form epithet or two for the literature. Yet such names, under the circumstances, would have no ecological, and probably no real taxonomic significance. Flow-respirometry of one of these *Halimeda* channels might be expected to reveal productivities as high as any found for the *Halimeda*-free reef flat.

The *Halimeda* species *lacunalis* f. *lata*, *taenicola*, *fragilis* and *micronesica* also lived in these "streams", but in more sheltered locations than *opuntia*. The relatively abundant *lacunalis* f. *lata* grew on the seaward and lee side of corals, often under overhangs provided by the undercut coral bases, or under promontories provided by the surface. Its segments, too, were sometimes dwarfed, and many of the apical segments grazed. In this inter-island channel it was the second most abundant *Halimeda* species; only *opuntia* was commoner. Other Udoteaceae were present too, but never prominent in any of the regions visited. This inter-island channel, lagoonward of midpoint, was one of the two sites with the greatest *Halimeda* species diversity encountered at Enewetak.

(d) *Atom bomb craters.* There are six nuclear craters underwater or in the reef flats of Enewetak which provide sites for *Halimeda* colonists, and I examined two of them, CACTUS and LACROSSE, in December 1975. Both are at the north end of Runit (Fig. 97). The larger, LACROSSE, formed in May 1956, is in the back-reef, whereas CACTUS, formed almost exactly two years later, is more an inpocketing of an inter-island channel (Fig. 85). Both craters are open to the sea, but CACTUS had most of the crater rim submerged, and so was

flushed, in its shallows at least, with flowing reef water. Both craters were floored with very fine sediments, probably including clay-sized particles. I saw no sediments of comparable fineness elsewhere in the atoll. Both sediment bodies were contaminated with radionuclides. These craters are particularly interesting as sites for colonizers, and sites, moreover, with sediments of a size fraction not widespread in the neighbourhood. Unfortunately it is reported that CACTUS crater, the more interesting one, has been filled in as part of the recent clean-up operation on the atoll.

There were no Halimedae in LACROSSE, but a dense, pure stand of a lax form of *incrassata* was found in the centre of CACTUS (Fig. 85). No population count was made of this stand, but it had the appearance of a density of 200 or more thalli per square metre. This stand was in 11 m of water, in the very centre of the crater, where light was poor (visibility was about 1 m), and the water murky with clay or a colloid-like suspension. The bottom was extremely soft and went into suspension at the flick of a flipper. It was also billowed, apparently by worm tubes.

Away from the centre of the crater where the slope of the floor was already apparent but at a depth of about 10 m, the straggling thalli of *incrassata* thinned out and merged into a grove of *Caulerpa ad serrulata*. Tube worms with chitinous tubes were collected in this community. No Halimedae were found in shallower water, and a quick survey during descent suggested that the sides of the crater were barren of plants. The crater also contained a black-tipped shark.

The dense *incrassata* population in CACTUS is of special interest because we found this species to be rare at Enewetak, locating no dense populations other than this one. The species *incrassata* is the principal Rhipsalian *Halimeda* in the sandy and muddy shallows at Glory Be in Jamaica. Possibly this species is restricted at Enewetak by a paucity of fine substrates. But it certainly was able to disperse to this unusual site at Enewetak, and this is one of the few pieces of data on dispersal in *Halimeda* that we possess. It is possible that the dense population was found in the deepest water at the centre of the crater because a vegetative propagule settled there. Had the crater not been filled in, it would have been extremely interesting to see if the resulting clone spread up the sides.

(e) *The lagoon: pinnacles.* With over 2000 coral knolls in the lagoon (Emery *et al.*, 1954) some considerable variation can be expected in their biota. Of the three on which I collected (Fig. 97), Pole pinnacle, north-west of Rex islet, was the most interesting for *Halimeda*, and

possessed the same high *Halimeda* species richness that was encountered in the fast-flowing lagoonward end of the inter-island channel between Lojwa and Alembel. Species of section Opuntia other than *opuntia*, the taxa *copiosa*, *distorta* and to a lesser extent *minima*, achieved prominence on these knolls.

The flattish top of Pole pinnacle lies approximately 4 m below the surface of the water at low tide; its base is reached at about −40 m. *Halimeda distorta* and *macrophysa* filled crevices between colonies of

FIG. 101. Cluster of *H. copiosa* on Pole pinnacle near Rex Islet at a depth of 12–15 m, in December. The thalli are relatively small, with the width of broadest segments shown being 10–14 mm.

living coral on the brightly lighted, essentially horizontal upper surface of this pinnacle, with sizeable, dense clumps of *macrophysa* in places providing almost closed cover. The species *copiosa*, although present near the top with the other taxa mentioned, was more prominent under overhangs lower down (Fig. 101), often growing from under protuberances of the pinnacle. The thalli tended to be small, but this may be a seasonal phenomenon. *Halimeda minima* occurred under such overhangs too, but was not as abundant as *copiosa*, and other *Halimeda*

FIG. 102a. Grove of *H. cylindracea* in the lagoon near Enewetak Islet, Enewetak Atoll, at a depth of approximately 1·5–2·5 m. Young, mature and old thalli are present, with many of the mature and older plants supporting relatively dense epifloral and epifaunal populations. The thalli are also silted. There is a spreading mat of blue-green algae over portions of the sand, and shed segments of *Halimeda* are visible in the sand. Height range of thalli is *c.* 11·5–14 cm.

species were only occasional. On the South Medren pinnacle *gigas* was the most prominent *Halimeda* near the surface, that is at about −10 m. The commonest *Halimeda* species on the three pinnacles in December, both on their more or less horizontal tops and their gently sloping or more often steep sides, was *macrophysa*. *Halimeda macrophysa* also grew in widely scattered clumps on rock patches away from the pinnacle base. These deep-water thalli had few segments, however, in this way differing from the more familiar shrubbier plants of the sun-flooded shallows.

On two of the pinnacles *Tydemania expeditionis* was draped over considerable areas, in water only 8 m deep. Gilmartin (1966) reported it as prominent at the sites of some of his deepest dives in the lagoon, to about −63 m. Lush patches of this alga, which generally has been considered a deep-water plant, were also observed at depths of −3 m

FIG. 102b. The lagoon floor, here near the base of south Medren pinnacle at approximately −40 m, appears to be essentially barren of Halimedae, although the occasional plants were observed. Some of the erect structures in this photograph in the sand near the rock outcrop, height approximately 8 cm, are *cylindracea*.

to −5 m on the lagoon reefs of Jimini. Among green algae *Tydemania* is second only to *Halimeda* as a carbonate producer at Enewetak.

Other noteworthy algal associates of *Halimeda* on vertical or near vertical faces of pinnacles, particularly below 20 m, were species of Cyanophyta, their reddish or purply filaments at times streaming from under overlapping plates of coral colonies. Masses of some of these filaments also grew out of the sand–rock substrate some distance from pinnacles.

These *Halimeda* populations of the sides of pinnacles require more study because they may well be principal suppliers of carbonate to the reef floor. Gilmartin (1960) showed, and our own dives confirm, that the lagoon floors have very low densities of Halimedae growing on them, and yet there are the various bits of drill-core evidence that *Halimeda* segments are important constituents of the lagoonal sediments (Section IX). *Halimeda macrophysa* and some of the Opuntioids growing

FIG. 103a. A part of the grove shown in Fig. 102a, showing the spreading algal mat over loose substrate in the foreground, and overgrowth of the older thalli. The animal mound in the upper left indicates some of the disturbances of the substrate in these communities which might effect the extent of cloning of Rhipsalian Halimedae by "runners" through the sand. Height range of the thalli in this and Fig. 103b is approximately 9 cm.

on the flanks of 2000 pinnacles may be the solution to this problem of the *Halimeda* sediments at Enewetak. We need *Halimeda* production data from pinnacles.

(f) *The lagoon shallows.* Coming to an atoll with the experience of a fringing reef, it would be logical to expect the unconsolidated sediments of shallows, with associated coral rock, to be a prime site of *Halimeda* and carbonate production. There is certainly some, but not what might be expected if the measure is the inshore reef of the Jamaican north shore at Glory Be. At Enewetak the densities of Rhipsalian Halimedae growing on sand are much less striking than on the Jamaican fringing reef. There are more hard-substrate species, but even these do not seem abundant by the standards of a fringing reef.

The shallows on the lagoon sides of the islets have much living or dead coral and rock debris, among which sandy surfaces are not

FIG. 103b. Many of the *H. cylindracea* populations at Enewetak develop in the vicinity of rock although it sometimes is buried, rather than in the more open patches of loose substrate. In the photograph, thalli of *cylindracea* have developed at the edge of rock substrate.

extensive. *Halimeda macrophysa* populations were prominent on rock surfaces or in crevices, sometimes accompanied with lesser amounts of *gigas*. *Halimeda opuntia* was much less extensive than in the island channels, though it sometimes festooned branching *Acropora*. All these populations were greatest in shallow water (as shallow as −1 m), but nowhere were there dense populations like those of *opuntia* in the rapidly moving waters of channels between islets. There also appears to be some geographic separation of populations of rock-attached forms within the atoll because in the northern parts the commonest species was none of the above three, but *lacunalis* f. *lata*. At depths of 1–2 m at low tide it was common near the undercut bases of coral heads and hidden in *Acropora* thickets. It is possible that it is left in these protected places by grazing pressure, for the segments showed clear signs of being nibbled, perhaps by the common parrot fish.

Two Rhipsalian species, *cylindracea* (Figs 102, 103) and *stuposa* (Fig. 72, bottom), were abundant on unconsolidated substrates of the

shallows. As with the rock forms, there seems to be a geographical separation of their ranges, at least to the extent that *stuposa* is mostly restricted to the northern parts of the lagoon (Fig. 98). In shallow parts in the north the two species together formed extensive meadows, though these are not really comparable to the *incrassata* meadows of Jamaica. Perhaps more significantly, these meadows in no way compare to the *Thalassia* meadows of Jamaica, not even in the apparent density of the *Halimeda* contribution to the Jamaican *Thalassia* meadows. It was remarked in the study of Glory Be that a *Thalassia*-dominated community seemed to be involved in stabilizing patches of sand, and that Rhipsalian Halimedae were more abundant near or in these communities than in the open. Part of the low density of Rhipsalian Halimedae at Enewetak, therefore, may be a reflection of the absence of sea grasses. And this absence of sea grasses may be significant to the economy of the atoll.

(g) *The lagoon floor.* If the flats of the lagoon floor were covered with dense stands of Rhipsalian Halimedae, the source of the bulk of the reef carbonate would be explainable in one observation. But the floor is not so covered. This was first demonstrated by Gilmartin (1960) and our observations confirm this (Fig. 102b). There are very low densities of *cylindracea* (called *monile* in Gilmartin's paper), particularly near the bases of coral pinnacles. But for the most part the lagoon floor has few populations of *Halimeda*, and the ones that are there are rock-attached forms on coral blocks, particularly *macrophysa*. Gilmartin (1960) noted changes in the form of *cylindracea* with depth (Fig. 104), and postulated that the paucity of the species on the lagoon floor was a function of two processes: low light intensity and disturbance by burrowing animals. The relative prominence of animal mounds and castings on the lagoon floor near the base of pinnacles in 40 m of water certainly encourages acceptance of Gilmartin's hypothesis. Mounds and diggings show that the bottom is constantly overturned (Fig. 103). Plants growing at light intensities of 5% or 10% of that at the surface may well not achieve sufficiently vigorous growth to survive such constant digging.

### 3. Halimeda *at Enewetak: summary*

There are no obvious rivals to Halimedae as carbonate producers among the green algal macrophytes at Enewetak. *Tydemania expeditionis* is second, but a much lesser producer.

FIG. 104. Habit variation in *H. cylindracea* thalli collected at different depths. The shallowest-growing (top left, −19 m) is bushier, less attenuate and possesses a considerably more extensive holdfast. (Modified from Gilmartin (1960), reproduced with permission.)

At least 14 species are present, of which *macrophysa*, *opuntia*, *cylindracea*, *gigas*, *distorta*, *copiosa* and *lacunalis* f. *lata* appear to be the commonest (Hillis-Colinvaux, 1977). These, then, are the species which would contribute most to the atoll's primary productivity and calcium carbonate budgets.

Except for one collection, we have no information of the species, their species richness or biomass, seaward of the algal ridge. The high cover they provided at this one site, approximately 15% of a spur, presents a marked contrast to the spurs of Jamaica where Halimedae are rare.

It is likely that the *Halimeda* populations of the sides of the pinnacles are the prime producers of the *Halimeda* segments incorporated into the reef mass and thus are prime builders of the atoll. There are few Halimedae on the lagoon floor, and the lagoon floor, therefore, is not a prime source of *Halimeda* sediment.

There are no sea grasses at Enewetak, and this appears to have important consequences for *Halimeda* populations in unconsolidated sediments. Some of the densest sand-growing populations of *Halimeda* elsewhere are in association with sea-grass stands, and these dense stands are therefore not found at Enewetak. Communities of *Halimeda* and other algae do not seem to be able to replace sea grasses on sand substrates of the shallows. Whatever cause keeps sea grasses from Enewetak probably lowers the contribution of the lagoon shallows to the carbonate flux of the atoll.

## XI. Acknowledgements

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# THE INFLUENCE OF TEMPERATURE ON THE MAINTENANCE OF METABOLIC ENERGY BALANCE IN MARINE INVERTEBRATES

R. C. NEWELL* and G. M. BRANCH

*Department of Zoology, University of Cape Town, Cape Town, South Africa*

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## I. INTRODUCTION

The influence of temperature in controlling the abundance and distribution of marine invertebrates has been studied for many years. Early work by Huntsman and Sparks (1924) and by Henderson (1929), for example, showed that the upper limits of thermal tolerance of a variety of marine organisms were associated with both latitudinal and local variations in the environmental temperature range experienced under natural conditions. Gowanloch and Hayes (1927) showed that in *Littorina* there was an intraspecific gradation in thermal tolerance,

* Present address: Institute for Marine Environmental Research, Prospect Place, Plymouth, Devon, England.

upper-shore individuals having a higher thermal tolerance than their counterparts from the lower shore. Subsequently Broekhuysen (1940), Evans (1948) and Southward (1958) have made detailed studies on the sequence of thermal death points in intertidal invertebrates and have established that temperature tolerance shows a general correspondence with local conditions prevailing in the environment. Since that time there have been many studies on the tolerance of extreme environmental conditions by marine organisms. Much of the earlier literature has been summarized by Gunter (1957) whilst the more recent work appears in the comprehensive reviews of Kinne (1970, 1971), Vernberg and Vernberg (1972), and Precht *et al.* (1973).

Briefly, it is generally recognized that the "zone of tolerance" of an organism is defined by an upper and a lower "incipient lethal temperature", both of these values often being modifiable by exposure to long-term changes in environmental temperature. Such acclimatory responses allow the organism to adjust the limits of its zone of tolerance until "ultimate" upper and lower incipient lethal temperatures are reached (Fry, 1947, 1957; Newell *et al.*, 1971b; Precht *et al.*, 1973). At this stage injury to the whole organism or to its biochemical components is irreversible and a great many studies have been carried out on the correlation between the thermostability of tissues and component proteins in marine organisms and environmental conditions (for reviews, see Troshin, 1967). The zone of tolerance is, however, influenced by a wide variety of biological factors as well as by environmental factors other than temperature itself (McLeese, 1956; Costlow *et al.*, 1960; Mihursky and Kennedy, 1967; Cain, 1973; Lough and Gonor, 1973a, b). Age of the test organism (Lough and Gonor, 1973a, b; Kennedy *et al.*, 1974), stages of moulting cycle (Roberts, 1957), water pressure (Schlieper, 1963; Naroska, 1968), the oxygen content of the water (McLeese, 1956; Haefner, 1959, 1960), exposure salinity (Costlow *et al.*, 1960; Zein-Eldin and Aldrich, 1965; Costlow, 1967; Cain, 1973) and the salinity to which the animals have been acclimated, as well as combinations of these factors (McLeese, 1956; Costlow *et al.*, 1960) have all been implicated in controlling the conditions under which survival is possible (for reviews, see Kinne, 1970, 1971; Vernberg and Vernberg, 1973; Newell, 1976, 1979).

Extreme conditions of temperature, especially cold, may have dramatic effects on the survival of marine organisms living intertidally or in shallow coastal waters (Crisp, 1964; Kinne, 1970) and under these conditions it must be assumed that the lower lethal temperature for the organism acquires an ecological significance. Equally, in the case of marine organisms penetrating marginal habitats such as the intertidal zone, saltmarshes and lagoons, the organisms experience environmental temperatures which approach the heat-lethal limit for the species.

In crabs such as *Uca*, for example, the tropical species *U. annulipes* (Milne-Edwards) and *U. chlorophthalmus* (Milne-Edwards) live near to their lethal temperature and have a high upper limit of thermal tolerance which varies rather little between individuals of the population (Edney, 1961, 1962). This would be anticipated as a result of strong selection pressure for a high thermal tolerance in the population (see also Wolcott, 1973).

In other less extreme environments, however, marine organisms normally live well within their limits of survival. This is true of the majority of marine invertebrates, and in this case their ability to survive in a particular situation is controlled not by the tolerance of the species to extreme conditions, but by its ability to grow and reproduce in competition with other organisms with similar tolerance limits. Subtle adjustments of the rates of physiological processes (or "rate functions") within the zone of tolerance of the organisms in response to changes in environmental conditions are identified as "capacity adaptations" to distinguish them from the "resistance adaptations" described above (Precht *et al.*, 1973; Prosser, 1973) and principally determine the ability of the organisms to compete with their neighbours. Of prime importance in this context are processes associated with energy gained from the environment and energy lost through metabolism and excretion, since the amount of energy available for an organism to grow and reproduce is defined by the difference between energy gain and loss. In order to quantify this relationship, the well-known balanced energy equation of Winberg (1956) (see also Odum and Smalley, 1959; Petrusewicz and MacFadyen, 1970) may be applied to the individual when written in the form:

$$A-(R+U)=P+G$$

where $A$ is the net energy absorbed from the food ration (i.e. input $C$ minus faeces production $F$)*; $R$ the energy equivalent of oxygen consumption; $U$ the energy equivalent of excretory and other dissolved organic losses; $P$ the energy equivalent of growth; and $G$ the energy equivalent of the gametes released from the adult (see Crisp, 1971).

If the term $A-(R+U)$ is positive, then there is a net gain of energy from the environment and the organism then possesses "scope for growth and reproduction" (see Warren and Davis, 1967; Bayne *et al.*, 1973, 1976). Alternatively, when utilization of energy exceeds the energy input, the value becomes negative and under these conditions

* Consumption ($C$) minus faecal losses ($F$) is commonly referred to as the "assimilated ration" ($A$). However we prefer to use the term "absorbed ration" for ($A$) and to refer to the net energy gain ($A-R+U$) as the "assimilated ration" actually available for utilization by the organism.

body reserves must then be utilized (Gabbott and Bayne, 1973; Thompson *et al.*, 1974; Gabbott, 1975; for review, see Bayne *et al.*, 1973, 1976c). Cook and Gabbott (1978) have recently explored the mechanism controlling the accumulation or mobilization of glycogen reserves in *Mytilus edulis* L. Except for short periods of time, the maintenance of a positive index of energy balance which allows scope for growth and reproduction is clearly essential for the survival of the individual and the species as a whole. The main purpose of this review is to show how some marine invertebrates may manipulate the components of the metabolic energy balance equation defined above so that scope for growth and reproduction is maintained, despite changes in local environmental conditions.

## II. The Effect of Temperature Change on Individual Physiological Processes

Temperature affects not only the ability of marine organisms to survive in particular environmental situations, but also has a profound effect on the rate of individual physiological functions. Oxygen consumption rates (see Kinne, 1970; Precht *et al.*, 1973; Prosser, 1973), heart rates (Rao, 1953; Segal *et al.*, 1953; Segal, 1956, 1961, 1962; Pickens, 1965; Ahsanullah and Newell, 1971; Bayne, 1975; Bayne *et al.*, 1976a, b, c, d), irrigation (Crozier, 1916), cirral activity of barnacles (Southward, 1964; Crisp and Ritz, 1967a, b; Ritz and Foster, 1968), ciliary activity (Vernberg *et al.*, 1963), feeding rates (Rao, 1953), locomotory activity (McLeese and Wilder, 1958; McWhinnie, 1964; Hand *et al.*, 1965; Rüppell, 1967; Schwab, 1967), egestion rates (Anderson and Reish, 1967; Hylleberg, 1975), enzyme reaction rates (see Somero and Hochachka, 1976), as well as many other processes, have each been studied as a function of temperature.

Much of the extensive literature on the effects of temperature on individual rate functions in marine organisms has been summarized by Kinne (1970), Vernberg and Vernberg (1972), Prosser (1973), Precht *et al.* (1973), Somero and Hochachka (1976), and Newell (1979). It is generally recognized that three distinct time phases can be distinguished in the response of any particular process to a change in environmental temperature.

(i) First, there is a direct (or acute) response of the physiological process to a change in temperature. This may be accompanied by an overshoot followed by a period of stabilization which takes place over a period of minutes or hours (see Precht *et al.*, 1973).

(ii) Second, following longer-term exposure to changed temperature conditions lasting days or weeks, the organism may show an adjustment of its rate functions. When in response to temperature itself, this phenomenon is known as "thermal acclimation" whereas a compensatory adjustment in response to more complex seasonal changes in environmental conditions is distinguished as "seasonal acclimatization" (Prosser, 1973). Caution must be taken when ascribing seasonal changes of metabolic rate to acclimation for, as Parry (1978) has shown, changes of growth rate and production of gametes may alone be sufficient to explain such changes.

(iii) Third, long-term changes in environmental temperature operating over many generations favour the appearance of genetic variants adapted to the new thermal regime.

Both Precht (1958) (see also Precht *et al.*, 1973) and Prosser (1967, 1973) have classified patterns of compensation made in response to a change in environmental conditions. Precht (1958) compared the rates of reaction of indicator processes following transference from one acclimation temperature to another. Following transference to a higher temperature, the rate of reaction increases, whereas when the organism is placed in a lower temperature regime the rate of reaction decreases. If, following this immediate response, there is no further change in the stabilized reaction rate, then no acclimatory adjustment has occurred. This is classified as Type 4. In many instances, however, the stabilized reaction rate in the new temperature regime rises or falls with time, and eventually approaches, but does not reach, the value which is attained in the initial acclimation regime. This is incomplete or partial acclimation (Type 3), whereas a complete return to the initial reaction rate despite the changed thermal regime is termed perfect compensation (Type 2). In certain instances the reaction rate shows excess compensation (Type 1). Paradoxical or inverse (Type 5) compensation occurs when, on transference to a new acclimation regime, the rate of reaction diverges from the original rate even further during the time course of acclimation.

Prosser (1967, 1973) (see also Bullock, 1955) has devised a scheme which includes measurements of the physiological process made not only at a new acclimation regime but also at a variety of other exposure temperatures. An acute rate : temperature curve for animals acclimated to a particular temperature is then used to compare the responses following acclimation to new environmental conditions. Pattern I applies when there is no acclimation, and rate : temperature curves are the same for animals from different acclimation regimes. Pattern IIA is used to describe the response when the rate : temperature curves

are translated to the right or left following warm or cold acclimation respectively. We shall see that this pattern forms an important basis for compensation of both energy input and expenditure in some marine animals. The reverse of this pattern is inverse translation where warm acclimation results in a shift to the left of the rate : temperature curve and vice versa. This is classified as Type IIB. Pattern III is used to describe curves where there is rotation of the rate : temperature curve in response to a change in acclimation conditions, and finally Pattern IV involves a combination of rotation and translation of the rate : temperature curve. Alderdice (1972) has, however, recently shown that the schemes of Precht *et al.* (1973) and Prosser (1973) both represent partial "sections" through complex response surfaces which are best described in multidimensional terms.

Examples of these responses to cold and warm acclimation are widespread in the literature, but are not necessarily of the same type for all physiological processes in one organism, even though processes such as ventilatory activity, feeding rate, heart rate and metabolic rate obviously must be regulated in an integrated fashion. Even though all the processes involved in an adjustment of the organism as a whole to a change in environmental conditions are linked in a complex and integrated fashion, it is convenient to regard the responses of individual physiological processes as falling somewhat arbitrarily into two main categories as far as the overall energy balance of the organism is concerned.

(i) Those, such as irrigation and feeding rates, involved in the acquisition of energy from the environment.

(ii) Those, such as metabolism, which are a measure of energy loss from the organism.

Clearly, in terms of energy conservation, the organism would be expected to make compensatory adjustments to each of these groups of processes in such a way that maximal rates of energy gain are maintained, and energy loss is minimized in the face of a change in environmental conditions.

## III. Strategies for the Maintenance of Energy Balance

Studies in which both feeding rates and corresponding energy expenditure have been measured simultaneously in marine invertebrates are scarce, although a good deal of data now exists on the effects of a variety of environmental factors on either feeding rates or oxygen consumption in marine animals. A further complicating factor is that

it is rather difficult to quantify the feeding rate synchronously with oxygen consumption except in suspension-feeding animals, where the rate of clearance of suspended algae can be used to estimate feeding rate. The work summarized below thus refers mainly to suspension-feeding animals, although some examples are given of the possible energy balance relationships of other organisms where there are data for feeding rates and energy expenditure.

The potential energy gain or loss at a particular food concentration by filter-feeding organisms in different concentrations of suspended food can be calculated from the ratio of the clearance rate ($V_w$, litres of water cleared of particles) to oxygen consumption ($V_{O_2}$, millilitres of $O_2$ consumed). This index (the "convection requirement") can be used as a basis for comparison between organisms under different environmental conditions. Jørgensen (1952, 1960, 1966) found values of 2–20 in *Ostrea*, *Pecten* and several ascidians, whilst similar data on *Pecten* by Van Dam (1954) and Chipman and Hopkins (1954) gave values of 10 (Jørgensen, 1960). Subsequently Vahl (1972, 1973a, b) showed that body size affects the ratio of $V_w : V_{O_2}$ in *Cardium edule*, *Chlamys opercularis* (L.) and *Mytilus edulis*. A decrease in the ratio with increase in body size results in a reduction in energy available for growth and reproduction with increase in body size. Bayne *et al.* (1976a, b) have shown that the ratio of litres of water cleared per millilitre of oxygen consumed varies also with $pO_2$ in *Mytilus* and according to the individual response to declining oxygen tensions. Starved individuals show oxygen-dependent curves (oxyconformers) and may show $V_w : V_{O_2}$ ratios as high as 17 at partial pressures of oxygen of only 40 mm Hg, but the ratio is normally 2–3 in aerated water. McLusky (1973) recently suggested that the ratio of litres pumped per millilitre of oxygen consumed in *Chlamys opercularis* may be modifiable according to seasonal conditions. He found similar values for the filtration rate of *Chlamys* to those reported by Vahl (1972) but the rate of oxygen consumption was higher, yielding a lower value for the $V_w : V_{O_2}$ ratio. Adjustment of the $V_w : V_{O_2}$ ratio may thus be an important index of the ability of suspension-feeding organisms to maintain optimal filtration efficiency in the face of changes in environmental conditions. Strategies for the maintenance or improvement of energy balance are likely to involve an adjustment of the $V_w : V_{O_2}$ ratio so that the maximal volume of water is cleared per unit of oxygen consumed, an increase in the $V_w : V_{O_2}$ ratio at constant ration conditions allowing a greater scope for growth and reproduction.

An alternative compensatory mechanism may involve an adjustment in the filtration rate in response to concentration of suspended matter. Griffiths and King (1979), for example, have shown that filtration in

the ribbed mussel *Aulacomya ater* (Molina) increases dramatically from 0·5 l $h^{-1}$ at algal concentrations of less than $2 \times 10^6$ cells $l^{-1}$ (0.5 mg dry weight $l^{-1}$) to 1·5 l $h^{-1}$ at algal concentrations of $16 \times 10^6$ cells $l^{-1}$ (3 mg dry weight $l^{-1}$). Again, in *Mytilus edulis*, a ration-induced increase in filtration rate occurs, but this is attained at a lower suspended particle concentration of $1 \times 10^6$ cells $l^{-1}$ (Thompson and Bayne, 1974; Schulte, 1975). Such increase in filtration in both *Aulacomya* (see Griffiths and King, 1979) and *Mytilus* (see Thompson and Bayne, 1974) is associated with an increase in metabolism which may partly reflect metabolic costs associated with digestion and absorption rather than with the mechanical costs of irrigation itself (Bayne and Scullard, 1977).

Since the clearance rate and the oxygen consumption may have quite different responses to temperature change, it is clear that various possibilities exist for adjustment of the $V_w$: $V_{O_2}$ ratio. (A) In the first possibility, which we may refer to as Response Type 1, the clearance rate may be adjusted so that maximal rates coincide with the environmental temperature, and at the same time the oxygen consumption, and hence metabolic energy losses, may be relatively reduced following a rise in environmental temperature. An adjustment of the $V_w : V_{O_2}$ ratio is thus a reflection of simultaneous adjustment of two components of energy balance, as occurs in the filter-feeding gastropod *Crepidula fornicata* L. (see Newell and Kofoed, 1977a, b; Newell *et al.*, 1977a). (B) In the second response pattern (Type 2) the clearance rate may be adjusted in response to a change in environmental temperature, but metabolic losses increase sharply with environmental temperature. In this case, compensation of the rate of clearance is solely responsible for the adjustment of the $V_w : V_{O_2}$ ratio, and must compensate for the increased respiratory losses at high environmental temperatures. This pattern of response occurs in the oyster *Ostrea edulis* (see Newell *et al.*, 1977b) and also in the bivalve *Donax vittatus* (see Ansell and Sivadas, 1973). (C) Finally, in the third response pattern (Type 3) the energy input is inflexible and shows no adjustment in response to a change in environmental temperature, but there is a relative reduction of metabolism following warm acclimation. This pattern of response may occur in *Littorina littorea* (see Newell *et al.*, 1971a) and barnacles (Southward, 1964; Crisp and Ritz, 1967a, b; Ritz and Foster, 1968) since in these organisms the rate of radular activity and cirral activity shows only minor compensation in response to a long-term change in environmental temperature. It also occurs in the limpets *Patella granularis* L. and *P. cochlear* Born which experience, for different reasons, reduced food availability (Branch and Newell, 1978; Branch 1978) (see also p. 379). The rate of oxygen consumption, how-

ever, appears to be highly flexible, and shows considerable seasonal adjustment (Barnes and Barnes, 1969; Newell and Pye, 1970a) as well as compensation in response to acclimation temperature (Newell, 1969; Newell and Pye, 1970b, 1971a, b). It may also occur in *Chlamys opercularis* since filtration rates appear to be similar in specimens collected in summer and winter, whereas data from different authors suggest that the rate of oxygen consumption may be subject to seasonal change (Vahl, 1972; McLusky, 1973).

The ability of organisms to sustain energy flow into secondary production, despite the increase in metabolic costs ($R$) which commonly occur with a rise in environmental temperature, may be controlled not only by an adjustment of consumption ($C$) but by an increase of absorption efficiency ($AC^{-1}$), or by a combination of both strategies. Winter (1969, 1970; for review, see Winter, 1978; Newell, 1979) has shown that in both *Arctica islandica* and *Modiolus modiolus* an increase in absorption efficiency, as well as an increase in filtration rate, is implicated in the maintenance of an energy gain as environmental temperatures rise during the summer months. In both bivalves, an increase in filtration rate between 4 °C and 12 °C results in an increased capture of food, although the absorption efficiency at each temperature is generally similar (Table I). However at 20 °C there is a marked

TABLE I. RELATIONSHIP OF FOOD INGESTED, ABSORPTION EFFICIENCY AND ASSIMILATED RATION TO TEMPERATURE IN TWO SPECIES OF BIVALVE[a, b]

| *Species* | *Temperature* (°C) | *Ingested ration* (*mg 24 h*$^{-1}$) | *Absorption efficiency* (%) | *Absorbed ration* (*mg 24 h*$^{-1}$) |
|---|---|---|---|---|
| *Modiolus modiolus* | 4 | 33·5 | 77·5 | 26 |
| (2·31 g dry tissue | 12 | 70·4 | 82·5 | 58 |
| weight) | 20 | 101·5 | 92·9 | 94·3 |
| *Arctica islandica* | 4 | 80·4 | 67·3 | 54 |
| (4·4 g dry tissue | 12 | 161·3 | 67·2 | 108 |
| weight) | 20 | 172·7 | 83·6 | 144 |

[a] After Winter (1969).
[b] In the presence of a suspended cell concentration of $20 \times 10^6$ cells $l^{-1}$.

increase in absorption efficiency and this results in a continuing increase of absorbed ration ($A$) over the entire temperature range of 4–20 °C despite the fact that filtration shows only a modest increase between 12 °C and 20 °C. This increase in absorbed ration may then largely offset the increased metabolic losses which occur as the

temperature rises, and maintains the energetic gain necessary for growth and reproduction.

Obviously, for an increase in absorbed ration to occur in response to an increase in environmental temperature, both digestion and absorption rates must be linked to feeding and ingestion in an integrated fashion. In the absence of a compensatory increase in digestion and absorption, for example, an increase in filtration and ingestion would lead merely to increased faecal losses. Rather suprisingly, there have been very few studies on the influence of environmental temperature on the activity of digestive enzymes in marine invertebrates. Recently, however, Seiderer and Newell (1979) have shown that the activity of the $\alpha$-amylase extracted from the crystalline style of the mussel *Choromytilus meridionalis* can indeed be increased following warm acclimation of the mussels; whether this is achieved by a compensatory increase in enzyme concentration with warm acclimation or by the synthesis of isozymes of $\alpha$-amylase appropriate to the new temperature regime is not yet known. The increased digestive activity may then form an integral part of the improved filtration, ingestion and assimilation which is necessary to offset increased metabolic losses during the warm conditions of the summer months.

### A. *Response Type 1: adjustment of feeding rate and metabolic energy expenditure in response to environmental temperature change*

It is well known that short-term changes in exposure temperature have a profound effect on the rate of ciliary activity and water transport in suspension-feeding animals. Gray (1923) showed that the rate of ciliary activity in *Mytilus* increases with temperature, and Rao (1953) showed that the acute rate : temperature curve for water transport ($ml\ g^{-1}\ h^{-1}$) by *Mytilus californianus* Conrad varied with latitude. Warm-acclimated specimens from latitudes of 34°N. had rate : temperature curves which were displaced to the right compared with curves for mussels collected from 39°N. and 48°N. Subsequently Ali (1970) and Walne (1972) have shown that the filtration rate of bivalves including *Crassostrea*, *Ostrea* and *Mytilus* increases with temperature up to a maximum and then there is a sharp decline. The filtration rate of *Chlamys* is also affected by time of acclimation at 5 °C (McLusky, 1973) and acclimation also affects the temperature relationships of filtration by *Mytilus* (Bayne *et al.*, 1976a, b; Widdows, 1978a). Unfortunately, there are insufficient data collected on these animals to make a detailed comparison of the effects of short-term exposure temperature on both filtration rate and oxygen consumption.

Recent data for the suspension-feeding gastropod *Crepidula fornicata* show that this animal conforms closely to the Pattern I response, in which both filtration rate and energy expenditure from respiration are capable of compensation following a change in environmental temperature (Newell and Kofoed, 1977a, b; Newell *et al.*, 1977a). The clearance rate of *Phaeodactylum* by *Crepidula* at a variety of exposure temperatures, following acclimation to 10, 15, 20 and 25 °C is shown in Fig. 1. It is evident that except following acclimation to 10 °C, the curves are all markedly dependent upon temperature with a well-defined peak within the range of temperatures likely to occur in the environment. An increase in temperature above that to which the organism is acclimated would then lead to a rapid decline in clearance activity unless a compensatory response occurred. In fact acclimation to temperatures above 15 °C results in an obvious lateral translation of the rate : temperature curves for particle clearance. Maximal rates of filtration occur approximately 5 °C above the temperature to which the animals are acclimated, but the lateral translation is not entirely in step with the acclimation, and at 25 °C the maximal filtration rates almost coincide with the temperatures to which the animals have been acclimated. This has the effect of allowing the filtration rate to increase with warm acclimation as is shown in Fig. 1B.

Routine metabolic energy expenditure measured synchronously in the same specimens of *Crepidula* shows a similar lateral translation of the acute rate : temperature curve following warm acclimation, but in this case the response serves to maintain energy expenditure at a uniformly low level despite an increase in environmental temperature. The rate : temperature curves for routine oxygen consumption of *Crepidula* at a variety of exposure temperatures between 5 °C and 32 °C following acclimation to temperatures from 10 °C to 25 °C are shown in Fig. 2. It can be seen that the curves generally increase with temperature throughout much of the range 5–32 °C and do not show the marked thermal optimum at lower temperatures which occurs in the rate : temperature curve for clearance in the same animals. Lateral translation of the rate : temperature curves in this case is in step with increase of acclimation temperature, so that the response serves to maintain oxygen consumption at an almost constant level of between 62 $\mu$l $h^{-1}$ and 75 $\mu$l $h^{-1}$ despite an increase in acclimation temperature from 10 °C to 25 °C. The acclimated rate : temperature curve (in which exposure temperature ($Te$) = acclimation temperature ($Ta$)) for routine oxygen consumption by *Crepidula* is shown in Fig. 2B.

The decline in filtration rate which occurs at temperatures above those to which the animals have been acclimated, coupled with the

FIG. 1. The clearance rates of *Phaeodactylum* by *Crepidula* at a variety of exposure temperatures following acclimation to temperatures (*Ta*) of 10, 15, 20 and 25 °C. (A) Acute rate : temperature curves. (B) Acclimated rate : temperature curve. (After Newell and Kofoed, 1977b.)

FIG. 2. The rate of routine oxygen consumption of *Crepidula* at a variety of exposure temperatures following acclimation to temperatures (*Ta*) of 10, 15, 20 and 25 °C. (A) Acute rate : temperature curves. (B) Acclimated rate : temperature curve. (After Newell and Kofoed, 1977b.)

increase in routine oxygen consumption, results in all cases in a decrease in the irrigatory efficiency ($V_w : V_{O_2}$) at high exposure temperatures. Ratios for $V_w : V_{O_2}$ in *Crepidula* are shown in Fig. 3A. However, the two complementary adjustments in potential energy gain and expenditure which occur in response to warm acclimation profoundly affect the energetics of water transport. Because the maximal clearance rates increase with the onset of warm environmental conditions, whereas routine energy expenditure from oxygen consumption is maintained at a relatively uniform level, it follows that the volume of water cleared per unit of oxygen consumed ($V_w : V_{O_2}$) increases with warm acclimation. The values for $V_w : V_{O_2}$ at each acclimation temperature are shown in Fig. 3B. Acclimation to temperatures from 10 °C to 20 °C evidently greatly enhances the filtration efficiency, whereas acclimation to temperatures above 20 °C results in little further improvement of the $V_w : V_{O_2}$ ratio. It also follows that the energetic cost of filtration ($V_{O_2} : V_w$), which includes a variety of energy-consuming processes other than ciliary activity itself (Newell and Kofoed, 1977a), declines with warm acclimation and reaches minimal values at 20 °C as is shown in Fig. 7A. This value defines the minimal maintenance energy requirement of the animal and can be used to calculate potential scope for growth and reproduction at different ration levels in suspension-feeding animals (see Newell *et al.*, 1977b).

Lateral translation of the rate : temperature curves for filtration and for oxygen consumption in relation to thermal acclimation in *Crepidula* are thus linked to maintain a balance between energy gain and expenditure in the Pattern 1 response. In this way the greatly increased cost of activity which would occur with increase of temperature in the absence of a thermal acclimatory response is avoided. The minimum maintenance energy requirement, and hence the greatest scope for growth and reproduction at a defined ration level, is thus adjusted to coincide with the temperatures prevailing in the environment. It seems likely that this pattern of response may be widespread in suspension-feeding animals. Certainly, in the case of *Mytilus*, an adjustment of filtration rates in response to thermal acclimation (Read, 1962; Widdows, 1973a, b; Bayne *et al.*, 1976a, b) and to latitudinal differences in environmental temperature (Rao, 1954; see also Bullock, 1955) may be associated with compensation in the rate of oxygen comsumption in response to seasonal changes in environmental temperature and thermal acclimation (Newell and Pye, 1970a, b; Widdows, 1973b; Bayne *et al.*, 1976a, b).

A different example is provided by corals which depend on the production of their symbiotic zooxanthellae. In this symbiotic relationship

FIG. 3. The influence of temperature on the $V_W : V_{O_2}$ ratios in *Crepidula*. (A) Acute rate : temperature curves. (B) Acclimated rate : temperature curve. (After Newell and Kofoed, 1977b.)

production by the algae contributes to the organic input available for assimilation. Coles and Jokiel (1977) have measured the rate of production by the zooxanthellae ($P$), and the rate of respiration by coral and zooxanthellae ($R$) at various temperatures. Comparing four species of coral from Hawaii, they showed that both $P$ and $R$ increase with temperature between 18 °C and 32 °C but that $R$ increases faster than $P$, the ratio $P : R$ consequently declining. Assuming that respiration occurs throughout the day and night but that production is limited to daylight, a $P : R$ value of less than 2 would indicate a net consumption of organic materials. For the four Hawaiian species this ratio is reached between 31 °C and 35 °C, which is very close to their lethal temperature of 31–32 °C (Jokiel and Coles, 1977). Corals from Enewetak Atoll experience consistently higher temperatures and their lethal temperatures fall between 34 °C and 35 °C. Two species which occur at both Hawaii and Enewetak have been compared and in both cases $P$ and $R$ appear to have acclimated to the higher temperatures at Enewetak, being lower than the rates for Hawaiian specimens (when measured at the same temperature). However, the ratio $P : R$ is much higher in the Enewetak specimens, only declining to a value of 2 at between 35 °C and 38 °C (Coles and Jokiel, 1977). Thus in this case adjustment of both production (organic input) and respiration has taken place.

### B. *Response Type 2: adjustment of feeding rate, but no adjustment of metabolic energy expenditure in response to environmental temperature change*

The scarcity of data on synchronous measurements of filtration activity and oxygen consumption in relation to temperature following acclimation to controlled thermal regimes again makes generalizations difficult on the possible occurrence of the Pattern 2 response. An absence of an acclimatory adjustment in metabolism is a recognized pattern of response which is widespread in many organisms (Precht, 1958; Precht *et al.*, 1973; Prosser, 1973). Davies (1966, 1967) showed that *Patella vulgata* L. is capable of metabolic acclimation, both seasonally and in relation to its position on the shore. *P. aspera* Lamarck, on the other hand, fails to acclimate and Davies suggests this is one of the reasons that this species is restricted to the lower shore. Similarly the high-shore *Actinia equina* L. acclimates to higher summer temperatures by a translation of its respiratory rate : temperature curve, while the subtidal *Anemonia natalensis* Carlgren fails to acclimate (Griffiths, 1977a).

On the other hand, studies of adjustment of the filtration rate in response to known acclimation regimes have rarely been carried out on the same organisms, neither is the precise environmental temperature known with sufficient accuracy to predict whether a lateral shift in the rate : temperature curve for filtration would result in an enhancement or a stabilization of the rate function with acclimation temperature. As has been shown for *Crepidula*, lateral translation can result in either pattern of acclimated response depending on the amount of shift of the curves in relation to a change in environmental temperature.

Recent work on the oyster *Ostrea edulis* suggests that the maintenance of a positive index of energy balance is achieved by an increase of the filtration rate following warm acclimation, but that this is not associated with a relative suppression of energy expenditure from metabolism (Newell *et al.*, 1977b). The rate : temperature curves for clearance of *Phaeodactylum* by oysters acclimated to temperatures from 5 °C to 25 °C and measured at exposure temperatures between 5 °C and 30 °C are shown in Fig. 4. The data are strikingly similar to those obtained in *Crepidula* under similar experimental conditions. Following acclimation to 5 °C or 10 °C, the oysters show little filtration activity at exposure temperatures between 5 °C and 30 °C. However, following acclimation to temperatures of from 15 °C to 25 °C there is an obvious increase in the thermal optimum for particle clearance which approaches 700 ml $h^{-1}$ at 20 °C in animals acclimated to 15 °C, 600 ml $h^{-1}$ (extrapolated from curve) at 24 °C in animals acclimated to 20 °C, and 500 ml $h^{-1}$ at 28 °C in animals acclimated to 25 °C (Newell *et al.*, 1977b). The acclimated rate : temperature curve (where $Te = Ta$) for filtration in *Ostrea* is shown in Fig. 4B. It is clear that thermal acclimation up to 20 °C results in a marked increase in filtration activity and that a sharp decline occurs above the optimal temperature, much as has been noted for many other bivalves (Ali, 1970; Walne, 1972; McLusky, 1973). The response of filtration activity following thermal acclimation thus resembles that in *Crepidula*, except that the rates decline at 25 °C. It seems likely, therefore, that in *Crepidula* maximal filtration rates can be sustained at higher environmental temperatures than in *Ostrea*.

Curves for the corresponding rates of oxygen consumption of the same animals at different exposure temperatures are shown in Fig. 5. In this case the rates increase throughout the range of exposure temperatures, much as in *Crepidula*, but show little evidence of a compensatory translation in response to warm acclimation (Newell *et al.*, 1977b). In contrast to *Crepidula*, the acclimated rate : temperature curve (where $Te = Ta$) increases with temperature and the routine metabolic energy expenditure of *Ostrea edulis* must therefore increase with

FIG. 4. The clearance rates of *Phaeodactylum* by *Ostrea* at a variety of exposure temperatures following acclimation to 5, 10,15, 20 and 25 °C. (A) Acute rate : temperature curves. (B) Acclimated rate : temperature curve. (After Newell *et al.*, 1977b.)

FIG. 5. The rate of routine oxygen consumption of *Ostrea* at a variety of exposure temperatures following acclimation to 5, 10, 15, 20 and 25 °C. (A) Acute rate : temperature curves. (B) Acclimated rate : temperature curve. (After Newell *et al.*, 1977b.)

FIG. 6. The influence of temperature on the $V_w : V_{O_2}$ ratios in *Ostrea*. (A) Acute rate : temperature curves. (B) Acclimated rate : temperature curve. (After Newell *et al.*, 1977b.)

environmental temperature despite acclimation for as much as 70 days in the laboratory. It follows that changes in the filtration efficiency ($V_w : V_{O_2}$) in *Ostrea* following thermal acclimation are controlled by compensatory responses of the filtration rate rather than by a relative reduction of energy losses from metabolism. Figure 6 shows the ratios for $V_w : V_{O_2}$ for *Ostrea* acclimated to temperatures from 5 °C to 25 °C and measured at exposure temperatures from 10 °C to 30 °C. As in *Crepidula*, the increase in metabolic energy expenditure, coupled with a decline in filtration rate at exposure temperatures above those to which the animals have been acclimated, results in a decline in the $V_w : V_{O_2}$ ratio with exposure temperature. But the increase in filtration rate following warm acclimation between 10 °C and 20 °C more than compensates for the increased metabolic losses, and there is a marked increase in the volume of water filtered per unit of oxygen consumed up to 20 °C. Above 20 °C, however, the ratio falls and reflects the decline in filtration coupled with increased oxygen consumption at 25 °C. As a result of these somewhat different strategies for the maintenance of metabolic energy balance, both *Crepidula* and *Ostrea* thus achieve maximal filtration efficiency at 20 °C. The minimal cost of filtration ($V_{O_2} : V_w$) is achieved at this temperature in *Ostrea* (Fig. 7B) and maximum scope for growth and reproduction thus coincides with that in *Crepidula*.

*Donax vittatus* (da Costa) also evidently exhibits Response Type 2, for Ansell and Sivadas (1973) have shown that between 10 °C and 20 °C acclimation to higher temperatures shifts the filtration-rate : temperature curve to the right so that as temperatures rise, acclimation maintains the filtration rate at a relatively constant level. On the other hand, Ansell and Sivadas suggest that the metabolic rate conforms, increasing as temperatures rise. In fact their data show that reverse acclimation occurs, the respiratory-rate : temperature curve being elevated and rotated anti-clockwise after the animals are acclimated to higher temperatures. The net effect is that at higher temperatures metabolic costs rise steeply while filtration remains relatively constant, placing heavy demands on the animals. The resulting stress is particularly severe when temperatures rise in the spring, for carbohydrate and lipid reserves are then at a low level, following depletion during winter when food is limited. Mass mortalities often occur at this stage as a result of the stress.

It seems likely from these examples that the environmental temperature range over which the clearance rates can be adjusted may restrict the competitive ability of species at the limits of their distributional range. Certainly, in the case of *Mytilus edulis* the filtration rate reaches its maximum in animals acclimated to 10 °C and is significantly

FIG. 7. The rate : temperature curves for the cost of filtration ($V_{O_2}/V_w$) for (A) *Crepidula* and (B) *Ostrea*. Curve for *Crepidula* expressed in terms of an animal of 160 mg dry tissue weight. (After Newell and Kofoed, 1977b.) Curve for *Ostrea* expressed in terms of an animal of 285 mg dry tissue weight. (After Newell *et al.*, 1977b.) Note that the cost of activity declines with warm acclimation and reaches a minimal value at 20 °C in *Ostrea* and 25 °C in *Crepidula*.

depressed at 25 °C (Widdows, 1978a). Although body size affects the rate of filtration (see also Winter, 1973; Thompson and Bayne, 1974; Widdows, 1978a) for similar-sized animals, *M. edulis* appears to be primarily adapted for optimal filtration between 5 °C and 15 °C (see Widdows, 1978a), whereas comparable curves for *Ostrea edulis* L. show an optimum at 20 °C (Newell *et al.*, 1977b) and those for *Crepidula fornicata* indicate that optimal filtration efficiencies can be maintained up to 25 °C (Newell and Kofoed, 1977b). One might predict, therefore, that the ability to maintain optimal values for the $V_w : V_{O_2}$ ratio over the range of environmental conditions prevailing in the habitat is one factor controlling the replacement of one species by another when both are competing for a potentially limiting food resource.

### C. *Response Type 3: no adjustment of feeding rate, but compensation of metabolic energy expenditure in response to environmental temperature change*

The third pattern of adjustment of the $V_w : V_{O_2}$ ratio involves an absence of compensatory adjustment in the feeding rate, but a major suppression of metabolic energy expenditure following warm acclimation. It may be a common response type in intertidal organisms which are subjected to wide and largely unpredictable cyclical changes in environmental temperature with the ebb and flow of the tide. A continuous thermal acclimation of feeding rates to conform with the high environmental temperatures encountered on exposure to air during the summer months would result in feeding rates which were not appropriate to aquatic conditions when feeding occurs. There are no detailed studies in which both feeding rate and routine oxygen consumption have been measured in relation to temperature in the same organism, but there are numerous data on feeding rates in intertidal organisms, some of which show no major adjustment in response to long-term temperature change.

Southward (1955a, b, 1957, 1962, 1964; see also Kinne, 1970), for example, has made detailed studies of the cirral activity of barnacles from a variety of latitudes in response to acute temperature change. He found some evidence of a compensatory adjustment in the rate : temperature curve for cirral activity in response to latitudinal changes in environmental conditions. Intraspecific differences occur in the cirral-activity : temperature curves of *Balanus balanoides* (L.) where the specimens near the southern limit of their distribution at Virginia Beach, U.S.A., continued beating up to 35 °C, whereas in those from Plymouth, U.K., a decline occurs after 31 °C, and in those from Alaska after 30 °C. Some differences also occur in the rate : temperature curves for cirral activity in *Tetraclita squamosa* Pilsbry, but in general the differences at the upper end of the temperature range are not great compared with the major latitudinal changes involved. Subsequently Crisp and Ritz (1967b) showed that in the barnacle *Elminius modestus* Darwin the proportion of animals which were actively beating their cirri varies with exposure temperature, and was modified following acclimation for five months in the laboratory. Maximum activity and cessation of activity occurred at successively higher temperatures as the acclimation temperature was increased from 4 °C to 25 °C. Ritz and Foster (1968) later showed that the rate of cirral-activity : temperature curves for *Elminius* was different in populations collected from Menai Bridge, North Wales, and from Leigh, New Zealand, and that the curves showed

lateral translation in response to warm acclimation (Fig. 8). There is thus a good deal of evidence that in *Elminius* some adjustments of the feeding response occurs following a change in environmental temperature, but the large body of data for other species (Southward, 1964; Kinne, 1970) suggests that although acclimation of cirral activity may account for latitudinal differences between populations (Crisp and Ritz, 1967a), in

FIG. 8. The effect of acute temperature change on the rate of cirral activity of specimens of *Elminius modestus* from Leigh, New Zealand, and Menai Bridge, North Wales. (After Ritz and Foster, 1968.)

most balanoids it is of only minor importance in compensation of energy balance.

Although the rates of particle clearance have not been determined in relation to exposure and acclimation temperature in barnacles, a comparison of the rates of cirral activity and of the oxygen consumption allows some comparisons to be made with $V_w : V_{O_2}$ ratios cited for suspension-feeding molluscs. The rate of routine oxygen consumption and the rate of cirral activity of different specimens of *Balanus balanoides* collected during the summer when the sea temperature was approximately 15 °C were measured by Newell and Northcroft (1965). These values can be used to calculate the cirral-activity : $V_{O_2}$ ratios

shown in Fig. 9. It can be seen that maximal values for the cirral-activity : $V_{O_2}$ ratio occur at, or near, the sea temperature at the time of collection, and that the ratio declines towards high exposure temperatures. In this respect the temperature relationships of the ratios resemble those for other suspension-feeding invertebrates, and it would be of considerable interest to estimate the particle clearance activity

FIG. 9. The effect of acute temperature change on the cirral activity : oxygen consumption (beats $h^{-1}$ : µl routine $O_2$ consumed $h^{-1}$) in a specimen of *Balanus balanoides* of dry tissue weight 1·5 mg. (Compiled from Newell and Northcroft, 1965.)

so that more direct comparisons can be made between the filtration efficiency of such organisms. Barnes and Barnes (1969) have also shown that oxygen consumption in the barnacles *B. balanoides* and *Chthamalus stellatus* (Poli) is subject to marked seasonal variation. The cirral-activity : $V_{O_2}$ relationships may thus be adjusted to coincide with environmental temperatures primarily by modification of the rate of energy expenditure through metabolism, rather than by major adjustment of cirral activity in response to seasonal changes in environmental temperature.

Radular activity in gastropods may also be used as an index of feeding rate (Cornelius, 1972). In the winkle *Littorina littorea* L., the

the radular activity occurs on immersion by the sea following a period of exposure to air. The rate of radular activity varies with short-term exposure temperature and with the period the winkles have been exposed by the tide. Feeding rates on immersion are thus faster in upper-shore animals and in this way the winkles are able to compensate for the reduced feeding time available at upper-shore levels (Newell *et al.*, 1971a). There is some indication of an adjustment of the rate : temperature curve for radular activity of *L. littorea* following acclimation for 14 days to temperatures between 5 °C and 25 °C (Newell *et al.*, 1972a), but compensation is only partial so that the acclimated rate : temperature curve (where $Te = Ta$) generally increases with temperature up to a maximum at 20 °C. The curve for radular activity of *Littorina* collected in July, and measured at a variety of exposure temperatures from 9 °C to 30 °C following acclimation to temperatures from 5 °C to 25 °C, is shown in Fig. 10.

The effects of temperature and other factors on the oxygen consumption of *L. littorea* are known from other studies on winkles from the same locality (Newell and Pye, 1970a, b, 1971a, b, c; Newell and Roy, 1973). These values can be used to calculate the radular-activity : $V_{O_2}$ ratio for *L. littorea* at different exposure temperatures following thermal acclimation. Table II shows the values recalculated from data on the oxygen consumption (Newell and Pye, 1970b) and the radular activity (Newell *et al.*, 1971a) of *L. littorea*. It is apparent that the radular-activity : $V_{O_2}$ ratio following thermal acclimation in these animals generally increases with exposure temperature, reflecting the increase in radular activity which occurs at high exposure temperatures. Following acclimation to low temperatures of 5 °C, however, a maximal ratio of radular-activity : $V_{O_2}$ is achieved at 17·5 °C after which a decline occurs. The acclimated curve (where $Te = Ta$) for the ratio of radular-activity : $V_{O_2}$ reflects more closely the values which are achieved on immersion by the sea. These are shown in Fig. 11 from which it is evident that the radular-activity : $V_{O_2}$ ratio increases with thermal acclimation from 5 °C to 15 °C and then declines at 20 °C. This form of curve is very similar to that achieved by the compensatory adjustments of both metabolism and activity in *Crepidula*, and by compensation of activity alone in *Ostrea*. In *L. littorea*, however, the modification of the radular-activity : $V_{O_2}$ ratio in response to thermal acclimation is achieved mainly by the maintenance of a relatively uniform energy expenditure despite an increase of environmental temperature, rather than by modification of the rate of radular activity. Rate : temperature curves for radular activity are thus similar to one another following thermal acclimation, whereas lateral translation of the curves for

FIG. 10. The effect of temperature on radular activity in the winkle *Littorina littorea* following acclimation to 5, 10, 16, 21 and 25 °C. (A) Acute rate : temperature curve. (B) Acclimated rate : temperature curve. (Based on Newell *et al.*, 1971a.)

TABLE II. $V_{O_2}$ AND CORRESPONDING RADULAR ACTIVITY OF *Littorina littorea* AT DIFFERENT EXPOSURE TEMPERATURES (*Te*) FOLLOWING ACCLIMATION TO TEMPERATURES FROM 5 °C TO 20 °C

| Te | $V_{O_2}$ (μl *mg dry tissue*$^{-1}$ *h*$^{-1}$) | *Radular activity movement* (*mg dry tissue*$^{-1}$ *h*$^{-1}$) | *Ratio radular-activity* : $V_{O_2}$ |
|---|---|---|---|
| *Acclimation temperature 5 °C* | | | |
| 5 | 1·6 | 16·4 | 10·26 |
| 10 | 1·8 | 25·1 | 13·96 |
| 15 | 1·9 | 30·9 | 16·28 |
| 17·5 | 2·0 | 35·8 | 17·89 |
| 20 | 2·3 | 33·8 | 14·69 |
| 25 | 2·2 | 30·0 | 13·64 |
| *Acclimation temperature 10 °C* | | | |
| 5 | 0·9 | — | — |
| 10 | 1·9 | 22·2 | 11·70 |
| 15 | 2·2 | 27·1 | 12·30 |
| 17·5 | 2·6 | 30·9 | 11·90 |
| 20 | 2·2 | 31·4 | 14·28 |
| 25 | 1·7 | 21·9 | 18·77 |
| 30 | 0·2 | 32·4 | — |
| *Acclimation temperature 15 °C* | | | |
| 5 | 1·8 | 15·5 | 8·59 |
| 10 | 1·5 | 20·3 | 13·53 |
| 15 | 1·6 | 25·1 | 15·71 |
| 20 | 2·1 | 32·9 | 15·65 |
| 25 | 1·7 | 40·6 | 23·88 |
| 30 | 1·4 | — | — |
| *Acclimation temperature 20 °C* | | | |
| 5 | 1·3 | 11·6 | 8·92 |
| 10 | 1·4 | 21·3 | 15·19 |
| 15 | 2·1 | 25·1 | 11·97 |
| 20 | 2·5 | 29·0 | 11·60 |
| 25 | 2·7 | 30·9 | 11·45 |
| 30 | 1·2 | 26·1 | 21·75 |

routine metabolism results in values for $V_{O_2}$ which are insignificantly different from one another despite an increase of acclimation temperature from 5 °C to 15 °C. Compensation over an even wider temperature range has been recorded seasonally (Newell, 1973a, b; Newell and Bayne, 1973). The fall in radular-activity : $V_{O_2}$ ratio which occurs at

FIG. 11. The effect of thermal acclimation on the radular activity : oxygen consumption (radular movements mg dry weight$^{-1}$ h$^{-1}$ : µl routine oxygen consumed mg$^{-1}$ h$^{-1}$) ratio in *Littorina littorea*. Compiled from Table II.

20 °C reflects an increase in routine metabolic energy expenditure, rather than a change in radular activity.

In animals such as the carnivorous anthozoans it is difficult to see how adjustment of feeding rate can take place in response to a temperature shift, for these animals rely on chance encounters with their prey. Metabolic compensation may thus be critical for energy conservation in such animals. Griffiths (1977a, b) has shown that in the high-shore *Actinia equina* metabolism is largely independent of temperature between 19 °C and 33 °C in winter ($Q_{10}$ = 1·24) and that acclimation increases this zone of temperature independence up to 37 °C in summer. In addition, exposure at low tide initially results in a high metabolic rate, but within two hours this declines to about 25% of the initial rate. Sassamen and Mangum (1970) demonstrated metabolic adaptation in three actinian species after increases in environmental temperatures. In such animals it can be anticipated that adjustment of metabolic rate will be important because the feeding rate cannot easily be adjusted.

Whether the Pattern 3 response, in which a compensation of feeding activity plays only a minor part in the maintenance of a positive index

of energy balance following a change of environmental conditions, is qualitatively distinct from the Pattern 1 response discussed on p. 338 is not yet clear. Certainly minor adjustments in the rate of cirral activity of barnacles and of radular activity do occur in response to a change of acclimation regime, but there are insufficient detailed data at this stage to establish whether such alterations in rate function make a significant contribution to the overall energy balance compared with the relative suppression of metabolic energy costs which occur with warm acclimation in these animals.

## IV. Conservation of Metabolic Energy Reserves during Periods of Reduced Food Availability

### A. *The energetic cost of activity*

The strategies outlined above suggest alternative ways in which organisms may maintain a positive index of energy balance in the face of a change of environmental temperature. But each mechanism presupposes the presence of food in at least sufficient abundance to meet the routine metabolic energy requirements of the organism. In some instances, such as during the ebb and flow of the tide, there may be cyclical variations in food availability. In this case there may be insufficient food, or environmental conditions may be unsuitable for feeding, so that routine energy requirements for feeding activity cannot be met. In other situations there may be seasonal variations in planktonic food availability such that the energy consumed in filtration and other postural activities associated with feeding exceeds the energy captured from the environment.

Gilfillan *et al.* (1977) have analysed the flux of carbon in the bivalve *Mya arenaria* L. and demonstrated that for seven months of the year, when environmental temperatures and food availability are low, respiratory losses exceed gains from absorption; and during this period both absorption and respiration are kept very low (Fig. 12). Only when temperatures rise and phytoplankton is at a relatively higher level does absorption increase sufficiently to exceed respiration, resulting in a net gain of carbon. The increase in absorption, between May and June, far exceeds the rise expected from the corresponding increase in temperature of 5 °C, rising from 15 $\mu$gC h$^{-1}$ to 121 $\mu$gC h$^{-1}$ in a 100 g animal. Conversely, although respiratory levels at first increase with rising temperature, they decline as sea temperatures rise further. The enormous increase in absorption and the decline of

FIG. 12. Rates of absorption and respiration in *Mya arenaria*. Measurements were made under the environmental conditions of temperature and food availability shown in the two upper graphs. The graph for chlorophyll levels is a running two-monthly mean. Data for carbon gains or losses are for a standard 100 mg (dry weight) animal. (After Gilfillan *et al.*, 1977.)

respiratory costs imply compensatory adjustments of both functions. Interestingly, these adjustments seem to be primarily a response to temperature and not to food availability, for both absorption and respiration remain low in March and April when the spring phytoplankton bloom is at its peak (Fig. 12). Greatest net losses of carbon are experienced in May and in October–November when temperatures are rising or dropping faster than at other times. Widdows and Bayne (1971) have shown that warm acclimation of *Mytilus edulis* results in a temporary calorific imbalance and it may be that temperature adaptation similarly stresses *Mya arenaria*.

It is not surprising to find, therefore, that in these situations marine invertebrates may show prolonged periods of quiescence and thus conserve metabolic reserves until suitable conditions for feeding prevail. For example, Menge (1972) has described how the starfish *Leptasterias hexactis* (Stimpson) has a very low feeding rate in winter, when available food levels are also low. Menge points out that in areas where there is a critical shortage of food, foraging activities will cease because an active starfish will be operating at an energy deficit, metabolic costs in an active animal exceeding the gains from foraging for sparse prey. The starfish *Pisaster ochraceus* (Brandt) similarly nearly ceases feeding in winter (Paine, 1969) and the opisthobranch *Navanax inermis* (Cooper) suffers from an energy deficit in winter and reduces its feeding activities to avoid fruitless searching for food (Paine, 1965).

The energy reserves which can be conserved by a reduction of activity level can be calculated by synchronous measurement of oxygen consumption and activity. In fishes it has been common practice to measure the oxygen consumption as a function of swimming speed in a water tunnel (see Bell and Terhune, 1970). This allows measurement of the maximal, or "active rate" of oxygen consumption as well as a variety of intermediate or "routine rates" of oxygen consumption. The extrapolated value for oxygen consumption at zero activity is then defined as the "standard rate" (Spoor, 1946; Fry, 1947; Fry and Hart, 1948; Beamish and Mookherjii, 1964; Muir *et al.*, 1965; Brett, 1971; Muir and Niimi, 1972). A rather similar approach can be used on motile marine invertebrates. McFarland and Pickens (1965), for example, measured the oxygen consumption of the grass shrimp *Palaemonetes vulgaris* (Say) swimming at various speeds against a water current. They showed that the active rate of oxygen consumption in this animal increased with exposure temperature from 0·4 ml $O_2$ $g^{-1}$ wet weight $h^{-1}$ at 10 °C to 1·0 ml $O_2$ $g^{-1}$ wet weight $h^{-1}$ at 30 °C. The standard rate of inactive animals was in the range 0·12–0·30 ml $O_2$ $g^{-1}$ wet weight $h^{-1}$ over the same temperature range, so that an approximately 3·5-fold reduction in energy expenditure can be achieved with the onset of

quiescence in this animal. In absolute terms, this is equivalent to a saving of between 1·4 and $3{\cdot}6 \times 10^{-3}$ cal $g^{-1}$ $h^{-1}$ depending on the temperature. This effect of temperature may be of importance in intertidal animals which are subject to reduced food availability coupled with high environmental temperature during the intertidal period. In much the same way, Halcrow and Boyd (1967) have shown that in the amphipod *Gammarus oceanicus* Segerstråle there is a 2·5-fold reduction in energy expenditure with the onset of quiescence following routine activity. This leads to a saving of up to $0{\cdot}5 \times 10^{-3}$ cal $g^{-1}$ wet weight $h^{-1}$ in the transition from routine activity to quiescence, and clearly this behavioural response could lead to important economy of metabolic reserves during periods of reduced food availability. Coleman (1976) describes how four species of intertidal neritid gastropod are active when first exposed to air by the receding tide, but as the duration of exposure increases they retreat under stones and into crevices and are quiescent for the remainder of the low-tide period. Respiratory levels are initially high during the active phase, but decline by 20–50% during quiescence.

Endogenous rhythms of activity are common in many animals. The sandy beach isopod *Tylos granulatus* Krauss burrows in the sand at the high-tide mark, only emerging during the nocturnal low-tide period to feed on cast-up kelp. Emergence is rhythmic but is delayed on each successive night to coincide with the low tide which is later each night (Kensley, 1974). Parallel with these activity rhythms, the oxygen consumption of individuals in the population is synchronized and increases from a daytime "basal" level of about 300 $\mu$l $g^{-1}$ ash-free dry weight $h^{-1}$ to a peak of up to 2500 $\mu$l $g^{-1}$ ash-free dry weight $h^{-1}$ during the three hours of emergence (Fig. 13). The lower rates which are maintained for much of the day represent a saving of about 1·373 cal $Kcal^{-1}$ of tissue (Marsh and Branch, 1979). The activity rhythms have a further metabolic advantage, for *T. granulatus* remains buried at a depth of about 30 cm and while surface temperatures rise to 37 °C the animals only experience 24 °C. Conversely when the animals emerge at night, surface temperatures are then about 6 °C lower than at a depth of 30 cm (Fig. 13).

Oxygen consumption as a function of irrigatory activity can be used to estimate the conservation of energy which can be achieved in sessile organisms. Mangum and Sassaman (1969) found a fall of $\times$ 3·45 between the active and standard metabolism of the polychaete *Diopatra cuprea* (Bosc.). Boyden (1972) estimated a value of $\times$ 1·9 for the cockle *Cardium edule*, and values of between 1·94 and 2·32 have been reported for the mussel *Mytilus edulis* (Fig. 14A) (Thompson and Bayne, 1972; Bayne *et al.*, 1973; see also Newell, 1976). This amounts to a saving of

FIG. 13. Rhythms of respiration in *Tylos granulatus*. Each point is the mean of 21 animals (± standard error). The height of the respiratory peak varies with the phase of the moon, being reduced at spring tides, and is shown here at its maximum. The lower graphs show substrate temperatures, at the surface and at a depth of 30 cm where most of the *Tylos* are buried throughout the day. (After Marsh and Branch, 1978.)

FIG. 14. The relationship between irrigatory activity and oxygen consumption in, (A) the mussel *Mytilus edulis* and (B) the gastropod *Crepidula fornicata*. (A) Ventilation rate (ml water $min^{-1}$) and oxygen consumption (ml $O_2$ g dry $weight^{-1}$ $h^{-1}$) in a 1·0 g specimen of *Mytilus edulis* at 15 °C. (After Newell and Bayne, 1973; data from Widdows, 1973b.) (B) Ventilation rate (ml water $h^{-1}$) and oxygen consumption (µl $O_2$ $h^{-1}$) in a specimen of *Crepidula* of 123·9 mg dry weight at 15 °C. (After Newell and Kofoed, 1977a.)

as much as $1{\cdot}8 \times 10^{-3}$ cal $g^{-1}$ dry tissue $h^{-1}$ and a greater saving is achieved at high temperatures, much as occurs in *Palaemonetes*. Estimates for other animals such as the gastropod *Crepidula* fall into a similar range to that cited above. In *Crepidula* the gross cost of routine activity, which includes not only the energetic cost of water transport but also a major component of postural responses, is approximately twice the rate of oxygen consumption of inactive animals (Fig. 14B). On exposure to air, the rate of oxygen consumption falls to a value which is similar to that of inactive animals in water, and the minimal oxygen requirements can then be largely met by aerial gas exchange as in many other intertidal animals (see Newell, 1976, 1979; Boyden, 1972; Newell *et al.*, 1972; Bayne *et al.*, 1976a, b). A reduction in food availability, especially when this occurs with the onset of exposure to aerial conditions, is thus associated with a reduction of activity level in many marine organisms and this yields an approximately two-fold conservation of metabolic reserves compared with those used during routine activity in the presence of food.

A reduction in oxygen consumption during starvation, even in the absence of aerial exposure, has been described in many invertebrates (Roberts, 1957; von Brand *et al.*, 1957; Vernberg, 1959; Duerr, 1965; Barnes *et al.*, 1963a) although in *Thais lamellosa* (Gmelin) an increase has been noted (Stickle and Duerr, 1970; Stickle, 1971). In the shrimp *Crangon vulgaris* Fabricius the active rate of oxygen consumption declines during starvation and steadily approaches the standard rate which is unaffected by starvation over seven days (Hagerman, 1970). In the crabs *Cancer pagurus* L. and *Carcinus maenas* (L.) both a general decline due to starvation and an increase following feeding have been cited (Ansell, 1973; Marsden *et al.*, 1973; Wallace, 1973; Aldrich, 1975a, b). Studies on the barnacle *Balanus balanoides* (Barnes *et al.*, 1963a, b), the limpet *Patella vulgata* (Davies, 1966, 1967), the winkle *Littorina littorea* (Newell and Pye, 1970a, b, 1971a, b) and *Mytilus edulis* (Thompson and Bayne, 1972) suggest that such nutritional factors may not only govern the level of oxygen consumption in these animals but also influence their temperature relationships. Again, in *Mytilus* the rate of oxygen consumption of starved individuals approaches the standard rate and this has a low temperature coefficient of about 1·2. Following presentation of food, however, the rate of filtration increases and oxygen consumption reaches the "active rate" after which it declines over a period of five days towards "routine" levels, the routine rate being more strongly dependent on temperature than the standard or active rates (Thompson and Bayne, 1972; Widdows, 1973b; Bayne *et al.*, 1976a, b).

Aldrich (1975b) has made a detailed study of the rates of oxygen consumption of individual *Cancer pagurus* and *Maia squinado* (Herbst) following starvation and subsequent presentation of food. He showed that both starved and fed crabs have a rhythmical rate of oxygen consumption and that there is a considerable individual variability in metabolism. The metabolism of both starved and fed crabs appears to be governed by the same rhythm, but the amplitude of the cycles of fed crabs is greater than that of starved crabs. This response allows crabs to make periodic feeding excursions whilst at the same time reducing their overall metabolic energy expenditure during periods of food deprivation. It is analogous to the energy conservation during torpor which can be induced by starvation in some desert mammals such as *Perognathus* (Tucker, 1965; see also Schmidt-Nielsen, 1975). Clearly, in this animal and in marine invertebrates periodic arousal is necessary to test the food availability even though it involves an increase in metabolic energy expenditure over a short period of time.

The sandy beach gastropod *Bullia digitalis* Meuschen remains buried in the sand for much of the time, but large numbers emerge when food is cast up on the shore, spreading their feet like sails so that waves transport the *Bullia* up the shore. While buried, *Bullia* consumes oxygen at a rate of about 947 $\mu g\ g^{-1}$ dry weight $h^{-1}$, whilst animals experiencing variable surges of currents (equivalent to tranport by waves) respire at about 2068 $\mu g\ g^{-1}$ dry weight $h^{-1}$. Thus remaining inactive for most of the tidal cycle, or more specifically responding only when food is available, can result in a considerable saving of energy (Brown, 1979). Again, the shallow-water sponge *Tethya crypta* (de Laubenfels) reduces pumping (and hence respiration) at night. Reiswig (1971) suggests the nocturnal reduction is adaptive because prevailing breezes decrease at sunset and water circulation is virtually absent, so that a reduction of pumping prevents "rehandling" of the same water. Pumping also virtually ceases during storms, avoiding sand scour. The crab *Petrolisthes cinctipes* (Randall) is stimulated to filter feed by the presence of amino acids and sugars in the water, all of which are released by plankton, so that feeding is increased or initiated in the presence of food (Hartman and Hartman, 1977). In both animals suspension of activity is related to reduced food availability.

In other animals, suspension of activity may be more long term. The isopod *Tylos punctatus* Holmes & Gay normally emerges nightly at low tide to feed on cast-up algae, but during winter it hibernates, remaining buried for about three to four months at a depth of 20–70 cm. Starvation decreases its rate of oxygen consumption from an initial

117 $\mu$l $g^{-1}$ $h^{-1}$ to about 19 $\mu$l $g^{-1}$ $h^{-1}$, and Hayes (1969) suggests a comparable decline occurs during hibernation.

It seems, therefore, that in the presence of food marine organisms maintain a high level of oxygen consumption and that both energy uptake and expenditure increase with exposure temperature. With a reduction in food availability, energy conservation is effected by a reduction in activity level and the rate of oxygen consumption may then be less affected by an increase in environmental temperature. Behavioural and morphological adaptations may also limit body temperatures and hence metabolic losses. Evaporation (Lewis, 1963; Vermeij, 1973), body or shell proportions and sculpture (Vermeij, 1971, 1973), crypsis (Kensler, 1967), burrowing (Marsh and Branch, 1979), nocturnal activities (Benson and Lewis, 1976) and seasonal migration down the shore in summer (Breen, 1972; Branch, 1975b) may all play a role. The temperature relationships of energy expenditure are discussed in more detail below.

### B. *The effects of temperature on metabolic rate functions*

As has been pointed out (p. 331) the level of metabolic energy expenditure under defined ration levels governs the "index of energy balance" and hence the scope for growth and reproduction which is available for an organism under a particular set of environmental conditions. The influence of temperature on metabolic energy expenditure is thus directly relevant to the maintenance of energy balance, and is of particular importance when ration levels fall below that required to maintain routine metabolism. A minor reduction in the temperature coefficient for oxygen consumption over the appropriate environmental temperature range may then acquire an ecological significance in the maintenance of metabolic energy balance under conditions of thermal and nutritive stress.

The rate of activity itself nearly always increases logarithmically with temperature, and it is not surprising to find that routine oxygen consumption is also dependent upon temperature in marine invertebrates. Rates of oxygen consumption associated with activity are markedly dependent upon temperature in several polychaetes (Mangum and Sassaman, 1969; Coyer and Mangum, 1973), in barnacles (Newell and Northcroft, 1965), in the decapod *Palaemonetes vulgaris* (McFarland and Pickens, 1965), in *Gammarus oceanicus* (Halcrow and Boyd, 1967), in *Crangon vulgaris* (Hagerman, 1969), in many molluscs including *Mytilus* (Bayne *et al.*, 1973), *Donax* (Ansell, 1973), *Chlamys* (McLusky, 1973), *Crepidula* (Newell and Kofoed, 1977a, b) and *Ostrea* (Newell

*et al.*, 1977b), in the echinoid *Strongylocentrotus* (Percy, 1972) and in many other invertebrates.

In contrast to the increase in routine rate of oxygen consumption which occurs with temperature, the standard rate of quiescent invertebrates may show different temperature relationships according to ecological and seasonal conditions. Many intertidal invertebrates including anemones (Griffiths, 1977a), mussels (Read, 1962; Widdows, 1973a, b), limpets (Davies, 1966), littorinids (Newell and Pye, 1970a, b; McMahon and Russell-Hunter, 1973, 1977), stenoglossans (Huebner, 1969), ostracods (Hagerman, 1969) and decapods (Vernberg, 1959) show discontinuities in the curve relating metabolism to temperature (for reviews, see Newell 1969, 1976, 1979; Newell and Bayne, 1973). In some cases there appears to be an ecological pattern in the occurrence of low temperature coefficients. In subtidal organisms such as *Strongylocentrotus franciscanus* A. Agassiz (Ulbricht and Pritchard, 1972), *Anemonia natalensis* (Griffiths, 1977a), lower-shore forms such as *Diopatra cuprea* (Mangum and Sassaman, 1969) and some bivalves (Kennedy and Milhursky, 1972), for example, the respiratory rate even during quiescence increases markedly with temperature. On the other hand, intertidal species which experience major variations in environmental temperature at times of reduced food availability often show very low coefficients for the standard rate of metabolism. *Littorina littorea* (Newell and Pye, 1970a, b, 1971a, b), *Strongylocentrotus purpuratus* (Stimpson) (Ulbricht and Pritchard, 1972), *Macoma balthica* (L.) (Kennedy and Milhursky, 1972), *Actinia equina* (Griffiths, 1977a), *Bullia digitalis* (Brown, 1979) and many freshwater invertebrates which experience wide changes in environmental temperature show standard rates of oxygen consumption which are essentially independent of temperature over at least part of the environmental temperature range. Other intertidal organisms such as *Mytilus* have very low temperature coefficients for standard oxygen consumption (Widdows, 1973b). In *Littorina littorea* the routine rate of oxygen consumption increases markedly with short-term exposure temperature whereas the standard rate of quiescent winkles is much less dependent on temperature, especially in small specimens collected in the summer months or acclimated to high environmental temperatures (Newell and Pye, 1970a, b, 1971a, b). But there are many apparent contradictions, with some intertidal organisms such as *Patella vulgata* (Davies, 1966) and *Patella oculus* Born (Branch and Newell, 1978) showing no major suppression of the temperature coefficient, and some subtidal forms such as the polychaete *Hyalinoecia* showing low values for the temperature coefficient even though this animal does not experience

marked temperature changes under natural conditions (Mangum, 1972).

It seems significant that the temperature range over which the metabolism has a reduced temperature sensitivity can change according to seasonal variations in temperature in *Littorina* (Newell and Pye, 1970a; Newell and Roy, 1973) and *Actinia equina* (Griffiths, 1977a, b) and in response to thermal acclimation in sea urchins (Ulbricht, 1973), *Littorina* (Newell and Pye, 1970b; Pye and Newell, 1973) and *Ligia* (Newell *et al.*, 1976), but many other factors including nutritional level may be involved in the induction of low temperature coefficients for

FIG. 15. The effect of acute temperature change on the routine oxygen consumption of active *Littorina littorea* and the standard rate of inactive animals with the onset of warm environmental conditions. Environmental temperature on the shore at the time of collection is indicated by *TA* 1, *TA* 2 and *TA* 3. (After Newell, 1973a.)

metabolism. Figure 15 shows, for example, the effect of temperature on the rate of oxygen consumption of the winkle *Littorina littorea* collected between May and June when the temperature on the shore rose from approximately 13 °C to 30 °C. It is evident that the oxygen consumption during routine activity generally increases with temperature, and that the temperature beyond which a decline occurs increases with the onset of warm environmental conditions. The routine rate of oxygen consumption thus shows "translation" as well as some evidence of

"rotation" (see p. 334), and is similar in this respect to the routine energy expenditure of many other invertebrates. The standard rate of oxygen consumption of the inactive *Littorina*, however, is much lower than the routine rate and emphasizes the extent to which energy conservation can be achieved in this animal by a reduction in activity during the intertidal period. The standard rate of the quiescent animal also shows a reduced temperature coefficient over the temperature range prevailing in the environment at the time of collection, which leads to a further economy of metabolic reserves as the temperature rises during exposure to air in the intertidal period.

FIG. 16. The effect of temperature on the rate of oxygen consumption of active and inactive *Littorina littorea* of 30 mg dry protein weight collected in June. Superimposed are the rates for subcellular preparations in the presence of various concentrations of pyruvate. (After Newell, 1976; based on Newell and Pye, 1971a.)

There has been a considerable amount of work carried out on possible cellular and enzymic mechanisms which might account for the adjustment of the oxygen consumption of ectothermic organisms in response to changes in environmental temperature. Much of this is outside the scope of this review and is summarized by Hochachka and Somero (1973), Precht *et al.* (1973), Prosser (1973) and more recently by Somero and Hochachka (1976). Nevertheless, it is of interest to note that rates of oxygen consumption of subcellular preparations fall within the range of rates recorded in intact *Littorina* (Newell and Pye, 1971a, b;

Newell, 1973a, b; Pye and Newell, 1973) and in *Porcellio* (Newell *et al.*, 1974), despite the fact that many of the possibilities of control are removed in the process of homogenization. In *Littorina*, for example, rates approaching the standard rate and the routine rate of intact animals can be induced in subcellular preparations by variation of the substrate concentration from 0·01 mM pyruvate to 0·5 mM (Newell and Pye, 1971a), and rate : temperature relationships similar to those occurring in intact *Littorina* can be obtained in subcellular preparations following thermal acclimation prior to homogenization (Newell and Pye, 1971b). The curves for the oxygen consumption of intact and subcellular preparations of *Littorina* acclimated to approximately 17 °C are shown in Fig. 16 and suggest that possibilities for the control of the level and temperature relationships of oxygen consumption can occur in subcellular preparations. Possible mechanisms have been recently reviewed by Somero and Hochachka (1976) and include branch points in metabolism (see Hochachka, 1965, 1967; Prosser, 1973; Markel, 1976) as well as isozymes with kinetic properties which could result in the occurrence of low temperature coefficients for metabolism in a variety of ectotherms (Somero, 1969; Baldwin and Hochachka, 1970; Baldwin, 1971; Hochachka and Somero, 1973; Somero, 1975).

## V. Factors Controlling Metabolic Energy Expenditure

Interpretation of the effects of temperature on the level of metabolic energy expenditure is complicated by the many different endogenous and environmental factors which interact with one another under natural conditions. Environmental factors including photoperiod (Dehnel, 1958; Webb and Brown, 1958; Roberts, 1964, 1967; Unglaub-Silverthorn, 1973), diet (Nelson *et al.*, 1977), salinity (Rao, 1958; Duncan, 1966; Klekowski and Duncan, 1966), oxygen availability (Mangum and Winkle, 1973; Newell *et al.*, 1977a), exposure to air or water (Sandison, 1966; Micallef, 1967; McMahon and Russell-Hunter, 1977; Branch and Newell, 1978) as well as temperature stresses (Newell and Bayne, 1973) have been implicated in control of the metabolic rate of marine invertebrates. Amongst the endogenous factors, excitation due to handling (Newell *et al.*, 1974; Aldrich, 1975a), rhythmical changes (Ansell, 1973; Aldrich, 1975b; see also Naylor, 1976; Marsh and Branch, 1979), body size (Zeuthen, 1953; Hemmingsen, 1960), activity level (McFarland and Pickens, 1965; Halcrow and Boyd, 1967; Thompson and Bayne, 1972; Bayne *et al.*, 1973; Newell and Kofoed, 1977a, b; Newell *et al.*, 1977a, b), nutritional conditions

(Hagerman, 1969; Thompson and Bayne, 1972; Wallace, 1972, 1973; Marsden *et al.*, 1973; Newell *et al.*, 1976) state of reproductive development (Barnes *et al.*, 1963a; Barnes and Barnes, 1969) and many other factors have been shown to affect the level of oxygen consumption.

A further complication is that interactions between environmental factors, between endogenous factors, and between combinations of both are well known. In *Littorina littorea*, for example, the metabolic energy expenditure of small individuals is less affected by acute temperature change than that of large ones (Newell and Roy, 1973; Newell, 1975). Similar effects have been noted in the amphipod *Talorchestia* and in the sand crab *Emerita* (Rao and Bullock, 1954), in the amphipod *Orchomonella* (Armitage, 1962), in *Uca* (Vernberg, 1959) and in the terrestrial slug *Arion* (Roy, 1969). Again, in *Carcinus*, the oxygen consumption of small individuals is not only less affected by acute temperature change than that of larger animals, but it is also more affected by starvation (Marsden, 1973; Marsden *et al.*, 1973). Presumably this is because the higher weight-specific metabolism of small individuals causes utilization of the metabolic reserves more quickly than in large crabs. Equally, in the supralittoral isopod *Ligia oceanica* (L.) the rate of energy expenditure of quiescent animals is influenced by an interaction between body size, temperature and nutritional level (Newell *et al.*, 1976).

The analysis of the possible factors controlling any one indicator process such as oxygen consumption is complicated and has been attempted in only a relatively few instances until recently when multiple regression techniques have been adopted (see Quenouille, 1952; Snedecor, 1956; Alderdice, 1972). The number of possible combinations of "independent variables" is $2^n$ (where $n$ is the number of independent variables) and it is often necessary to use a stepwise analytical solution to reduce the complexity of the final equation (see Effroymson, 1960; Fredette *et al.*, 1967; Roy, 1969). Independent variables are introduced one by one, tested for statistical significance at a prescribed level, and either retained in the equation, replaced by another one or removed. The final result obtained is a shortened mathematical model in which the partial regression coefficients are ranked in order of importance and in which all are statistically significant, but which is less cumbersome than the complete theoretical model based on all combinations of the independent variables. It should be stressed, however, that it is often difficult to combine all possible independent variables into one experimental situation and for this reason the multiple regression models obtained are best regarded as useful

descriptive tools rather than as being of predictive importance in situations where additional variables are exerting an effect.

An analysis of factors affecting the oxygen consumption of the winkle *Littorina littorea* showed that metabolic energy expenditure (log metabolism, *Lm*) varies with log body weight (*Ld*), activity level (*Ac*) and exposure temperature (*Te*) (Newell and Roy, 1973). The curves relating oxygen consumption to temperature were, however, of a complex form, and third- and fourth-order curvilinearity terms for *Te* were necessary to describe the rate : temperature curves. Finally, interaction terms were added. Since small animals were differently affected by exposure temperature than large animals, an interaction term for weight (*Ld*) and exposure temperature (*Te*) appears. Equally, the activity level (*Ac*) varies seasonally, so that an activity term multiplied by the day of the year (*Da*) is necessary. Finally, the effect of exposure temperature varies seasonally, so that we find an interaction between terms for exposure temperature (*Te*) and day of the year (*Da*). The resultant equation based on a total of 697 different observations accounted for 94·9% of the variability of log metabolism (*Lm*) about its general mean and is as follows:

$$\begin{aligned} Lm = & -0{\cdot}003873 \\ & +0{\cdot}3029 . Ld \\ & +0{\cdot}6286 . Ac \\ & +0{\cdot}03359 . Te \\ & -0{\cdot}4441 . 10^{-4} Te^3 \\ & +0{\cdot}8539 . 10^{-6} Te^4 \\ & +0{\cdot}007743 . Ld . Te \\ & +0{\cdot}001123 . Ac . Da \\ & -0{\cdot}8523 . 10^{-4} Te . Da. \end{aligned}$$

This equation may then be used to generate a series of curves relating log metabolism to combinations of different environmental factors. Hypothetical curves for inactive and active *Littorina littorea* on days 56, 125, 147 and 191 are shown in Fig. 17. The development of regions of low-temperature coefficient with the onset of warm conditions during the summer months can be seen. The principal advantage of such a technique is that experimental data, which are often extremely difficult to interpret by mere inspection, can be simplified and the independent variables together with their mutual interactions can be ranked in order of importance.

The technique has also been used to analyse factors affecting the oxygen consumption of the isopod *Ligia oceanica* (Newell *et al.*, 1976). Starvation, as well as exposure temperature, acclimation temperature and body size were introduced as independent variables into the

FIG. 17. The predicted effect of exposure temperature (*Te*) on log metabolism (*Lm*) in *Littorina littorea* collected in February (day 56), May (day 125), June (day 157) and July (day 191) 1970. Data expressed in terms of an animal of 160 mg dry tissue weight ($Ld = 2{\cdot}2$). (A) Active animal. (B) Inactive animal. (Data from Newell and Roy, 1973; Newell, 1975.)

multiple regression equation. The final equations were then used to generate multidimensional stereodiagrams illustrating the effects of combinations of independent variables on energy expenditure in *Ligia*. It was found that in this animal, both thermal acclimation and nutritional level affected the energy expenditure. Regions of reduced temperature sensitivity shifted from 15–25 °C at low acclimation temperatures to 20–35 °C at high acclimation temperatures, much as in the seasonal adjustment noted in the oxygen consumption of *Littorina*. The effects of starvation, as in *Carcinus*, are controlled by body size, starvation time and acclimation temperature. Metabolism is suppressed in small animals sooner than in large ones at each acclimation temperature, and high acclimation temperatures enhance the onset and magnitude of such effects. Thus the complex relationships between the independent variables and metabolism, which could not be interpreted by examination of the 3130 individual observations constituting the raw data, could be quantified and are found to agree well with results for other marine invertebrates.

Clearly, in terms of energy balance, it would be preferable to apply similar analytical techniques to combinations of several indicator processes such as feeding rate, energy expenditure and growth, as well as to combinations of the independent variables cited above. Multifactorial experimental designs and response-surface techniques (see Alderdice, 1972) have been used in a number of studies on the combined effects of several independent variables such as temperature, salinity and $pO_2$ on the survival and development of marine invertebrate larvae (see Haefner, 1959, 1960; Cain, 1973; Lough and Gonor, 1973a, b; Kennedy *et al.*, 1974). More recently, Widdows (1978a, b) has analysed the effects of body size, food concentration, exposure temperature and season of the year on four different indicator processes: oxygen consumption, filtration rate, assimilation efficiency and ammonia excretion in the mussel *Mytilus edulis*. The multiple regression equation obtained could be used to describe and illustrate the complex effects of the environment on integrated physiological indices such as scope for growth, growth efficiency and oxygen : nitrogen ratio (see Bayne, 1975; Bayne *et al.*, 1976c, d; Widdows, 1978b). Response-surface contours can then be generated to predict growth and reproduction under combinations of environmental conditions. As pointed out on p. 331, such indices yield a more complete model of the ability of an organism to grow and reproduce under particular environmental conditions. Such indices of competitive ability of an organism may then help to explain why one species can replace another when both are apparently living within their zone of physiological tolerance.

## VI. Food Availability—a Major Factor Influencing Exploitative Strategy

The metabolic responses of animals to temperature may ultimately depend on the availability of food, in terms of both absolute amounts and predictability of food. For species with abundant food, energy conservation by reduction of metabolic losses may not be necessary or even desirable, whereas in species suffering from a food shortage, metabolic adjustments to reduce energy losses may be critical. Such adjustments can be made by reducing the rate of oxygen consumption or reducing its temperature dependency, or by translation of the metabolic rate : temperature curve.

The relative availability of food can be fairly easily established for some groups of animals. Intertidal barnacles, by virtue of their filter-feeding habits, have progressively less time to feed the higher they occur in the intertidal zone. Barnes and Barnes (1959) have shown that the subtidal *Balanus crenatus* Brugière and *B. rostratus* Hoek have high metabolic rates, low- and mid-shore species *B. cariosus* (Pallas), *B. glandula* Darwin and *Pollicipes polymerus* Sowerby have intermemediate rates, while the extreme high-shore *Chthamalus dalli* Pilsbry and *C. fissus* Darwin have very low rates (Fig. 18). Curiously,

Fig. 18. Logarithmic plot of respiration (μl $O_2$ $g^{-1}$ $h^{-1}$) against body weight (mg) for seven species of barnacles which occur in the upper, mid-, lower- or sub-tidal zones of the shore. (Modified after Barnes and Barnes, 1959.)

high-shore species appear to be unable to compensate for their shorter feeding time by a faster rate of feeding. In fact Southward (1955a, b) has shown the rate of cirral beat to be greatest in the low-level species, although Crisp and Ritz (1970) found that high-water animals have a higher food intake than low-shore individuals of *Balanus balanoides* when first brought into the laboratory. Most low-shore or subtidal species also grow much faster than their high-shore counterparts. Thus the low-shore species, having relatively more food, also have a higher turnover and higher rates of feeding, with less need of respiratory adjustment to minimize energy losses.

A similar comparison can be made between the high-shore actinian *Actinia equina* and the subtidal *Anemonia natalensis*, for sessile high-shore predators have the same problem of limited feeding time. Griffiths (1977a) has shown that on the subtropical South African east coast *Actinia* has a respiratory rate which is about half that of *Anemonia* (Fig. 19). Furthermore, the respiratory-rate : temperature curve for *Actinia* is very flattened between 19 °C and 33 °C in winter ($Q_{10}$ of 1·6 between 19 °C and 28 °C, and 1·0 between 28 °C and 33 °C) while in summer this zone of temperature independence extends to 36 °C due to acclimation. Griffiths (1977a, b) has also shown that *Actinia* acclimates when held at different experimental temperatures while *Anemonia* seems incapable of acclimation (Fig. 19). Thus the high-shore *Actinia* compensates for less food by a reduced level of respiration, temperature independence and seasonal acclimation, while none of these occur in the subtidal *Anemonia*.

Childress (1971) states that pelagic crustaceans and fishes living in deep waters (900–1300 m) have lower metabolic rates than occupants of midwaters (400–900 m), while species living above these depths have the highest respiratory rates. Food availability also declines at depth so that a decrease in the level of metabolism may again be a compensatory adaptation. Almost all carnivorous arachnids have a rate of oxygen consumption which is considerably less than the value predicted by Hemmingsen's (1960) generalized regression for poikilotherms, and Anderson (1970) suggests this is adaptive because food availability is unpredictable. He also draws attention to the particularly low metabolic rates of cavernicolous spiders and harvestmen and relates this to the sparsity of food in caves.

Brown *et al.* (1979) have recently compared oxygen consumption of the temperate South African *Bullia digitalis* with that of the tropical *Bullia* (*Dorsanum*) *melanoides* Deshayes from India, and shown that when measured at temperatures equivalent to those experienced in the field (15 °C and 30 °C for the two species respectively) the respiratory

FIG. 19. Comparison of oxygen consumption in the subtidal *Anemonia natalensis* with that of the high-shore *Actinia equina*. Points are the mean of nine animals (±2 standard errors). (After Griffiths, 1977a.)

rate of *B. digitalis* is an order of magnitude lower than that of *B. melanoides* (Fig. 20). Brown *et al.* (1979) suggest that this is an example of non-acclimation. They show that the rate of reproduction is higher in *B. melanoides* which breeds twice a year as opposed to once, and that *B. melanoides* has a shorter life span of two years while *B. digitalis* has a longevity of at least six years. Brown *et al.* suggest that the slower pace of living in *B. digitalis* may be because of fairly lengthy periods of starvation, which make energy conservation important. Brown and da Silva (1979) have further shown that even in active animals the respiratory-rate : temperature curve for *B. digitalis* is remarkably flat between 10 °C and 25 °C (with a $Q_{10}$ of 1·10) so that the metabolic energy losses are not elevated during exposure to high

FIG. 20. (A) Effects of temperature on the rate of oxygen consumption by *Bullia digitalis*. Data for a standard 750 mg (dry weight) animal. (After Brown and da Silva, 1979.) (B) Comparison of oxygen consumption by *B. digitalis* and *B. melanoides*, measured at their normal environmental temperatures of 15 °C and 30 °C respectively. (After Brown *et al.*, 1979.)

temperatures while the animals are feeding in the intertidal zone. *B. digitalis* failed to acclimate to experimental or seasonal changes in temperature, but this is hardly surprising in an animal whose respiration is independent of temperature over the full environmental range (Brown and da Silva, 1979). It remains to be seen if *B. melanoides*, with its higher living pace, has sufficient food to obviate the need for metabolic adjustments, as its very high respiratory rate suggests. The tropical *Donax incarnatus* Gmelin also respires much faster at its environmental temperature of 30 °C than the temperate *D. vittatus* at 15 °C, suggesting this is a further example of non-acclimation. *D. incarnatus* also has a far higher growth rate, a shorter life and a very high filtration rate (McLusky and Stirling, 1975).

Recent comparisons of the respiratory rates for four patellid limpets (Branch and Newell, 1978; Branch, 1978) support the concept that respiratory adjustments are most important in species experiencing food shortage, and also throw further light on the possible mechanisms of adjustment. Of the species examined, *Patella cochlear* occurs at the low-tide mark, but in such high densities that it is short of food, with consequent density-dependent reduction of growth rate and reproductive output (Branch, 1974a, b, 1975a, b). *P. granularis* is a high-shore species, also experiencing food shortage because of competition (Branch, 1976) and more particularly because food is scarce on the upper shore. In contrast, *P. oculus* and *P. granatina* L. are mid-shore species with abundant food. Feeding rates for the four species are not easily quantified but the rate of faecal production under field conditions (Fig. 21) suggests that *P. granatina* and *P. oculus* have much higher feeding rates than *P. granularis* or *P. cochlear*. Cumulative metabolic costs for the four species (over a period of 24 hours) are given in Fig. 22. *P. cochlear* and *P. granularis* have relatively low metabolic costs when compared with the other two species. *P. cochlear* achieves this low cost because it occurs low on the shore where its body temperature rises above that of seawater only for brief periods. Consequently its respiratory-rate : temperature curve is not adjusted in any obvious way to reduce energy losses. On the other hand, the high-shore *P. granularis* faces the joint problems of food shortage and high air temperatures, and has a number of adaptations minimizing loss of energy. First, the level of its respiratory-rate : temperature curve is suppressed relative to that of the other three species (Fig. 23). Secondly, it has low $Q_{10}$ values (mean 1·6 between 5 °C and 30 °C) so that the high temperatures experienced during low tide do not elevate respiration excessively. Finally, *P. granularis* migrates progressively up the shore so that larger animals are found high on the shore while

FIG. 21. Rate of faecal production in four species of *Patella* at 18 °C. (G. M. Branch and K. Damstra, unpublished data.)

juveniles occur well below mid-tide. Comparison of the respiratory-rate : temperature curves in air and water (Fig. 23) shows that small specimens respire slower in water than in air, so that their occurrence low on the shore ensures low respiration for most of the tidal cycle. The reverse is true of larger animals which occur high on the shore yet respire slower in air. Thus they too ensure low respiratory rates and hence low metabolic energy losses.

In contrast, both *Patella oculus* and *P. granatina* have very high metabolic rates, not only in comparison with *P. cochlear* and *P. granularis*, but also when compared with other species of limpets (Branch, 1978). These high levels are maintained by a number of mechanisms. Firstly the levels of the respiratory-rate : temperature curves are high. Secondly, in *P. oculus* $Q_{10}$ values are also high (mean 2·83 between 5 °C and 30 °C) so that as heating occurs at low tide respiratory rates rise sharply. The oxygen consumption of *P. granatina* has lower $Q_{10}$ values (mean 1·61, 5–30 °C) which indicates the maintenance of a high metabolic rate in spite of the low temperature experienced in the cold water of the west coast to which *P. granatina* is confined. Figure 23H shows that, relative to the other species,

FIG. 22. Cumulative daily oxygen consumption (and expenditure of energy) for standard 100 mg (ash-free dry weight) individuals of four *Patella* spp. Dotted lines indicate the aerial phase of the tidal cycle, and solid lines the aquatic phase. (After Newell and Branch, 1978; Branch, 1978.)

respiration of *P. granatina* is particularly high over the lower temperature range. Finally, *P. granatina* migrates up the shore, so that as in the case of *P. granularis* larger specimens occur highest on the shore. However, the respiratory response of *P. granatina* is quite different from that of *P. granularis*. Small animals occur low on the shore and respire faster in water, while the high-shore larger specimens respire faster in air (Fig. 23). Respiration in both size ranges is thus kept high. Small *P. oculus* remain in shallow intertidal pools where water temperatures may reach 30 °C, while larger specimens occur on bare rocks and are exposed for most of the tidal cycle. Rate : temperature curves for respiration of small and large *P. oculus* (Fig. 23) show that rates differ in air and in water, and that the small animals respire faster in water, particularly over the upper temperature range. Larger animals respire faster in air at higher temperatures (which are only experienced during exposure at low tide), but faster in water over the lower temperature range (experienced during submergence). These responses again

FIG. 23. Rate of oxygen consumption for four species of *Patella* in air and in water. Data for standard animals of 10 mg and 1000 mg ash-free dry flesh weight. (After Branch and Newell, 1978; Branch, 1978.)

elevate the effective rate : temperature curves of both small and large *P. oculus* and *P. granatina*.

Both the lower-shore *Patella cochlear* and the high-shore *P. granularis* may be considered as "conservationist" species. *P. cochlear* has a very slow growth rate and a low reproductive output (Branch, 1976), and experiences food shortage because of intense competition on the lower shore. In this case metabolic losses are reduced because body temperatures are kept low. On the other hand, *P. granularis* experiences extreme conditions on the upper shore and consequently has a relatively low longevity requiring at least a moderate growth rate and high reproductive output to compensate. Since food resources are scarce, conservation of energy is of the greatest importance to *P. granularis*. Conversely, *P. oculus* and *P. granatina* maintain very high respiratory levels, which can be related to extremely high growth rates and reproductive output (Branch, 1974a, b). It seems that these two species are capitalizing on high food availability and adopt an "exploitative" strategy of high energy turnover, which necessarily involves maximizing metabolic energy expenditure.

Thus several animals which experience food shortage (e.g., *Chthamalus* spp., *Actinia equina*, *Bullia digitalis*, *Patella granularis* and *P. cochlear*), either at high shore levels or due to intense competition on the lower shore, can be shown to conserve energy by reducing their metabolic energy losses. On the other hand, other species belonging to taxonomically equivalent groups (e.g., subtidal barnacles, *Anemonia natalensis*, *Bullia melanoides*, *Patella granatina* and *P. oculus*) have more food or a greater time for feeding, and adopt an exploitative strategy with high respiratory rates. Metabolic energy losses can thus be adjusted to allow for conservation or exploitation, and this compensation may involve the level of metabolism, the degree of temperature dependence, relative abilities to acclimate, and relative rates of respiration in air and in water.

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# A HISTORY OF MIGRATORY SALMON ACCLIMATIZATION EXPERIMENTS IN PARTS OF THE SOUTHERN HEMISPHERE AND THE POSSIBLE EFFECTS OF OCEANIC CURRENTS AND GYRES UPON THEIR OUTCOME

LESLIE STEWART

*The Lodge, Claughton, Nr. Lancaster, U.K.*

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## I. INTRODUCTION

In 1973, at the request of the Overseas Development Administration and on behalf of His Excellency the Governor of the Falkland Islands and his Executive Council, I investigated the fisheries in the Islands where acclimatization experiments had taken place with Atlantic salmon, *Salmo salar* L., and with sea trout and brown trout, the migratory and non-migratory forms of the species *S. trutta* L. (During the 1960s I had been responsible for first supplying, and then both supplying and sending, Atlantic salmon and sea trout ova from the hatcheries of the then Lancashire River Board to the Falkland Islands.) I found that, whilst the brown trout had developed and there were sea trout infiltrating into the rivers of the two main islands of the Falklands, the

Atlantic salmon had failed to establish there. In my report (Stewart, 1973) I put forward a theory as to the possible reason for the failure of this species to establish in the Islands and suggested that, as migratory runs of a Pacific salmon species, namely quinnat salmon, *Oncorhynchus tschawytscha* (Walbaum), had been established in the Southern Hemisphere, in New Zealand, investigations of these runs should be made to discover their relevance to the Falkland Islands' experiments and the suitability of this species for possible introduction into the Islands.

Subsequently, I visited New Zealand for about four weeks in March and April of 1975 to investigate the salmon fisheries there, including the intensity of the quinnat salmon runs, characteristics of the rivers and other relevant factors. My investigations led me, ultimately, to visit Tasmania where the first acclimatization experiments with Salmonidae in the Antipodes had taken place and where, I was informed, runs of sea trout were still thought to be present. The Hatchery and Research Station of the Fisheries and Wildlife Division of the Ministry of Conservation at Snobs Creek, Victoria, was visited because of information received that viable brood stocks of quinnat salmon had been established there. Whilst on the mainland of Australia, I also followed up reports that salmon were being caught off the coast near Melbourne, particularly in view of the fact that salmon acclimatization experiments had taken place in Victoria; however, as anticipated, the fish I saw were actually *Arripis trutta* (Forst.), a species of sea fish commonly referred to as "Australian salmon".

There are many complexities involved in establishing populations of salmon species. With certain exceptions, the salmon requires two different environments for various stages of its life-cycle, namely, a freshwater environment for the reproductive and nursery stages and a period in the sea, where it quickly grows, for its main feeding phase. Whilst the freshwater stages of the salmon's life-history can be managed, both in rivers and in hatcheries, no control can be exercised over their natural feeding and migrating habits in the sea; indeed, little factual evidence appears to be available concerning their marine life. As there is such a small amount of critical data to be found on this subject, the drift hypothesis described in this article should not be discounted as unreasonable until it is shown that salmon in the sea move faster to and from their feeding grounds than the mean drifts developed within the ocean currents.

Whilst the Pacific salmon species *O. tschawytscha* has many popular names, including chinook and Sacramento, the term "quinnat" is the one most widely used in New Zealand for this species and this is the term that has been used in this article.

## II. Introduction of Salmonids into Tasmania, New Zealand and the Falkland Islands

There are no indigenous Atlantic or Pacific salmon or trout (Salmonidae) in the Southern Hemisphere and natural infiltration of these species from the Northern Hemisphere cannot occur because of the temperature barrier at the Equator. For more than a century, attempts were made to establish sea-going runs of Atlantic salmon, *Salmo salar*, and some species of Pacific salmon (genus *Oncorhynchus*) in Tasmanian and New Zealand rivers. Migratory runs of quinnat salmon, *O. tschawytscha*, have been established in certain rivers of the South Island of New Zealand but all attempts to introduce sea-going runs of other Pacific salmon species and Atlantic salmon have failed, although small land-locked populations of salmon species can be found in some New Zealand natural and man-made lakes as a result of these experiments. More success has been experienced with efforts to introduce brown trout, *S. trutta*, and rainbow trout, *S. gairdneri* Richardson, which, as a consequence, have become established in some rivers and lakes of Australia (particularly Tasmania) and New Zealand. Trout can also be found in other areas of the Southern Hemisphere, such as parts of Chile and Argentina, where they have been successfully introduced.

One of the most recent attempts to introduce salmonids into the Southern Hemisphere has taken place in the Falkland Islands. Brown trout and runs of sea trout are now established in rivers there though efforts to introduce Atlantic salmon have failed.

### A. *Introduction of salmon into Tasmania and New Zealand*

Motives for introducing species of the genus *Salmo* from the British Isles into Tasmania and New Zealand in the first experiments would appear to be obvious. Colonists arriving from Britain to start new lives there found a dearth of suitable indigenous freshwater fish species to provide both recreation, in the form of angling, and a welcome source of food. According to Thomson (1922), the rivers and lakes of New Zealand originally contained a poor and rather sparse fish-fauna consisting of the grayling, *Prototroctes oxyrhynchus* Gunther, the smelt, *Reptropinna richardsoni* Gill., several species of *Galaxias*, a mud-fish, *Neochanna apoda* Gunther, a lamprey, *Geotria chilensis* Gray, and species of eel. The colonists may also have wished for a tangible link with their old homeland, of which the naming of many of the rivers in the new settlements after British rivers would seem to be an indication. Perhaps, too,

there was a wish to establish game-fish rivers free of all the restrictions experienced in the British Isles. These reasons would also apply in the case of the later Pacific salmon experiments (except for the homeland link) with, presumably, the added incentive of exploitation of any substantial runs established by means of a canning industry or other food-processing procedures.

Whatever the motives, the history of the attempts to introduce salmon species, in particular, into Tasmania and New Zealand is an interesting one.

## 1. *Introduction of salmon into Tasmania*

The island state of Tasmania is the smallest of the Australian states and is separated from the mainland by the 240 km of the Bass Strait. It extends 290 km north to south and 305 km east to west, and is broken up by a continual succession of hills and mountains. The altitude, which rises to over 1220 m on the central plateau, causes a considerable variability of climate. Yearly rainfall varies from an upper limit of 368·3 cm at Lake Margaret on the west coast to a lower limit of 48·2 cm in the midlands. Topography and rainfall result in high-altitude lakes and many swift rivers flowing from the central highlands, which have now been extensively harnessed for the production of hydro-electric energy. Tasmania has a cool temperate climate similar to that of New Zealand, with a warm summer, mild winter and considerable diurnal range of temperature; the mean annual temperature at Hobart is 12·4 °C. February is generally the hottest month, when the mean maximum temperature at Hobart is 21·4 °C. The island is substantially free from mist, fog, dust and other air impurities. In winter, frosts are common. Tasmania was first settled by the British in 1803.

(a) *Atlantic salmon* (Salmo salar). As long ago as the 1840s thought was being given by the colonists as to methods whereby Atlantic salmon from the British Isles could be introduced into Tasmania. In 1849, Sir William Denison wrote to Earl Grey on the subject, saying, "Several attempts have been made to bring out the spawn, but they have all failed", though there is no record of such experiments which possibly utilized convict vessel sailings to carry ova. The first documented attempt was that made by a Mr Gottlieb Boccius, who was officially employed by the home government, through the Land and Emigration Commissioners, to transport 50 000 salmon and trout ova from England to Tasmania on the ship *Columbus* in 1852. Mr J. L. Burnett described the method used, thus:

> About 50,000 ova of salmon and trout were placed in a large oval tub or vessel with a false bottom, 4ft. 6in. by 3ft. 4in., 1ft. 8in. deep, double sided, made of wood, cased in lead, and capable of containing 60 gallons of water, besides the requisite quantity of gravel . . . . The tub was slung just under and on one side of the fore hatchway, with directions that every six hours a fresh supply of six gallons of water should be added by means of a funnel inserted in a tube entering below the false bottom, the old or original quantity (or the greater portion of it) being drawn off by a stop-cock placed for that purpose in the upper part of the tub, and that the six gallons of water were to be supplied six times a day as the vessel approached the Equator, making 36 gallons in the 24 hours, and to be again reduced in the cooler latitudes to the original quantity of 24 gallons per diem.

The ship having sailed on 31 January, 1852, Boccius fixed 15 and 20 April as the dates upon which the trout and salmon ova would hatch, but hatching actually commenced on 1 March, in latitude 14° 30′ N., longitude 26°W., and alevins were seen in the tub until the water became thick and putrid. No traces of either ova or fish were found when the ship reached Hobart. The experiment, which had cost £300, failed because, it was said, Boccius did not shelter the ova from injury resulting from the motion of the ship and because he made no provision for maintaining a low water temperature.

In 1854, Mr James, later to become Sir James, Arndel(l) Youl, a Tasmanian (Fig. 1), began to study the subject and came to the conclusion that the governing principle in transporting ova must be the retardation of the development of the embryos beyond the average natural period. Experiments which were carried out at Crystal Palace in London established the extreme limits of hatching time from the date of fertilization as being between 35 days and 140 days, depending upon temperature. (Whilst Youl and others considered the introduction of ova as the best means of establishing salmon in the Antipodes, there was a body of opinion in Tasmania which favoured the introduction of "live salmon" for this purpose, and, in fact, a Royal Society of Tasmania committee reported "that the mere introduction of spawn . . . ought not of itself to entitle the person introducing it to any portion of the reward" (i.e. a Parliamentary reward of £500 for the introduction of salmon into Tasmania). Sir Thomas Brady demonstrated the possibility of carrying live fish to the Antipodes when he successfully conveyed some 12-month-old fish to the south of the line "where their deaths were caused by improper food" (Seager, 1889).) In 1860, Youl arranged for 30 000 salmon ova to be collected from the River Dovey in Wales and shipped in the *Sarah Curling* sailing from Liverpool, in an experiment

FIG. 1. Sir James Arndel(l) Youl. (Photograph: Inland Fisheries Commission, Tasmania.)

carried out through the efforts of a body of colonists then in England, known as the Australian Association. The ova travelled in an ice-house, with a gentle and continuous stream of water passing over them as they lay in swing trays, but the 15 tons of ice gave out and the last of the ova was found to be dead when the ship was 68 days out, the temperature then being 23·8 °C.

Despite this failure, the Governments of Tasmania, Victoria and Southland (New Zealand) voted £3000, £500 and £200 respectively for further experimentation. Another shipment of salmon ova from the British Isles, under the direction of the Australian Association, was authorized by the Tasmanian Government and, after visiting breeding establishments in Scotland and Ireland and journeying to France to study methods used there for transporting fish ova, Youl arranged for the charter of a small steamer, *Beautiful Star*, which sailed on 4 March, 1862, with 80 000 salmon ova, chiefly obtained from the River Dovey,

on board. Most of the ova were laid on gravel in swing trays with a constant supply of water flowing over them and the whole was enclosed in an ice-house. As an experiment, 300 of the ova were packed in moss in a perforated pinewood box and embedded in the ice. The ice gave out on the voyage, being all gone by 17 May, but the ova in the box survived for eight hours after the death of all the others.

The preparation of ponds on the Plenty River in Tasmania to accommodate the expected salmon, together with the experiment, had cost £1410 and, although Youl had contributed his time and also £200 of his own money towards the perfection of details, he was abused by most of the colonists and the colonial press. Honorary Salmon Commissioners had been appointed by the Tasmanian Government in 1861 to manage the acclimatization of salmonids in the island and the Commissioners gave the conduct of another trial to send out ova again to the Australian Association, which immediately delegated the sole superintendence of it to Youl, a member of the Association. After carrying out, in 1863, further experiments with ova in one of the vaults of the Wenham Lake Ice Company in London, Youl took advantage of free space offered in the sailing ship *Norfolk* (Fig. 2) in 1864 to send 100 000 salmon and 3000 brown trout ova, from various British rivers, in 181 perforated pinewood boxes, each containing charcoal, broken ice and living moss; these boxes were packed closely together on the floor of an ice-house, with nine cubic feet of ice piled on top of them. The ship sailed from London on 21 January and, when the ice-house was unsealed in Melbourne on 15 April following, it was found that many of the eggs were still alive. Four thousand salmon ova were left for the colony of Melbourne and the rest were sent to Hobart by Government steamer, thereafter to be taken by another steamer to within four miles of the Plenty Hatchery, to which they were transported overland by bearers. According to the 1864 report of the Tasmanian Salmon Commissioners, the first trout made its appearance on 4 May, followed on the succeeding day by the first salmon. By 25 May, when all the surviving trout eggs had hatched, there were 300 trout and 700 salmon alevins in the hatchery. The salmon ova continued to hatch in thousands until 8 June and 2000 of the survivors were allowed to migrate to sea as smolts from the ponds in 1865. Of the 300 trout, many died; about 30 were liberated in the River Plenty whilst six pairs reached maturity and spawned in their ponds. The descendants of these trout are now to be found in many rivers, streams and lakes of Tasmania, Victoria and New Zealand.

Once Youl had achieved success with his methods of transportation, other shipments of Atlantic salmon ova were made. Table I gives details

FIG. 2. *Norfolk*. (Photograph: National Maritime Museum, Greenwich, England.)

TABLE I. SUCCESSFUL ATLANTIC SALMON OVA SHIPMENTS TO MELBOURNE AND TASMANIA, 1861–1887[a]

| *Year* | *Number of ova shipped* | *River of origin (British Isles)* | *Ship and consigner* | *Destination* | *Number of ova survived journey* |
|---|---|---|---|---|---|
| 1864 | 100 000 | Dovey, Ribble, Hodder, Severn, Tweed | *Norfolk* (Youl) | Melbourne<br>Tasmania | 4000<br>29 700 |
| 1866 | 102 500 | Ribble, Hodder, Itchen and tributaries, Severn, Teme, Tyne, Tweed | *Lincolnshire* (Youl) | (Melbourne)<br>Tasmania | —<br>40 000 (including sea trout) |
| 1876 | ? 85 000 (Total of 175 000 intended for Australia and New Zealand) | Hodder, Severn, various Lancashire rivers | *Durham* (Youl and Buckland) | Melbourne | > 30 000 |
| 1884 | > 80 000 | Irish rivers | *Abington* (Youl) | Tasmania | > 4400 |
| ? | 10 000 | ? | *Tainui* | Tasmania | "Large percentage" |
| 1885 | 160 000 | Erne, Blackwater | *Yeoman* (Youl) | Tasmania | > 27 900 |

[a] Of a total of more than 452 500 Atlantic salmon ova shipped from the British Isles to Melbourne and Tasmania during the years 1864–1885, at least 136 000 ova survived the journey. The comparative failure of the *Abington* shipment in 1884 was due to a defect in the drainage of the ice-house on board ship.

of successful shipments of Atlantic salmon ova from the British Isles to Tasmania (and Melbourne) during the 26-year period, from 1861 to 1887, first managed by the Tasmanian Salmon Commissioners. Experiments took place for over 50 years (Thomson, 1922).

After the first successful importation of Atlantic salmon ova into Tasmania, the colonists were sanguine in their hopes of establishing migratory runs of these fish in the Antipodes, using the Plenty Hatchery as a centre to produce and distribute ova and fry to the colonies on the mainland of Australia and New Zealand. Of the successful establishment of such runs in Tasmania itself, they had little doubt. In 1864, the Salmon Commissioners said, in their report to the Governor-in Chief:

> Few countries of the same extent possess more rivers suited to the nature of this noble fish than Tasmania. A stranger acquainted with the Salmon rivers of Europe could scarcely behold the ample stream and sparkling waters of the Derwent without fancying that they were already the home of the king of fish.
>
> And the Derwent is but one of many other large and ever-flowing rivers almost equally suited to become the abode of the Salmon. When these rivers have been stocked, they cannot fail to become a source of considerable public revenue, and of profit and pleasure to the people.

From personal observation of many of the rivers of Tasmania, I can verify that their appearance is similar to some of the salmon rivers of the British Isles.

In the years that followed, the brown trout flourished; it still flourishes today in Tasmanian and New Zealand rivers and lakes and in certain rivers and lakes on the mainland of Australia. (Other freshwater fish species, including rainbow trout, *Salmo gairdneri*, and American brook trout, *Salvelinus fontinalis* Mitchill, were introduced into Australian waters later.) Regarding the sea trout, 900 fry were raised from the *Lincolnshire* consignment of 1866, of which 12, after reaching maturity, spawned in the Plenty ponds; 500 fry hatched from this stock were released into the River Huon. For several years, a breeding stock of sea trout was kept in the Plenty ponds to produce ova for distribution in the rivers of Tasmania and of the other colonies and, whilst the fertility of the imprisoned sea trout was at first exceptional, the Tasmanian Salmon Commissioners' report for 1876 noted, "It has been found . . . for the last two seasons that an increasing proportion of the ova of the last named fish (salmon trout) have proved infertile". Despite subsequent importations of sea trout ova into Tasmania, very few records now exist concerning any stocks of these fish there, although rumours of their presence in the waters off the west coast still persist.

There is no conclusive evidence that migratory runs of sea trout have ever established in the rivers of Tasmania or of the mainland of Australia.

After my return to this country, I examined a number of scales which were taken from trout caught in the Derwent and Gordon river system and kindly supplied by Mr D. D. Lynch, Commissioner of the Inland Fisheries Commission, Hobart, Tasmania. These fish varied in length and weight from 44 cm to 58 cm and from 992 g to 2·26 kg respectively. With one exception, all were five years of age. Three had spawned once during their lifetime and one had spawned three times. From my examination of the scales, I concluded that all these fish had fed in areas highly productive of food but none had the usual characteristics found in sea trout around the British Isles.

During the early years of the attempts to naturalize Atlantic salmon in Tasmanian waters, an amount of £30 was offered by the Government of Tasmania for the capture of the first salmon or grilse. This reward was claimed by Mr Joseph Cronly, in December 1873, in respect of a fish captured from a pool on the mud-flat immediately below the causeway at Bridgewater and he was paid on the recommendation of the Salmon Commissioners after inspection and examination of the fish. Captures of other fish believed to be salmon were made and it was reported that many were being netted and sold in Hobart. The head of a fish weighing 13·2 kg, caught in February 1878, was sent to a Professor McCoy who, after examination, pronounced it to be from a "true salmon (*Salmo salar*)" and a further specimen captured by rod near New Norfolk was forwarded to the International Exhibition at Sydney.

Despite this and other scanty evidence, there is reasonable doubt that a substantial sea-going run of Atlantic salmon was ever established in Tasmania and there is no evidence that such a run exists there today. In the words of W. Saville Kent, the Queensland Commissioner of Fisheries, when referring to this subject in 1872: "the attempts to stock Tasmanian streams with the true salmon have utterly failed. The young fish have thriven magnificently until their departure for the sea as smolts, at which stage they have simply vanished from human sight . . .." With regard to the mainland of Australia, there is no proof that a migratory run of this species was ever established.

(b) *Pacific salmon* (*genus* Oncorhynchus). In 1872, the United States Commission of Fish and Fisheries, later the United States Bureau of Fisheries, established a station (Baird Station, California) on a tributary of the Sacramento River for the purpose of collecting ova from quinnat salmon, *O. tschawytscha*, for transplantation into foreign waters, and

this station formed the source of supply for millions of ova which were shipped to many parts of the world. Additional stations were subsequently established in Oregon and Washington by the Bureau of Fisheries and, after 1900, they supplied ova and young of other species of Pacific salmon to various parts of the world for transplantation purposes.

Quinnat salmon ova sent from the Sacramento in 1874 died in transit to Australia (D. Lynch, personal communication). Nicols (1882) states that a consignment of 50 000 ova from the Sacramento was despatched to Australia in 1876 by Spencer F. Baird; half of these ova were unloaded at Sydney and according to Baird "most of the living eggs were successfully treated and placed in Australian waters". In 1877, 500 eyed ova arrived and it appears that fry developed from them were liberated in the rivers between the Glenelg River in the west and the Snowy River in the east (D. Lynch, personal communication). There have been subsequent importations of quinnat salmon into Victoria. I saw several fish of this species retained in outdoor tanks at the Snobs Creek Hatchery and Research Station, Victoria, but they were far from resembling the bright, healthy specimens of fresh-run quinnat salmon that I witnessed being caught in the Rangitata and Waitaki Rivers in New Zealand.

In Tasmania, the Salmon and Freshwater Fisheries Commissioners began to think of importing quinnat salmon from New Zealand some decades after the first Atlantic salmon importations had taken place there. Importations of quinnat salmon ova, including 494 000 received direct from the Sacramento during the period from 1901 to 1910, continued on a regular basis for many years; for example, 75 000, 100 000 and 25 000 ova were imported into Tasmania from New Zealand during the years 1928, 1929, and 1934, respectively. Quinnat salmon were liberated in the Derwent and Forth Rivers but, apart from one fish caught at the mouth of the Plenty River in March 1931, records of other catches, if any, are not available. Following the lack of success of liberations in streams, quinnat salmon were liberated in Great Lake in April 1930, and several females were caught in the spawning run at Liawenee in 1936 (D. Lynch, personal communication). An attempt to introduce sockeye salmon, *O. nerka* (Walbaum), from Canada into Tasmania at the beginning of this century appears to have failed.

It seems that attempts to establish sea-going populations of Pacific salmon species, particularly quinnat salmon, in rivers of Tasmania and of the mainland of Australia have met with the same lack of success experienced in the efforts to establish sea-going populations of Atlantic salmon there. Davidson and Hutchinson (1938) say that a

demonstration of the unfavourable influence of coastal waters of high temperature and salinity on the marine survival of quinnat may be found in the failure of these attempts.

## 2. *Introduction of salmon into New Zealand*

New Zealand is composed of two main islands, the North Island and the South Island, with areas respectively of 114 244 $km^2$ and 149 879 $km^2$; the combined length of the North and South Islands is approximately 1600 km and neither exceeds 448 km in width. The Islands lie between latitude 34° S. and 47° S.

New Zealand is a geologically new land of volcanoes, earthquakes, alpine ranges and restricted lowlands. Less than one-quarter of the land surface lies below 198 m and an area almost as large exceeds 1069 m in elevation. The landscapes in both Islands are often spectacular as, in addition to the high mountain ranges and volcanoes already mentioned, glaciers, geysers and pumice deserts can be found there.

At Auckland, North Island, the mean air temperature for January is 19·3 °C and for June 10·7 °C, whilst at Invercargill, South Island, the mean air temperature for January is 14 °C and for June 5·2 °C; between the east and west coasts of both Islands, there is a variation of about 3 °C. Temperatures in the mountainous regions of the South Island often fall below freezing point and, on some of the mountains, there are permanent snowlines. Most parts of the Islands have a maritime type of climate and there are large annual totals of clear blue skies with frequent periods of sunshine. Winds are westerly and the movement of air is far from being regular. The strongest wind speeds generate anticyclones which move towards the north. Storms are confined, in the main, to the mountainous regions.

There are marked rainfall and temperature differences across both the Islands. In the North Island, where cyclones of tropical origin can cause heavy downpours to fall over the greater part of the Island, the average rainfall is about 101 cm per annum. In the South Island, there is a difference in the amount of rain falling on the east and west sides of the mountain ranges, with the Southern Alps producing the highest rainfall. An average of 304 cm per annum falls on the western part of the South Island and, in Fiordland, around Milford, rainfall of up to 635 cm per annum has been recorded. In contrast, the annual average rainfall is between 76 cm and 89 cm in the lowlands of Canterbury and even less on the interior plains of Otago, where the average is between 50 cm and 63 cm per annum.

The magnitude of the river flows of New Zealand overshadows completely those of the British Isles. Table II shows the comparative peak discharges of various major rivers of Great Britain and New Zealand.

New Zealand was settled by the British in the nineteenth century. Efforts to introduce Salmonidae there commenced within a few years of the first Tasmanian experiments.

TABLE II. COMPARATIVE PEAK DISCHARGES OF VARIOUS RIVERS OF GREAT BRITAIN AND NEW ZEALAND

| *River, Great Britain* | *Year* | *Flow* (cusec)[a] | *River, New Zealand* | *Year* | *Flow* (cusec)[a] |
|---|---|---|---|---|---|
| Tay | 1954 | 42 400 | Buller, S.I. | 1950 | 437 300 |
| Tyne | 1962 | 42 000 | Wairoa, N.I. | 1948 | 404 100 |
| Dee | 1937 | 40 000 | Haast, S.I. | 1950 | 260 000 |
| Spey | 1956 | 34 200 | Rangitikei, N.I. | 1897 | 232 000 |
| Thames | 1894 | 27 000 | Waiapu, N.I. | 1924 | 230 000 |
| | | | Mohaka, N.I. | 1938 | 225 000 |
| | | | Wanganui, N.I. | 1904 | 219 000 |
| | | | Waimakariri, S.I. | 1950 | 195 000 |
| | | | Mataura, S.I. | 1913 | 177 000 |
| | | | Rakaia, S.I. | 1947 | 160 000 |

[a] 1 cusec × 0·0283 = 1 $m^3 s^{-1}$.

(a) *Atlantic salmon* (Salmo salar). The first attempt to acclimatize Atlantic salmon in New Zealand was made in 1864 by a Mr A. M. Johnson, who shipped 600 "young fish" on board the *British Empire*, bound from London to Canterbury, as part of a consignment of several freshwater fish species including gudgeon, *Gobio gobio* (L.), barbel, *Barbus barbus* (L.), and tench, *Tinca tinca* (L.). He provided snails and plants in the fish tanks, contrivances for aerating the water and a framework case for the tanks, lined with double mattings of cane which were kept constantly wet throughout the journey through the tropics. With the exception of a few golden carp, *Carassius auratus* (L.), which survived the journey, the whole experiment was unsuccessful (Thomson, 1922).

The next attempt was made by the Provincial Government of Otago which ordered 300 boxes of 100 000 salmon ova, mostly from the River Tay with some from the River Severn, and these were sent out on the *Celestial Queen* in 1868. The boxes were packed by Youl according to

his successful method and, whilst all the ova died in 77 of them, about 8000 healthy ova were taken from the others after arrival in New Zealand; approximately 500 smolts developed from these and escaped into the Waiwera, a tributary of the Clutha River, in 1869.

Details of shipments of Atlantic salmon ova made to New Zealand from 1868 to 1911 are shown in Table III. The ova were chiefly obtained from rivers of the British Isles though some were also obtained from the River Rhine and Canadian rivers. In addition to the ova shipments, 500 parr from a British river appear to have been shipped to New Zealand in 1885, of which none survived the journey. Most of the effort of introducing Atlantic salmon, particularly in the nineteenth century, was undertaken and carried out by the Acclimatization Societies situated in various parts of the North and South Islands, such as Wellington and Canterbury; Acclimatization Societies still exist in New Zealand today.

Table III has been compiled mostly from information contained in the book, "The Naturalisation of Animals and Plants in New Zealand", by G. M. Thomson (Thomson, 1922). Whilst Thomson endeavoured to make a complete list of importations and the subsequent results, it appears that some of the records were incomplete or misleading. This table, therefore, should not be taken as being an absolutely accurate record, particularly as the numbers of ova which survived the journey would seem to have been greater than those shown here. It does serve, however, in indicating the scale of the operations and the persistence of the efforts made to establish migratory Atlantic salmon runs.

The records indicate that, even after the apparent safe arrival of ova in New Zealand, many subsequently failed to develop. Mr S. C. Farr, Secretary to the North Canterbury Society, attributed the high losses prior to 1884 to a 90% infertility rate but, as with the earlier Atlantic salmon ova shipments to Tasmania, it is more likely that mortalities would have been due to lack of adequate temperature control and to the shock caused to uneyed ova by the ships' movements at sea. (The terms "uneyed" and "green" ova are used to describe the period of development in salmonids from fertilization to formation of an advanced embryo with pigmented eyes in the egg capsule, which is known as the "eyed" stage; in the Atlantic salmon species, the eyed stage is usually completed approximately 70 days after fertilization has taken place, depending upon water temperature. During the period of development from the uneyed to the eyed stage, Atlantic salmon eggs are very susceptible to shock and vibration and can be quickly killed as a result.) Interestingly, it was arranged that, when Youl's shipment of Atlantic salmon ova was transported to Tasmania in the small, iron

TABLE III. ATLANTIC SALMON OVA SHIPMENTS TO NEW ZEALAND, 1868–1911[a]

| *Year* | *Number of ova shipped* | *River of origin* | *Ship and consigner* | *Destination and consignee(s)* | *Number survived journey* |
|---|---|---|---|---|---|
| 1868 | 100 000 | British rivers (Tay and Severn) | *Celestial Queen* (Youl) | Port Chalmers | 8000 |
| 1869 | 110 000 | British river(s) | *Mindora* (Youl) | Port Chalmers (Canterbury, Southland and Otago) | Ova never hatched out |
| 1871 | 3000 | British river(s) | Ship (Buckland) | ? via Melbourne (Southland) | Ova never hatched out |
| 1871 | Not known | British river(s) | Ship and rail | ? via San Francisco (Auckland) | None |
| 1873 | 120 000 | British river (Ribble) | *Oberon* (Youl) | Port Chalmers (Southland and Canterbury) | > 10 000 |
| 1875 | 300 000 | British river(s) | *Timaru* (Buckland) | Bluff (Otago) | None |
| 1876 | 90 000 | British river(s) (including Hodder and Severn) | *Durham* (Youl and Buckland) | Bluff and Canterbury via Melbourne (Southland and Canterbury) | > 10 000 |
| 1878 | 45 000 | British river(s) | *Chimborazo* (Youl and Buckland) | Bluff and Invercargill via Melbourne (Otago and Southland) | 2500 |
| 1881 | 100 000 | British river(s) | Ship (Capel) | ? (Otago and Marlborough) | None |
| 1884 | Not known | British river(s) | *Ionic* | — | — |
| 1885 | 198 000 | British river (Tweed) | Ship (Farr) | Lyttelton (Napier, Wellington, Otago, Waitaki and Canterbury) | < 120 000 |
| 1886 | 200 000 | British river(s) (Tay mostly) | *Ionic* (Agent-General for N.Z.) | Wellington (Wellington, Nelson, North Canterbury, Otago, Southland and Lakes, etc.) | > 99 600 |

| | | | | | |
|---|---|---|---|---|---|
| 1887 | 160 000 | British river(s) (Tay, Forth and Tweed) | *Kaikoura* (N.Z. Govt) | Wellington (Otago and Southland) | 75 000 |
| 1887 | 330 000 | British river(s) (Tay, Forth and Tweed) | *Doric* (N.Z. Govt) | Wellington (Otago, Southland and Oamaru) | > 71 000 |
| 1887 | 120 000 | British river (Tweed) | *Tongariro* (N.Z. Govt) | Wellington (Dunedin and Oamaru) | 75 000 |
| 1887 | 100 000 | River Rhine | *Tongariro* (N.Z. Govt) | Wellington (Canterbury and Wellington) | > 8620 |
| 1889 | 150 000 | British river (Forth) | *Arawa* (N.Z. Govt) | Wellington (Southland and Otago) | 129 000 |
| 1889 | 483 000 | British river (Tweed) | *Aorangi* (N.Z. Govt) | Wellington and Port Chalmers (Dunedin, Otago and Invercargill) | 320 000 |
| 1895 | > 200 000 | Presumably British river(s) | *Kaikoura* (N.Z. Govt) | ? (Wellington) | 20 000 |
| ? | > 16 500 | Presumably British river(s) | Ship (N.Z. Govt) | ? (Southland, Westport, Greymouth, Hokitika, Buller and Marlborough) | 20 000 |
| 1901–1902 | 150 000 | British river(s) | *Gothic* (? N.Z. Govt) | ? | > 51 200 |
| 1901–1902 | 50 000 | British river(s) | *Paparoa* (? N.Z. Govt) | ? | > 25 500 |
| 1907 | 50 000 | Canadian river(s) | Ship (Canadian Govt) | ? (Canterbury) | > 47 000 |
| 1908 | 150 000 | Canadian river(s) | Ship (C. L. Ayson) | ? (Marine Dept) | 140 000 |
| 1909 | 500 000 | Irish rivers and Tay | *Turakina* (L. F. Ayson—N.Z. Govt) | ? (Marine Dept) | 447 000 |

TABLE III (*cont.*)

| *Year* | *Number of ova shipped* | *River of origin* | *Ship and consigner* | *Destination and consignee(s)* | *Number survived journey* |
|---|---|---|---|---|---|
| 1909 | 175 000 | British rivers (Test and Dee) | *Rakaia* (L. F. Ayson—N.Z. Govt) | ? (Marine Dept) | 6900 |
| | 340 000 | River Rhine | *Rakaia* (L. F. Ayson—N.Z. Govt) | ? (Marine Dept) | 103 440 |
| 1910–1911 | 400 000 | British river (Wye) | *Ruahine* (C. L. Ayson) | ? ( Marine Dept) | Total of 930 000 |
| | 600 000 | River Rhine | *Ruahine* (C. L. Ayson) | ? ( Marine Dept) | |

[a] There have been few importations in more recent years, and those experiments that have occurred, such as the importation of Scottish salmon ova by the Southland Society in 1956, appear to have met with little or no success in the establishment of sea runs.

steamer of 120 tons, the *Beautiful Star*, in 1862, the ship was to sail under a jury rig and not use her steam power. After this experiment, Youl negotiated for space in the *Great Britain* for another shipment but the expense involved was greater than anticipated and he was "afraid of the effect of the vibration of the screw on the vitality of the ova" so this particular shipment did not take place (Seager, 1889).

As can be seen from Table III, Atlantic salmon eggs were imported into New Zealand on a large scale for nearly 50 years. According to Thomson, the total number of ova introduced, commencing in 1868, was 4 813 000; in addition, some 120 000 were obtained from pond-reared fish. The total number of fry liberated, at various stages of growth, including those obtained from pond-reared fish, was more than 2 000 000, which were turned out into the rivers, or their tributary lakes and rivers, shown in Table IV (Thomson, 1922).

As a result of various implantings, there are today a few land-locked Atlantic salmon in Lake Te Anau and possibly other lakes in the South Island of New Zealand. (A land-locked species of salmon, *Salmo sebago* (Girard), was introduced into New Zealand in 1905, though no major stocks seem to have developed as a result, and, in 1910, 20 000 ova of this species were also introduced into Tasmania, of which I have no further information.)

Despite the consistency of the efforts of the various Acclimatization Societies and the New Zealand Government, however, there is no evidence that a migratory run of Atlantic salmon has ever been established in any New Zealand river. As Thomson states in his book:

> Fish (Atlantic salmon) have been hatched by the million, and liberated in a great number of the rivers both of the South and North Islands. Glacial streams, rivers from the great lakes, rivers from the Canterbury mountains, rapid streams, sluggish streams—all have been tried. In several cases the same river has been stocked with young fish for many years in succession. In many cases salmon have been reared from the egg, have been kept in confinement till they spawned, and their fry have been liberated—always in the same stream—for a succession of years, by the hundred thousand. The fish have grown well to a certain age in our waters and have then gone to sea in a normal manner, just as they do in European streams, but from that point they are lost . . . . The fish has absolutely failed to establish itself.

(b) *Pacific salmon* (*genus* Oncorhynchus). Attempts to establish sea-going runs of Pacific salmon species in New Zealand rivers have also been made, with some degree of success being achieved in the case of quinnat salmon.

TABLE IV. ATLANTIC SALMON FRY PLANTINGS IN RIVERS AND LAKES OF THE NORTH AND SOUTH ISLANDS OF NEW ZEALAND

| *River or lake* | *Numbers of fry* |
|---|---|
| South Island | |
| Lake Ada, Milford Sound | 5 200 |
| Aparima | 494 000 |
| Ashley | 180 |
| Avon | 50 (?) |
| Clarence | 725 |
| Clutha | 146 900 |
| Heathcote | 240 |
| Hurunui | 1000 |
| Kakanui | 200 |
| Leith | 500 |
| Mataura | 8000 |
| Nelson, Marlborough, Grey, Buller and Hokitika | 15 000 |
| Opihi | 1500 |
| Owaka | 7000 |
| Perceval | 200 |
| Rangitata | 1000 |
| Selwyn | 13 250 |
| Temuka | 1500 |
| Waiau | 1 767 000 |
| Waitaki | 162 000 |
| North Island | |
| Hawke's Bay | ? |
| Hutt | 8400 |
| Manawatu | 3800 |
| Ruamahanga | 400 |
| Streams in Taranaki | 2800 |

(i) *Quinnat salmon* (O. tschawytscha). In 1875, the first shipment of ova from quinnat salmon was arranged by the Hawke's Bay Society through Spencer F. Baird, Chairman of the United States Commission of Fish and Fisheries, but it never reached Napier. After the steamship carrying the consignment had failed to obtain a fresh supply of ice at Sydney, it was found that the ova had begun to hatch out on the trip to Auckland. Accordingly, of the 20 000 ova which arrived, about 10 000 were placed in the Waikato and the upper tributaries of the Thames River, the remainder being placed in the hatching boxes; about 1450 fry were forwarded to the Thames, Wairoa and Tauranga districts and 1000 fry retained in Auckland. (I have been unable to ascertain whether or not this is the same shipment as that mentioned by Nicol in his book. If it is,

then the original consignment consisted of 50 000 salmon ova from the Sacramento River, of which half were left in Sydney. However, Nicol stated that the remainder died on their way to New Zealand.)

Following upon this, the Acclimatization Societies and the Government of New Zealand imported further supplies of quinnat salmon ova from California. Thomson's figures of shipments are given in Table V.

TABLE V. QUINNAT SALMON OVA SHIPMENTS TO NEW ZEALAND 1875–1878 AND 1901–1907

| *Year* | *Number of ova shipped* | *Number of ova survived journey* |
|---|---|---|
| 1875 | > 20 000 | > 12 450 |
| 1876 | > 264 000 | > 128 000 |
| 1877 | > 350 000 | > 269 000 |
| 1878 | 100 000 | ? |
| 1879–1900 | No shipments | — |
| 1901 | 500 000 | > 75 000 |
| 1904 | > 300 000 | > 294 000 |
| 1906 | 500 000 | > 469 833 |
| 1907 | 500 000 | > 482 000 |

The importations of quinnat salmon up to and including 1878 failed to establish any migratory runs of this species. Rivers into which ova, fry, parr and/or smolts were introduced in these early experiments are given by Thomson and enumerated below.

1875. Thames, Waikato, Wairoa district and Tauranga district.

1876. Tuakau, Mahurangi, Mangakahia, Punui and Hutt, Napier district, Southern Wairoa, Manawatu, Wanganui, Grey, Wairau, Hurunui, Waimakariri, Rangitata, Heathcote, Shag and Oreti.

1877. Northern Wairoa, Mangakahia, Punui and Hutt, Wairau, Motueka, Hurunui, Waimakariri, Heathcote, Rangitata, Shag, Kakanui, Waipahi and Makarewa.

1878. Upper Thames.

1880. Hutt.

Importations of quinnat salmon ova recommenced in 1901 when the Government entered on a continuous policy in this matter. Control of the operations was given to Mr L. F. Ayson, Chief Inspector of Fisheries, and to him should go chief credit for the establishment of the quinnat salmon runs in existence in New Zealand today. Of the ova received in

TABLE VI. QUINNAT SALMON LIBERATIONS FROM OVA SHIPMENTS TO NEW ZEALAND, 1901–1904

| *Year of shipment* | *Number of ova shipped* | *Year liberated into N.Z. waters* | *Stage of development* | *Number liberated* | *River or lake in which liberated* | *Remarks* |
|---|---|---|---|---|---|---|
| 1901 | 500 000 | 1902 | Yearlings | 23 600 | Tributaries of R. Waitaki | |
| | | 1903 | 20 months | 12 600 | R. Hakataramea | |
| | | 1903 | 26 months | 20 000 | R. Hakataramea | |
| | | 1904 | 3½ years | 5000 | R. Hakataramea | |
| | | 1905 | 4 years | 448 | R. Hakataramea | Presumed location |
| | | 1906 | 5 years | 73 | R. Hakataramea | |
| 1904 | >300 000 | 1905 | 3 months | 162 613 | R. Hakataramea | Presumed location |
| | | 1905 | 8 months | 224 252 | R. Hakataramea | Presumed location |
| | | 1905 | 1 year | 12 000 | R. Hakataramea | Presumed location |
| | | 1906 | 2 years | 12 587 | R. Hakataramea | |
| | | 1907 | 3 years | 62 | R. Hakataramea | |
| | | 1908 | 4 years | 103 | R. Hakataramea | |

the shipments made from 1901 to 1904 inclusive, some were sent to the River Hakatamarea and others to Lake Ohau. Table VI, based on Thomson's figures, shows the disposal of fish developed from these ova.

Regarding the 1904 shipment, Thomson commented to the effect that, though 300 000 ova (of which 98% hatched out) were shown as having been received, evidently far more had actually been received in view of the numbers of fish developed from the ova and later liberated. Both the 1901 and the 1904 shipments were sent as gifts from the United States Commission of Fish and Fisheries.

This pattern of liberations was continued with the 1906 and 1907 shipments, with fish being reared to different stages of development before release. The report of the Marine Department for 1906–1907 states that: "This year, fish which are undoubtedly Quinnat salmon have been caught in the Hakataramea River, up which they are going to spawn", and, during May and June, the manager of the salmon station on the Hakataramea (Fig. 3), which is the major tributary of the Waitaki River, obtained 30 000 ova, the first to be taken in New Zealand from migrating quinnat.

From this time onwards, ova for propagation purposes could be collected from fish returning to the rivers from the sea in order to spawn and, only a few years later, New Zealand was able to send quinnat salmon ova to Tasmania for the acclimatization experiments carried out there with this species. In New Zealand, stocking of waters continued; the Selwyn, Seaforth–Mackenzie, Leith, Waikouaiti and streams flowing into the Hokitika River were amongst those stocked in these early years. However, it was in the east coast rivers of the South Island that the establishment of sizeable (in some cases) and self-perpetuating runs of quinnat proved to be successful, and this was effected by fish from the Waitaki spreading along the east coast and infiltrating certain other rivers. (Infiltration has not taken place in all the east coast rivers; those situated below the Clutha River and above the Waiau River do not have even sporadic sea runs of quinnat in them, though the occasional fish may enter from the sea, and neither do certain other rivers situated between the Clutha and the Waiau.) Figure 4 shows a fresh-run salmon which was caught by an angler at the mouth of the Rakaia River in 1975.

In addition to the migratory runs mentioned, some quinnat salmon are land-locked, either voluntarily or involuntarily, in certain natural lakes and impounds of hydro schemes in the South Island. Figure 5 shows involuntarily land-locked quinnat from Lake Coleridge.

There are no quinnat salmon, resulting from the acclimatization experiments described, in the North Island of New Zealand.

FIG. 3. The Hakataramea Salmon Station, South Island, New Zealand. L. F. Ayson is on the left. (Photograph: Laboratory Collection, Fisheries Research Division, Ministry of Agriculture and Food, New Zealand.)

FIG. 4. Fresh-run quinnat salmon 68·5 cm long caught in a sea-washed lagoon on an east coast river, South Island, New Zealand. (Photograph: L. Stewart.)

(ii) *Sockeye salmon* (O. nerka). A shipment of 500 000 sockeye salmon ova was sent from Canada, via San Francisco, to New Zealand in 1901–1902. They arrived in poor condition but sufficient numbers survived to provide a stock to be introduced into tributaries of the Waitaki River and streams flowing into Lake Ohau, in the South Island. In 1906, a fish caught at the mouth of the Hakataramea River was identified as a sockeye and it seems that a small sea run did develop, although it disappeared after only a few years. Later, sockeye salmon were found to be living in Lake Ohau; they were small fish which had apparently adopted a completely freshwater life. Figure 6 shows land-locked sockeye salmon from Lake Ohau.

Hardy (1970) records that, in March 1969, shortly after the man-made Aviemore spawning channel below the Aviemore Dam, on the Otago bank of the Waitaki River had been commissioned, about 200 mature sockeye unexpectedly appeared and began to spawn. They were small fish, averaging 30·5 cm in length and 0·68 kg in weight, and quite different in appearance from sea-going sockeye salmon, noticeably in their body colour. Some of the male fish had humped backs and were very aggressive.

FIG. 5. Land-locked quinnat salmon from Lake Coleridge, South Island, New Zealand. (Photograph: M. Flain.)

FIG. 6. Land-locked sockeye salmon from Lake Ohau, South Island, New Zealand. The top fish is 43·2 cm long. The coin is a New Zealand two-cent piece which has a diameter of 2·1 cm. (Photograph: R. Goode.)

No attempt has been made in this article to make a complete record of all efforts to establish salmon species, particularly sea-going runs of those species, in Tasmania and New Zealand. Perhaps, however, sufficient has been set down to illustrate the great perseverance of many of the efforts, which eventually resulted in limited success in that sea-going runs of quinnat salmon are established in certain New Zealand rivers and land-locked salmon species are present in some natural and man-made lakes of New Zealand.

### B. *Introduction of salmonids into the Falkland Islands*

The Falkland Islands, a British colony, lie in the South Atlantic between 51° S. and 53° S., and are situated approximately 480 km east and to the north of the Straits of Magellan. Separated from each other

by the Falkland Sound, the two main islands, the East and West Falklands, are surrounded by about 200 smaller islands. The combined area of the East and West Falklands, together with adjacent islands, totals some 12 220 km$^2$. A number of the islands have deeply indented coastlines and some possess good harbours and anchorages. Terrain is mostly hilly, attaining its maximum elevation of 701 m in Mount Usborne on East Falkland, and of a wild moorland character, interrupted by outcrops of rock and peculiar collections of angular boulders known as "stone runs". There are few or no trees, and the soil is chiefly peat. The economy of the Falkland Islands, which have a population of less than 2000 (almost entirely of British origin), is based mainly on sheep-farming.

The Islands are subject to strong south-westerly winds and rapid daily variations in temperature occur. This is caused by air masses and fronts which are generated in the Andes, pass over the Patagonian Plateau and then over 480 km of cold sea to the Falklands, influencing the climate of the islands considerably. Generally, the weather is cloudy with an average of two hours' sunshine a day in midwinter and seven in midsummer. As a consequence of the large amount of cloud, extremes of seasonal temperature are unusual; 21·1 °C is rarely exceeded in summer and the minimum seldom falls below −4·4 °C in winter. The average temperature for the whole of the year is about 5·5 °C, with a mean of 13·8 °C during the day in summer and a mean of −1 °C in winter. Rain falls on one or two days out of three, with an annual fall of about 681 mm. A third of the rain falls in frequent and sometimes heavy showers during the summer months of December and January.

The rivers in the Falkland Islands, which vary in length from 12 km to 40 km and in width from 4 m to 30 m, are small when compared with many of those in the British Isles. None is very deep, except in the tidal reaches, and the majority are sluggish in character. Spate flows seldom develop and, as a result, the gravel substratum forming the beds of the rivers is frequently compacted. The pH of most of the rivers and streams examined throughout the islands ranged from 6·0 to 6·8. Figure 7 shows the mid-reach of the Malo River in East Falkland, which is typical of most of the larger rivers in the Islands.

There are only two indigenous fish species to be found in the Falkland rivers, namely *Aplochiton zebra* Jenyns, which is also known along the Chilean side of the Andes, from the Rio Callecalle system south to Tierra de Fuego, and *Galaxias maculatus* Richardson, often referred to by islanders as "minnow" when in the freshwater stage, which is to be found in Australia, New Zealand and South America. A marine fish, *Eleginus falklandicus* Richardson, with a distribution

FIG. 7. The mid-reach of the Malo River, East Falkland, Falkland Islands. (Photograph: L. Stewart.)

extending from the Rio Plata on the east coast of the Argentine to northern Chile, enters from the sea at certain times of the year; specimens weighing up to 6·3 kg have been recorded in Falkland estuaries and weights of 1–5 kg are common.

In 1935–1937, Argentina succeeded in establishing brown trout, *Salmo trutta*, rainbow trout, *S. gairdneri*, and American brook trout, *Salvelinus fontinalis*, in some of the Tierra del Fuego rivers and, in 1939, it was decided to investigate whether these species could be successfully introduced into some of the rivers of the East and West Falklands. The first attempt was made during the Second World War when small quantities of eyed ova of brown trout, rainbow trout and American brook trout were obtained from Chile and incubated in a hastily built hatchery near the only town, Stanley, which is situated on East Falkland. The rainbow trout did not survive but the brown trout prospered.

In August 1947, 30 000 trout ova, a gift from the Chilean Government, were flown to Montevideo and then taken by ship to Stanley. They were said to be ova from *Salmo fario*, sometimes wrongly used as a species name for brown trout, but were actually from *S. trutta*. Records do not show in detail which streams were stocked with fry but it is believed that most were put into the Moody Brook, near Stanley,

and some of the remainder in the Murrell River; apparently, none was placed in rivers on the West Falkland. In the same year an English trout farm despatched 10 000 brown trout ova by air from London to Montevideo and thence by ship to Stanley, where they arrived in January 1948. Following this, 15 000 eggs were sent, arriving in Stanley in January 1949, and 10 000 in each of the years 1950, 1951 and 1952, all from the same trout farm. (Some of the eggs came from wild trout obtained from an English lake and the rest from trout in a Scottish loch. Whilst it is understood that no sea trout had access to the waters from which the fish supplying the ova came, there is always the possibility that restocking of these lakes may have taken place, at some time in the past, with fish produced from parents which had access to the sea.) In all, 85 000 brown trout ova were received in the Falkland Islands from 1947 to 1952 but, unfortunately, nothing is positively known of the numbers of fry developed from them or the locations where they were planted out.

In 1954, anglers float-fishing with mutton for *Aplochiton zebra* Jenyns (1842) began to catch brown trout and, on 25 February, 1956, nine years after the first introduction of the species, a brown trout weighing 1·6 kg was caught in the Malo River. By April 1957, trout fishing had become popular with the islanders and, in the two angling seasons from 1957 to 1959, 300–400 fish, varying in weight from 0·9 kg to 5·4 kg, were taken from the Murrell River, near Stanley. These fish, and those caught in a few other rivers, appeared to have been feeding in the sea and resembled the anadromous sea trout, *Salmo trutta*.

Because some brown trout appeared to have developed a sea-running habit in the Falklands, it seemed logical to assume that migratory runs of Atlantic salmon, *S. salar*, might be established there with success. Accordingly, from 1959 to 1964 inclusive, 240 000 eggs from Atlantic salmon were supplied from the hatcheries of the then Lancashire River Board in England for this purpose, and a total of 28 000 eggs from established runs of sea trout were also supplied in the years 1961–1962. At first, the ova were incubated to the eyed stage in the London laboratories of the Ministry of Agriculture, Fisheries and Food before onward shipment by air and sea to the Islands, but satisfactory results were not obtained. To overcome the difficulty, from 1962 onwards the Lancashire River Board incubated the ova in its hatcheries and flew them out direct from Manchester to Montevideo for onward shipment by sea. This system of incubating and transporting ova to the Islands reduced losses considerably.

It may be of interest to describe here the methods used by the former Lancashire River Board for transporting sea trout ova to New

Zealand and salmon and sea trout ova to the Falkland Islands in the 1950s and 1960s. The procedures adopted for shipping ova by air were on similar lines to those pioneered by Youl a century earlier, except that it was possible to send eyed ova because of the faster means of transport. Despite the swiftness of the journey, however, there were still some hazards involved such as when, on one occasion, the aircraft carrying the eggs was delayed at Dakar and Montevideo, where the temperatures were between 26·6 °C and 32·2 °C. For transportation by air, the ova were laid on nylon-mesh trays covered with sphagnum moss. These were packed in a strong wooden case, in the top of which were perforated wooden compartments filled with ice which was replenished by airport staff at the different points of touchdown. After noting that some eggs in an early shipment by the Board had died because of the increase in the temperature of the aircraft's floor when the hotter countries had been reached, ice compartments were incorporated into the bases of the packing cases. Using this method, several successful shipments of ova were made.

Details of brown trout, sea trout and Atlantic salmon ova shipped to the Falkland Islands during the years from 1947 to 1964 are shown in Table VII. In addition to the numbers of ova shown here, 50 000 Atlantic salmon ova were supplied in 1962 by the Lancashire River

TABLE VII. SHIPMENTS OF OVA FROM SALMONIDS TO THE FALKLAND ISLANDS, 1947–1964

| | | *Brown trout ova* | | *Sea trout ova* | | *Atlantic salmon ova* | |
|---|---|---|---|---|---|---|---|
| *Year* | *Source* | *Number shipped* | *Number survived journey* | *Number shipped* | *Number survived journey* | *Number shipped* | *Number survived journey* |
| 1947 | Chile | 30 000 | Unknown | — | — | — | — |
| 1948 | English | 10 000 | Unknown | — | — | — | — |
| 1949 | lake | 15 000 | Unknown | — | — | — | — |
| 1950 | and | 10 000 | Unknown | — | — | — | — |
| 1951 | Scottish | 10 000 | Unknown | — | — | — | — |
| 1952 | Loch | 10 000 | Unknown | — | — | — | — |
| 1953– | No | | | | | | |
| 1959 | shipments | — | — | — | — | — | — |
| 1960 | Rivers | — | — | — | — | 60 000 | 21 000[a] |
| 1961 | in area | — | — | 20 000 | 15 000 | 40 000 | 3000 |
| 1962 | of Lancs. | — | — | 8000 | 7000 | 20 000 | 18 000 |
| 1963 | River | — | — | — | — | 40 000 | 36 000 |
| 1964 | Board | — | — | — | — | 30 000 | 27 000 |
| | Totals | 85 000 | Unknown | 28 000 | 22 000 | 190 000 | 105 000 |

[a] Died before planting.

Board but they died in London before they could be shipped to the islands. The probable locations for planting are given in Table VIII.

There are no records of any biological surveys of rivers and streams being carried out prior to the introduction of trout and salmon into the

TABLE VIII. PROBABLE LOCATIONS OF BROWN TROUT, SEA TROUT AND ATLANTIC SALMON OVA AND FRY PLANTINGS IN THE FALKLAND ISLANDS, 1948–1964

| *Year* | *Species* | *Probable locations of plantings* |
|---|---|---|
| 1948 | Brown trout | Hill Cove, Chartres, Warrah (Port Howard), Malo, Murrell |
| 1949–1950 | Brown trout | Fox Bay East and West, Hill Cove, Port San Carlos, Elephant Beach, San Carlos, Lorenzo Pond, Swan Inlet, Fitzroy, Kidney Pond, Pebbly Pond, Johnson Harbour |
| 1950–1951 | Brown trout | Pebble Island, Chartres, Hill Cove, Darwin, Warrah (Port Howard), Port Stephens, Malo, Port San Carlos, Fitzroy |
| 1951–1952 | Brown trout | Malo, Swan Inlet, Darwin, North Arm, Port San Carlos, Murrell |
| 1952–1953 | Brown trout | Lorenzo Pond, Murrell, Malo, John's Brook, Fitzroy, Swan Inlet, North Arm, Pebbly Pond, Kidney Pond |
| 1961 | Sea trout | Mac's Paddock Brook |
| | Salmon | John's Brook, Pasa Maneas, Warrah (Port Howard) |
| 1962 | Sea trout | Felton's Stream, Mile Pond, Round Pond, Pebbly Pond, Salvador Camp (a few only) |
| | Salmon | John's Brook, Pasa Maneas, Warrah (Port Howard), Hill Cove, Dean's River (Port Stephens), Fitzroy, Murrell, Salvador Camp, stream entering Brazo Mar |
| 1963 | Salmon | John's Brook, Pasa Maneas, Warrah (Port Howard), Hill Cove, Dean's River (Port Stephens), Fitzroy, Murrell |
| 1964 | Salmon | John's Brook, Pasa Maneas, Warrah (Port Howard), Hill Cove, Dean's River (Port Stephens), Fitzroy |

islands and no accurate information could be obtained concerning the numbers of fry developed and the locations of ova and fry plantings. One of the islanders was able to supply details of probable locations of plantings (Table VIII). (Few, if any, of the plantings seem to have taken place in that part of East Falkland known as Lafonia and lack of time precluded me from investigating the rivers there.)

When my investigation of Falkland rivers was carried out in 1973, it was found that brown trout were present in most of the rivers and streams of the two main islands, often supplanting the indigenous species. The largest brown trout captured during the survey measured 47·5 cm and weighed 1·9 kg. Food for trout in the rivers is not abundant and there was evidence of some predation by the larger brown trout on their own species. Restricted food supplies in Falkland rivers is likely to be one of the reasons for slob trout being found in the estuaries; these are brown trout which feed in brackish waters and, in the British Isles, they do not usually attain the same size as sea trout returning from

FIG. 8. A sea trout (top) and a slob trout (bottom) taken from the upper saline limits of the Malo Estuary, near the Gorge, East Falkland, Falkland Islands. (Photograph: L. Stewart.)

the sea. Numbers of good-sized sea trout were found widely throughout the East and West Falklands and it is understood that specimens weighing up to 9 kg each are now being caught by anglers. Figure 8 shows a sea trout and a slob trout taken from the upper saline limits of the Malo Estuary during the survey. Figure 9 illustrates growth curves calculated for non-migratory, slob and migratory trout from the survey findings.

Examination of scales taken from Falkland sea trout showed that the majority of them migrated seawards at 3+ years of age, with a far

FIG. 9. Age: length curve, Falklands fish. (After Stewart, 1973.)

lesser number migrating at 2+ years; the ratio was 6·725 : 1. In the British Isles, the majority of sea trout migrate seawards at 2 years. The pattern of sea feeding habits revealed a high degree of conformity in the Falkland sea trout but was markedly different from that which occurs in British sea trout, and indicated that the seaward environment off the Falkland Islands has an abundance of food which is greatly in excess of that to be found in the sea around the British Isles. Figure 10 shows samples of sea trout obtained from the Malo River during the survey.

Frost and Brown (1967), writing about the taxonomy of trout, said that typical brown trout transplanted to some parts of New Zealand and the Falkland Islands had found their way to the sea and become anadromous. The migratory habit which had developed in Falkland trout was observed by the islanders as long ago as the 1950s and confirmed by readings of trout scales sent to England. A number of the migratory trout were examined during my survey but it was not possible to determine whether they were descendants of fish developed from the brown trout importations of 1947–1952 or whether, possibly, at least some were descended from fish developed from the 1961–1962 sea trout importations.

FIG. 10. Sea trout, weighing 4·5 kg (top) and 3·6 kg (bottom) from the Malo River, East Falkland, Falkland Islands. (Photograph: L. Stewart.)

The survey of the Falkland rivers and streams failed to reveal any evidence that the efforts to introduce Atlantic salmon into the Islands had met with success and it appeared that, once again, sea runs of this species had failed to establish in the Southern Hemisphere. It was my opinion that, in the case of the Falkland Islands experiments, the reasons for this failure deserved closer attention. River conditions there are suitable for supporting migratory runs of salmonids, as is demonstrated by the sea trout runs now to be found widely in the two main islands. It appeared almost certain, from my findings, that some salmon smolts would have developed from implantations, eventually to migrate seawards, and eye-witness reports would seem to confirm that this was the case. If the known river conditions did not preclude the establishment of Atlantic salmon runs in the Falklands, then it was reasonable to assume that the likely cause of failure lay in the unknown oceanic habitat. My conclusions, which led me to speculate that oceanic conditions were possibly also responsible for the eventual outcome of other efforts made to establish sea-going populations of salmon species in the Southern Hemisphere, are given in Section IV.

It may be argued that too few Atlantic salmon ova were imported into the Falkland Islands over too short a period to ensure success, but the much more intensive efforts to establish sea runs of this species in Tasmania and New Zealand in earlier years fared no better. Migratory

runs of trout have established and thriven in the Falklands after introduction of trout ova on a similarly small scale to that of Atlantic salmon. It is interesting to note that the successful runs of quinnat salmon, *Oncorhynchus tschawytscha*, in New Zealand were also established in a comparatively short period, though, in this case, initial attempts carried out some years previously had failed. These appear to be the only sizeable and self-perpetuating sea runs of a salmon species existing in the Southern Hemisphere and, because of their relevance to the Falkland experiments and the possibility that this species could prove to be a suitable subject for any further experimentation, I visited New Zealand during 1975 to examine the quinnat salmon fisheries there.

## III. The Quinnat Salmon Fisheries of New Zealand

The quinnat salmon fisheries of New Zealand were established in the early years of this century as the result of importations of ova from California. They are situated in the South Island and, in addition to the sea runs contained by certain rivers, there are quinnat salmon landlocked, both voluntarily and involuntarily, in some of the natural and man-made lakes of the Island. There are no quinnat in the North Island. Figure 11 shows Flain's (1972) analysis of quinnat salmon distribution in New Zealand.

My special interest was in the migratory fisheries and particular attention was paid to the east coast rivers containing sea-going populations of quinnat and to the fish themselves; these rivers are situated between, and include, the Waiau River and the Clutha River. (The major quinnat salmon runs indicated for some of the rivers are by New Zealand standards and cannot compare in intensity with some of the runs of certain rivers in the Northern Hemisphere.) Outside these limits, the east coast rivers do not contain sea runs, though it is possible that the occasional fish may enter at times, and neither do certain east coast rivers within these limits. I visited the Catlins and a few other of these rivers and found that, at the point of inspection, their physical characteristics appeared to be similar to the quinnat salmon rivers I had examined. Certain west coast rivers, including those where small runs of quinnat were said to be present, were also visited.

Many of the lakes and rivers in the North Island of New Zealand were visited, particularly those where salmon species had been introduced in acclimatization experiments. The streams of both the North

Fig. 11. Quinnat salmon distribution in New Zealand. (1) Waiau R. (occasional sea run); (2) L. Sumner (voluntarily land-locked); (3) Hurunui R. (sea run varies); (4) Ashley R. (sea run varies); (5) Waimakariri R. (major sea run); (6) L. Coleridge (involuntarily land-locked); (7) Selwyn R. (very occasional sea run); (8) Rakaia R. (major sea run); (9) Ashburton R. (good sea run); (10) Rangitata R. (major sea run); (11) L. McGregor (involuntarily land-locked); (12) L. Alexandrina (involuntarily land-locked); (13) Opihi R. (good sea run); (14) Hakatamarea R. (major sea runs decreasing (hydro development)); (15) Waitaki R. (major sea runs decreasing (hydro development)); (16) L. Hawea (involuntarily land-locked); (17) L. Wanaka (involuntarily land-locked); (18) Clutha R. (sea run varies); (19) L. Wakatipu (involuntarily land-locked); (20) Taramakau R. (small sea run); (21) Whataroa R. (small sea run); (22) Okarito R. (small sea run) and Lagoon (voluntarily land-locked); (23) L. Mapourika (voluntarily land-locked); (24) Mahitahi R. (unconfirmed sea run); (25) L. Paringa (voluntarily land-locked) and Paringa R. (small sea run); (26) L. Moeraki (voluntarily land-locked) and Moeraki R. (small sea run); (27) L. Ellery (voluntarily land-locked) and Jackson R.; (28) L. Heron (voluntarily land-locked). (After Flain, 1972.)

Island and the South Island are often quite similar in character, with most of the larger ones originating in mountain lakes and flowing rapidly to the sea over gravelly and rocky beds. Nevertheless, on the evidence available, it would appear that no sea-going populations of salmon are

present in any of the rivers of the North Island, and it was thought, by many of the interested persons spoken to on this subject, that water temperatures, offshore and in the rivers, and/or offshore salinity tolerances, could have been responsible for the failure of the salmon acclimatization experiments carried out there in earlier years. Brown trout, *Salmo trutta*, and rainbow trout, *S. gairdneri*, are to be found in some of the rivers and lakes of the Island as a result of the introduction of these species many years ago.

Whilst examining the rivers and lakes of both Islands, many hydro-electric power generation schemes were observed to be in operation, some of them on rivers holding sea runs of quinnat. Certain New Zealand rivers are utilized for irrigation purposes.

In comparison with the majority of the New Zealand rivers seen, most British salmon rivers are stable, with some having famous salmon holding pools which have been in existence for centuries. However, the abundant river flows and the presence of gravel suitable for spawning in New Zealand rivers must have convinced the experimenters that their importation of ova had a reasonable chance of eventually establishing sea-going populations of salmon in them. Although the experiments with Atlantic salmon, *Salmo salar*, failed completely in this respect, their optimism was justified, to a limited extent, by the establishment of sea runs of quinnat salmon, *Oncorhynchus tschawytscha*, in certain rivers of New Zealand, which, according to Flain (1972), is the only country in the world where this species has been successfully acclimatized and has resulted in self-propagating sea-run fish.

### A. *The quinnat salmon rivers of New Zealand*

During my visit to New Zealand, the rivers on the east coast of the South Island where sea runs of quinnat had been established, namely, (from north to south), the Waiau, Hurunui, Ashley, Waimakariri, Selwyn, Rakaia, Ashburton, Rangitata, Opihi, Waitaki and its main tributary, the Hakataramea, and the Clutha, were examined in detail. Most of these rivers are very similar in character, being fed with water coming from the glacial complex in the Southern Alps, and the majority are affected with detritus in the form of glacial flour. The resultant opacity of the water can be seen in Fig. 12, which shows members of a local Acclimatization Society netting gravid salmon, for propagation purposes, from a power-station tailrace on the River Rakaia. Hobbs (1937) reported the mean monthly temperatures of salmon-bearing

FIG. 12. Members of a Local Acclimatization Society, South Island, New Zealand, netting gravid quinnat salmon from a power station tailrace. Note the glacial flour in the water. (Photograph: L. Stewart.)

streams on South Island as ranging from 3 °C in midwinter to 16·5 °C in midsummer.

The lengths of the east coast rivers containing sea runs vary from approximately 56 km for the Opihi to approximately 240 km for the Clutha. Highest recorded flood peak flows for these rivers, up to 1968, were 90 000 cusecs (2547 $m^3/s$), 1951, for the Ashburton, 100 000 cusecs (2830 $m^3/s$), 1951, for the Ashley, 180 000 cusecs (5094 $m^3/s$) for the Clutha, 59 000 cusecs (1670 $m^3/s$), 1952, for the Opihi, 160 000 cusecs (4528 $m^3/s$), 1940, for the Rakaia, 88 000 cusecs (2490 $m^3/s$), 1968, for the Rangitata, 21 700 cusecs (614 $m^3/s$), 1951, for the Selwyn, 195 000 cusecs (5519 $m^3/s$), 1940, for the Waimakariri and 85 000 cusecs (2406 $m^3/s$), 1931, for the Waitaki; information for the Hurunui and the Waiau was not available. The majority of these rivers are wide, some being over 4 km in width, and there are no shortages of suitable gravel in which salmon can spawn. Unfortunately, much of the gravel is unstable and accretes into large shoals and terraces so that river flows are discharged through numerous channels. Figure 13, an aerial view of the River Rakaia, illustrates this particular feature. Figure 14 shows an aerial view of the same river in flood.

FIG. 13. The Rakaia River, South Island, New Zealand, during normal flow conditions. (Photograph: V. C. Browne and Son, Christchurch, New Zealand.)

FIG. 14. The Rakaia River, South Island, New Zealand, in flood. (Photograph: V. C. Browne and Son, Christchurch, New Zealand.)

Another feature of these rivers is the absence of the delta and chevron types of estuaries. Instead, at the outlets to the sea, the rivers are contained in large sea-washed lagoons, finally emptying through channels enclosed by gravel accretion. These outlets varied from 30 m to 250 m in width for the various rivers, at the time of my visit.

Between the limits formed by the Waiau River at the top and the Clutha at the bottom, on the east coast, there are other rivers—such as the Clarence River—which apparently do not hold sea runs of quinnat. Although a few of these rivers were visited very briefly, lack of time precluded my examining them in detail.

Because there were said to be small sea runs of quinnat salmon in certain of the South Island's west coast rivers, namely, the Taramakau, Whataroa, Okarito, Paringa and Moeraki, as well as an unconfirmed sea run in the Mahitahi, visits were made to these and other west coast rivers. Some of them appeared to have certain characteristics of salmon rivers at the points visited but others were most uncharacteristic and seemingly much affected by rotting vegetation. Discussions with various fishery scientists and field officers in New Zealand failed to convince me that even minor established runs of quinnat are present on the west coast of the South Island.

### B. *The quinnat salmon of New Zealand*

In the Northern Hemisphere, quinnat salmon, *Oncorhynchus tschawytscha*, also known as the spring, king, Sacramento, Columbia River, tyee or chinook salmon, is to be found, in America and Canada, between the Ventura River of California and the Coppermine River in the Arctic and, in Asia, from the Anadyr River in Siberia to rivers on Hokkaido Island in Japan. The distribution of this species suggests that it is adaptable and can tolerate marked changes in its habitat. In the Northern Hemisphere, the principal spawning time is August–September and the resulting young stay in freshwater for a period varying from a few days up to two years; the length of ocean life varies from one to five years and mature fish can measure between 40·6 cm and 152·4 cm (average length 91·4 cm) and weigh between 1·1 kg and 56·7 kg (average weight 11·8 kg) (Netboy, 1974).

The first attempt, made from 1875 to 1878, to acclimatize quinnat in New Zealand waters with ova obtained from Californian fish was a failure. Marshall McDonald, Commissioner of the United States Department of Fish and Fisheries, when applied to for information, said (Thomson, 1922):

> We have attributed the failure [to acclimatize quinnat salmon on eastern coasts of America] to the different temperature conditions prevailing in the rivers of the east and west coasts at the spawning season, which is from July to September . . .. On the east coast at this season of the year our rivers are warmer than the adjacent seas, and we have concluded therefore that the failure to enter our streams is due to the higher temperature conditions prevailing in them. This is probably true in regard to your own waters.

In 1915, after the success of the second acclimatization experiment in New Zealand, Mr L. F. Ayson, Chief Inspector of Fisheries, wrote to Thomson:

> Quinnat salmon begin spawning about 1st April, and are finished by the end of May. In America there are two distinct runs, which are called the summer and winter runs. Marshall McDonald in the report you quote evidently referred to the summer run. The winter run commences well on in October, and finishes in December. The quinnat eggs with which we stocked the Waitaki were all from the winter-run fish, and it is interesting to note that we have only a winter run of spawning salmon, so far, in the Waitaki; which would go far to show that eggs taken from winter-run fish in America only develop winter-run fish in this country.

A further interesting point emerges from the Marine Department's report for 1915–1916:

> . . . One of the reasons why the Waitaki River was chosen in the first instance for the salmon was because of the northerly set of the ocean current along the east coast, so that by stocking the Waitaki all the rivers north of that would in time be stocked by the fish being carried northward.

This did occur, though only as far north as the Waiau River, thus confining the major salmon runs to the Canterbury Bight; also, not every river between the Waitaki and the Waiau has developed such runs.

The original stocks of New Zealand quinnat came from the Baird Station on the McLeod River, a tributary of the Sacramento River in California. Prior to the completion of the Shasta Dam, commenced in 1938, the Sacramento had spring and autumn runs of these fish; it also had a small winter run. Since the dam was completed, the spring run in the Sacramento has decreased, the autumn run been sustained at its former level and the winter run increased from a few hundred fish to over 60 000 (Netboy, 1974). Winter runs enter the rivers late in the year and spawning does not take place until the following April, with many of the fish spawning just above the tidal limits whilst others travel as

much as 960 km or more from the sea. The main upstream spawning of New Zealand salmon takes place in March–April. (Many fish were personally observed spawning in the headwaters of the Rakaia, downstream of the Glenariffe trap, on the last day of my visit.)

The major New Zealand quinnat salmon rivers, i.e. the Rakaia, Rangitata, Waimakariri and Waitaki, are all glacial-fed. The Sacramento River is also a large, glacial-fed river. In America, a number of other rivers and streams holding quinnat are glacial-fed; such rivers and streams are the Hok, Puyallup, Misqually and the Klickitat (L. Verhoeven, personal communication). Some of the streams holding quinnat salmon, in America, have large estuaries or pronounced deltas with multiple channels. L. Verhoeven (personal communication) also states that some fishery scientists feel that juvenile quinnat require a fairly large estuary in which they can adjust slowly from freshwater to saline water but that there are many streams holding quinnat which do not have deltas but which do have very small estuaries.

It is thought that salmon from different rivers, and their tributaries, differ in their migration patterns and oceanic distribution. Fry and Hughes (1951) concluded that by far the greater majority of salmon from the Sacramento River are what could be termed "stay at home" fish, i.e. fish that do not move northwards as far as the Californian/Oregon border some 320 km away; also, that some quinnat salmon are always to be found off the mouths of their respective rivers.

It is likely that the magnitude of flow from a river has a direct bearing upon the salinity of the seawater off its coastline. The salinity of water off the Sacramento River has a lower limit of 29·5 ‰ (Robinson, 1957). According to Eggleston (1972), the temperature and salinity tolerances in the Canterbury Bight off New Zealand's South Island are similar to those found off the mouth of the Sacramento. It was his opinion that the high-salinity water outside the Southland Front off the east coast of the South Island acts as a barrier to long-distance sea migration of the New Zealand quinnat, which has the effect of confining them to a zone within the Canterbury Bight. If Eggleston is right, then the magnitude of the glacial flows from the Waimakariri, Rakaia and other east coast rivers must have some bearing on the salinity and the presence of quinnat in the Canterbury Bight.

Between 1963 and 1968, the Marine Department in New Zealand carried out investigations into the intensity of the salmon runs in certain rivers. Commercial salmon netting has not been practised in the estuaries at all in recent years and so no records from this source were available. Information obtained from anglers' diaries, therefore, was used for the purpose of the investigations. Table IX shows the estimated

numbers of fish caught in ten rivers by anglers in 1968, as extracted from the New Zealand Fisheries Technical Report No. 83 (Graynoth, 1972).

Graynoth showed that 50% (9700) of the fish were caught immediately upstream of a point where the rivers enter the sea, which is a situation not dissimilar to that applying on the River Malo, in the Falkland Islands. Another 40% (7760) were caught within a distance of 16 km from the mouths of the rivers and the remaining 10% (1940) were presumably caught in the mid and upper reaches of the rivers.

TABLE IX. ESTIMATED NEW ZEALAND QUINNAT SALMON CATCHES, 1968

| *River* | *Catch (numbers of fish)* |
|---|---|
| Ashburton | 2300 |
| Ashley | 200 |
| Clutha | 100 |
| Hurunui | 200 |
| Opihi | 1400 |
| Rakaia | 2600 |
| Rangitata | 5100 |
| Waiau | 300 |
| Waimakariri | 1400 |
| Waitaki | 5800 |
| Total | 19 400 |

Figure 15 shows salmon anglers fishing a sea-washed lagoon on an east coast river of the South Island.

The escapement of salmon from the anglers on the Rakaia River, as counted at the Glenariffe trap in 1968, was 3275 (Galloway, 1972). In that same year, the recorded rod catch for this river was 2600 salmon, which means that the escapement of fish for spawning was at least 55·8%, not allowing for fish escaping into other, untrapped tributaries of the Rakaia. Taking the figure of 55·8% as a basis for calculating the spawning escapement on all the rivers listed in Table IX, then the salmon stocks for these rivers would have been about 30 070 fish. When a further percentage, say 50% in view of the absence of consistent commercial netting activities, is added in respect of the escapement not recorded by the Glenariffe trap and used as a basis for calculation, then the total estimated stock for the listed rivers would have been in the region of 40 000 fish.

Table X indicates the months when most fish were caught in the majority of the New Zealand quinnat salmon rivers, according to

FIG. 15. Salmon anglers fishing a sea-washed lagoon on an east coast river, South Island, New Zealand. (Photograph: R. Goode.)

TABLE X. PERCENTAGE MONTHLY CATCHES OF QUINNAT SALMON IN CERTAIN NEW ZEALAND RIVERS, 1968

| *River* | *December* (%) | *January* (%) | *February* (%) | *March* (%) | *April* (%) |
|---|---|---|---|---|---|
| Ashburton | 1 | 8 | 26 | 48 | 17 |
| Ashley | 1 | 8 | 26 | 48 | 17 |
| Hurunui | 1 | 8 | 26 | 48 | 17 |
| Rakaia | 1 | 8 | 26 | 48 | 17 |
| Rangitata | 5 | 26 | 26 | 26 | 17 |
| Waiau | 1 | 8 | 26 | 48 | 17 |
| Waimakariri | 1 | 8 | 26 | 48 | 17 |

information obtained from anglers in 1968. Percentage monthly catches for the Clutha and Opihi rivers were not shown by Graynoth (1972), from which the figures in this table were taken.

The percentage monthly catches of the Falkland Islands' sea trout for the years 1969–1973 are given in Table XI. Although the Falklands

TABLE XI. PERCENTAGE MONTHLY CATCHES OF SEA TROUT IN RIVERS OF THE FALKLAND ISLANDS, 1969–1973

| *September* | *October* | *November* | *December* | *January* | *February* | *March* |
|---|---|---|---|---|---|---|
| 27·2% | 30·6% | 1·9% | 0·03% | 20·04% | 15·9% | 3·93% |

are situated several thousand miles away from New Zealand, these seem to be the only two places in the Southern Hemisphere where sizeable sea runs of salmonids have been successfully established, which makes the Falkland figures of interest for comparison purposes.

Research carried out by the New Zealand Marine Department indicates that quinnat salmon smolts there migrate to sea after feeding for 18 months in freshwater. Grilse return most frequently after two years of sea feeding, sometimes in considerable numbers, but many of the females are not mature (Flain, 1972). The salmon runs consist mainly of three-year sea-feeding fish, with four-year sea-feeding fish

TABLE XII. AVERAGE LENGTHS AND WEIGHTS OF YEAR CLASSES OF NEW ZEALAND QUINNAT SALMON

| *Sea feeding (years)* | *Average length (cm)* | *Average weight (kg)* |
|---|---|---|
| 2 | 58·4 | 2·2 |
| 3 | 76·2 | 4·9 |
| 4 | 88·9 | 6·8 |
| 5 | 101·6 | 9·9 |

being the second most abundant; five-year sea-feeding fish are uncommon and no six-year sea-feeding fish had been encountered up to the time of my visit. Table XII shows the approximate average lengths and weights of New Zealand quinnat in the various year classes (Flain, 1972).

For the purposes of comparison, Table XIII shows the maximum and minimum lengths, together with the average weights, of the year classes of sea-feeding sea trout in the Falkland Islands. These figures indicate that the weights of sea trout in the Falkland Islands are in

TABLE XIII. MAXIMUM AND MINIMUM LENGTHS AND AVERAGE WEIGHTS OF YEAR CLASSES OF SEA TROUT IN THE FALKLAND ISLANDS

| *Sea feeding (years)* | *Maximum length (cm)* | *Minimum length (cm)* | *Average weight (kg)* |
|---|---|---|---|
| 1 | 48·0 | 37·0 | 0·878 |
| 2 | 66·0 | 37·5 | 0·960 |
| 3 | 67·0 | 55·0 | 4·13 |
| 4 | 73·0 | 68·5 | 4·57 |

reasonable conformity with the growth rates of New Zealand quinnat returning from the sea.

In order that growth rates of New Zealand Pacific salmon species *Oncorhynchus* which do not go to sea may be seen, the average lengths and weights of land-locked quinnat salmon, *O. tschawytscha*, and sockeye salmon, *O. nerka*, at different ages, are given. Table XIV shows average lengths and weights, at various ages, of land-locked quinnat (Flain, 1972). The average lengths and weights of mature sockeye salmon in the enclosed waters of the Waitaki catchment are given in Table XV (Flain, 1972).

TABLE XIV. AVERAGE LENGTHS AND WEIGHTS AT VARIOUS AGES OF NEW ZEALAND LAND-LOCKED QUINNAT SALMON

| *Age (years)* | *Average length (cm)* | *Average weight (kg)* |
|---|---|---|
| 2 | 35·5 | 0·68 |
| 3 | 45·7 | 1·1 |
| 4 | 50·8 | 1·4 |
| 5 | 58·4 | 1·8 |

TABLE XV. AVERAGE LENGTHS AND WEIGHTS OF MATURE LAND-LOCKED SOCKEYE SALMON IN NEW ZEALAND

| *Age (years)* | *Average length (cm)* | *Average weight (kg)* |
|---|---|---|
| 3 | 27·9 | 0·45 |
| 4 | 31·7 | 0·56 |

During the Falkland Islands' survey, over 2000 scales were removed from trout to ascertain their life-histories. The numbers of scales taken were far in excess of the numbers normally required for analysis because a preliminary examination had revealed that 90% of scales removed had regenerated. For some unknown reason, an extremely large number of trout in the Falkland rivers sustain injury in their early stages of development.

To facilitate the determination of the life-histories of the trout, the rings in all the scales were counted to find if any consistent annual growth pattern was present, with the results shown in Table XVI.

Lengths of fish in the various year classes defined in Table XVI were analysed and the results, showing the age : length relationship of

the Falkland trout, can be seen in Table XVII. (The total ages of the migratory fish can be obtained by the addition of three years to the ages of the non-migratory trout.)

Figure 16 shows a scale, with a complete nucleus, removed from a slob trout, measuring 73 cm in length and weighing 4·1 kg during the survey in the Falkland Islands. This fish had fed for three years in the

TABLE XVI. NUMBERS OF RINGS ON SCALES OF FALKLAND TROUT AT DIFFERENT AGES

| *Year of growth* | *Definition* | *Number of rings on scales* | *Average length of fish (cm)* |
|---|---|---|---|
| One year | 0+ | 7–11 | 7 |
| Two years | 1+ | 10–16 | 13 |
| Three years | 2+ | 10–16 | 18 |

TABLE XVII. GROWTH OF TROUT IN THE FALKLAND ISLANDS

| *Non-migratory trout* | | | *Migratory trout* | | |
|---|---|---|---|---|---|
| *River feeding (years)* | *Length (cm)* *Minimum* | *Maximum* | *Sea feeding (years)* | *Length (cm)* *Minimum* | *Maximum* |
| 0+ | 5·8 | 8·2 | 1 | 37·5 | 48·0 |
| 1 | 8·5 | 14·7 | 2 | 37·0 | 67·0 |
| 2 | 12·2 | 22·8 | 3 | 55·0 | 66·0 |
| 3 | 16·5 | 25·0 | 4 | — | 73·0 |
| 4 | 20·5 | 30·5 | — | — | — |
| 5 | 29·0 | 46·0 | — | — | — |

sea and four years in the estuary. It is typical of scales removed from slob trout in English waters.

Figure 17 shows a scale taken from a sea trout caught in the River Malo in the Falklands; the fish had fed in the river for at least two years and in the sea for two years. Again, it is typical of scales removed from sea trout in English waters.

The scale shown in Fig. 18 is atypical of the other sea trout scales examined during the survey. It is extremely unlikely that this fish was a hybrid, i.e. progeny developed from a sea trout ovum fertilized by a salmon parr, but the feeding bands on the scale are most unusual. The bands indicate that the fish had fed for three years in the river before

FIG. 16. Scale from a Falkland slob trout, showing regularly spaced feeding bands—3 years river life, 4+ years estuarine life. (Photograph: Department of Zoology, Freshwater Fisheries Unit, University of Liverpool.)

migrating seaward, at which time it would have measured approximately 17·8 cm and weighed 85 g; it then fed in the sea for two years and consistently put on weight prior to its capture in the Malo River. In common with other sea trout entering the Falkland Islands' rivers from the sea, this fish had no sea lice *Lepeophtheirus salmonis* (Krøyer) on its body such as are found on the bodies of salmon and sea trout returning from the sea to rivers in the British Isles.

A comparison of the Falkland sea trout scale illustrated in Fig. 18 with the scale shown in Fig. 19, which was removed from a quinnat salmon caught in the sea-washed lagoon of the Rangitata River in New Zealand, is of interest for it reveals that the configurations of the sea feeding bands on both scales are in close conformity. The quinnat scale in Fig. 19 clearly shows the feeding band laid down whilst the fish was feeding in freshwater and the sea feeding bands can also be seen; the fish had fed for one year in freshwater and for three years in the sea.

From examination of scales, it is reasonable to deduce that, whilst the food resources for salmonids in the rivers of the Falkland Islands

FIG. 17. Scale from a Falkland sea trout—? 3 years river life, 2 years sea life. (Photograph: Department of Zoology, Freshwater Fisheries Unit, University of Liverpool.)

are not so prolific as in New Zealand rivers, the food resources in the seas around the Falklands are suitable for sea trout and appear to be much more bountiful than in the seas around the British Isles. There are no closely defined winter feeding-bands occurring on the scales of Falkland trout such as can be found on the scales of Atlantic salmon in the Northern Hemisphere.

FIG. 18. Scale removed from a sea trout caught in the Malo River, East Falkland, Falkland Islands. (Photograph: Department of Zoology, Freshwater Fisheries Unit, University of Liverpool.)

The utilization of plentiful food resources in the sea by migrating runs of salmon species in order to provide for seasonal cropping by commercial and sporting interests is an attractive proposition which has led to many efforts to establish such runs in the Southern Hemisphere but, to date, only in New Zealand has success been achieved to any degree. The quinnat salmon fisheries there, although limited in extent and perhaps not substantial enough to allow consistent commercial exploitation on a large scale, are nevertheless viable and provide sport for anglers. New Zealand quinnat appear to possess certain characteristics of Sacramento fish, from which they are descended, and to be well matched to the rivers they now inhabit. Whilst the freshwater habitat is of very great importance in the life-cycle of migrating salmon, however, the provision of suitable river conditions is not the sole requirement for successful acclimatization as can be seen

FIG. 19. Scale removed from a quinnat salmon caught at the mouth of the Rakaia River, South Island, New Zealand. (Photograph: Department of Zoology, Freshwater Fisheries Unit, University of Liverpool.)

in the experiments with Atlantic salmon, *Salmo salar*, in both Tasmania and New Zealand, where the fish thrived well in the rivers to the smolt stage only to disappear, never to return, after migration to the sea. From this, it would appear that the oceanic habitat is at least as important as the freshwater habitat for the establishment and maintenance of salmon runs. The conditions in the sea which possibly influence migration are discussed next.

## IV. Possible Influences of Oceanic Currents and Gyres on Salmon Migration

During the Falkland survey, it was found that, whilst the rivers there are not large, their food resources are sufficient to support immature salmonids and the bed gravel, although compacted, is of a size suitable for salmon spawning in certain areas. Even allowing for trout predation on immature fish in the freshwater habitat, it seems almost certain that some smolts developed from the implantations of Atlantic salmon, *Salmo salar*, would have made their way downstream

to reach the rich feeding grounds of the sea. Assuming that a proportion of the ova and/or fry implanted in the rivers from the consignments received from 1961 to 1964 did survive to reach the smolt stage, migration to sea would probably have taken place after two or three years of river feeding and, allowing for a period in the sea of 4+ years (which was the longest sea-feeding period found in the larger sea trout), adult salmon could reasonably have been expected to return from 1969 onwards. No evidence was found during the 1973 survey that Atlantic salmon were present in Falkland rivers.

Many ideas have been propounded and much controversy engendered concerning the migration habits and swimming capabilities of salmon species. Theories have been presented about their journeys to and from oceanic feeding grounds using a so-called "homing instinct" capable of operating over long distances or other means, and the relevance of factors such as navigation by the sun, magnetic influences, water velocities and wind drift has been considered. It has been hypothesized, for example, that the odour of juvenile salmon residing in the natal stream may act as the prime stimulus for guiding the returning adult back to the stream from the sea. In the context of salmon acclimatization experiments, if this theory is correct, it means that the experiments must be carried out for several years in succession so as to ensure that the first returning adults come back whilst young fish are still present in the home stream; such a theory may possibly explain the failure of the Falkland Atlantic salmon experiments which were of a short duration but does not provide an answer in respect of the failed New Zealand Atlantic salmon experiments spanning half a century where, as Thomson (1922) commented, in several cases the same river had been stocked with young fish for many years in succession. There is evidence that the pheromone theory has some credence, according to Hara (1970), Døving *et al.* (1972, 1973) and Scholz *et al.* (1976), but there seems to be little factual evidence available as to the effects of an olfactory influence upon salmon in their marine habitat. In evaluating the various hypotheses, it may be asked whether an adult salmon can detect the pheromone emanating from its natal stream when feeding perhaps thousands of kilometres distant in the ocean, or whether it is able to navigate to and from the feeding grounds by using solar cues (also taking into account that salmon are capable of swimming at depths where light penetration is negligible or certainly not directional), or whether magnetic influences do play a part in enabling salmon to swim on fixed compass bearings, or whether there are any geophysical parameters caused by the rotation of the earth which can effect migration. The Tasmanian and New Zealand Atlantic salmon experiments

would seem to indicate that the theory of a homing instinct effective over substantial distances could largely be discounted, for, if such an instinct was present in sea-run salmon, it might have been expected that at least a proportion of the smolts seen migrating seawards over many years would have returned as adult fish.

When discussing the existence of a homing instinct in salmonids, it seems to me to be essential to differentiate between inshore and upstream migration and open-sea navigation. A migrating salmon requires two different environments—freshwater and saline—for various stages of its life-cycle and it is too often assumed, without supporting evidence, that the factor (or factors) which enable a salmon eventually to locate and return to its natal stream is the same as that which facilitates its movements to and from its feeding grounds in the sea. Very little is yet known of the marine life of salmon but it may eventually be found that their journeying in the sea is affected by different factors than those affecting their movements inshore and upstream. It may even be found that their movements at sea are affected by physical forces such as ocean currents which return them to a point where they are influenced by discharges from their natal stream.

After analysing the results of the Falkland survey, it occurred to me that the real explanation for the return of adult salmon from the sea was of a simple, physical nature and I came to the conclusion that the absence of integral land masses in the Southern Hemisphere and the lack of suitable oceanic gyres developing as a result was probably the main reason for the failure of almost every attempt to establish sea runs of salmon there. The general disposition of the gyrals around the coastlines of the highly integrated land masses in the Northern Hemisphere develops within a comparatively short distance of the coastlines of countries producing sea-going Atlantic salmon, *Salmo salar*, and the same also applies in the case of regions where sea-going Pacific salmon species (genus *Oncorhynchus*) are produced. (In the context of this article, the terms "gyres" and "gyrals" refer to rotating currents in the ocean.) Figure 20 gives a general outline, indicated by arrows, of the movements of various oceanic "drifts" and the disposition of gyrals around the coastlines of the land masses in the early part of the year in the Northern and Southern Hemispheres, the most important being those produced and maintained by permanent or predominant winds. The coastlines marked in bold on the figure are approximately those where sea runs of Atlantic or Pacific salmon species are now to be found, whilst the stippled areas show the approximate main habitats for sea-feeding salmon, cod, herring, hake and other fish, where food is available in quantity.

FIG. 20. General outline of movements in February of various oceanic drifts and gyres in the Northern and Southern Hemispheres, with coastlines where sea runs of Atlantic or Pacific salmon are now to be found shown in bold; their principal marine habitats are stippled.

It has been known for some time that some fish and the larvae of certain species can and do drift passively from one land mass to another, relying, for their movement, upon oceanic currents which, in many cases, are gyrational in character. In my opinion, it is possible that, when a salmon smolt leaves the offshore waters, it will meet an oceanic gyre or current in which it will drift along with other species of fish fauna. During this time, it will be preying upon marine aquatic organisms, the degree of feeding increasing or decreasing according to the physiological condition of the fish; its life-cycle will thus be controlled by the rotation of the gyre and be related to gonad development. At certain stages of its physiological development, the fish can leave or rejoin or even transfer to other associated gyres. The ultimate result, if it kept within or re-entered its original gyre, will be its return to the point at which it embarked as a smolt. (In this hypothesis, should a salmon fail to re-enter or keep within the gyre in which it started its original oceanic journey, it would be unable to return to its natal stream, such as could possibly have occurred in the cases of an Atlantic salmon smolt tagged in the Yorkshire Ure in Britain caught off Labrador and a few of the pink or humpback salmon, *Oncorhynchus gorbuscha* (Walbaum), introduced into the White Sea area by the Russians caught in Scottish and English rivers.) It is possible that, at the adult stage of its life, a smell imprint takes over and acts as a signal for the salmon to change its offshore habitat for that of freshwater and that, as it closes in to the river of its birth, the flows therefrom are detected; it then follows the coast until it recognizes the familiar scent or pheromone which impels it to enter its natal stream.

Concerning the Falkland Islands' salmon experiments, there are at least two enclosed gyres known to be present off the Antarctic coastline, shown on Fig. 20 at points 30° S., 40° E. and 60° S., 30° W., and in the context of suggestions made by Joyner *et al.* (1974) that the ocean surrounding the Antarctic continent should be used for the development of commercial salmon fisheries, an investigation into the possible exploitation of these gyres might be rewarding. Otherwise, a study of the currents around the Islands, where the wind is permanently blowing, shows that the movement of water is towards the Benguela Current where it meets up with the South Equatorial and Brazilian Currents (Fig. 21). If the passive drift hypothesis is valid, then it is likely that any Atlantic salmon smolts migrating from Falkland rivers would have been carried towards the Equator and into water temperatures in excess of 25 °C, which could have been lethal to them. Alternatively, if they had moved passively into the West Wind Drift, where temperatures fall within the non-lethal ranges for this species,

FIG. 21. Circulation of the North Atlantic Ocean and the South Atlantic Ocean. (Adapted from U.S. Navy Hydrographic Office Pilot Chart No· H.O. 1400 N.A. January 1961. After Collier (1970); reproduced by permission of John Wiley and Sons, Ltd.)

they would then have passed the southernmost tip of New Zealand between 50° S. and 60° S., several thousands of kilometres away.

Findings from investigations of ocean currents carried out by the Sea Fisheries Branch of the Department of Industries, Republic of South Africa, have some relevance to the Falkland salmon experiments. For seven years, from 1965, approximately 50 000 red, polythene drift cards were released in the oceans around Southern Africa by the Sea Fisheries Branch; of these cards, 1·6% were recovered locally and also overseas from North and South America, Australia and New Zealand as well as from numerous islands in the Atlantic and Indian Oceans. (During my visit to New Zealand, I picked up a South African drift card on the east coast of the South Island.) The points from which cards were recovered on the coastlines of Australia and New Zealand are shown in Fig. 22.

From information received with returned drift cards, Shannon *et al.* (1973) were able to calculate the average velocity of water movements in the South Atlantic and South Indian Oceans. In the case of the South Indian Ocean gyre and the Transverse Agulhas Current, as shown in Fig. 23, it takes approximately three years to make a complete circuit. This rate of water movement also applies to many currents in the North Atlantic Ocean. On the basis of velocities calculated for the West Wind Drift by Shannon and co-workers, an Atlantic salmon entering this current from the Falkland Islands and drifting passively in it would take between 3 and 4 years to pass the tip of New Zealand and $1\frac{1}{2}$–2 years to travel from New Zealand to Chile and the Falklands. The total journey time of approximately 5–6 years would constitute a period beyond the known maximum sea life of Atlantic salmon. Even if allowances were to be made for the fish swimming at a higher rate than the drift speed and for the time required for the developing smolt to mature to the adult stage whilst in the sea, it is unlikely that a reduction of 2 years in the period of travel would be the result; if it was, however, there would still be 4+ years of sea feeding to be accounted for. Grilse, with their sea-life span of 1+ year, are well within this period and the majority of British salmon normally spend 2 or 2+ years in the sea before returning to their natal streams.

One of the card recoveries in the South African investigations illustrates the type of passive drift of fauna in an ocean current which has been described. A drift card dropped east of Vema Seamount, 31°38′ S., 08°20′ E., was recovered on Tristan da Cunha. This card could only have reached the island by travelling in the South Atlantic gyre where the average velocity throughout a complete circuit is 16 cm/s or 13·8 km/d. In the Tristan da Cunha area, the rock lobster,

FIG. 22. Recoveries of drift cards from Australia and New Zealand. (After Shannon *et al.*, 1973.)

FIG. 23. Current patterns and velocities deduced from plastic drift card recoveries. (After Shannon *et al.*, 1973.)

*Jasus tristani* Holthuis, is common and its discovery on the isolated Vema Seamount, some 2897 km eastward, stimulated considerable interest amongst marine biologists as to how this population is maintained. The recovered card is an indication that the Vema rock lobster population may be augmented by larvae from Tristan da Cunha drifting in the South Atlantic gyre.

If it can be accepted that oceanic gyres may have some effect on the presence or otherwise of sea-going populations of salmon in rivers, it may well be asked why the second attempt at establishing quinnat salmon runs in New Zealand succeeded whereas the first one, and all the attempts to establish runs of Atlantic salmon there, failed. It is possible that one reason for eventual success is Ayson's selection of ova from winter-run fish in the Sacramento River for introduction into New Zealand rivers of the same (glacial) type and the similarity of the New Zealand quinnat in many respects, including the "stay at home" characteristic, to the Sacramento fish from which they are descended. Another possible reason is that, whilst the first attempt introduced quinnat salmon in many areas, particularly in the North Island, where conditions in the rivers and/or sea may not have been suitable for this species, Ayson stocked only the Waitaki River on the east coast of the South Island in the second attempt so as to take advantage of the ocean current along that coast for stocking rivers northwards. It is the opinion of Eggleston (1972) that the high-salinity water of the Southland Current confines the New Zealand quinnat to the inshore water on the coastal side of the Current, where temperature and salinity conditions are similar to those off the mouth of the Sacramento River. It is likely that the high-salinity water of the Southland Current would have had little effect upon the Atlantic salmon smolts going out into the Canterbury Bight during the acclimatization experiments, in my opinion, for they and adult Atlantic salmon are able to tolerate high salinities in the true oceanic environment. The failure of the Atlantic salmon to develop self-perpetuating runs in New Zealand is probably due to the disposition of the currents forming the Southland Front.

Between 1960 and 1973, over 20 000 drift cards were dropped by the New Zealand Government and merchant vessels at distances of up to 322 km offshore of the east and west coastlines of New Zealand and Australia. In respect of New Zealand, cards were returned from many places along the coastlines. No cards released off the west coast were recovered on the east coast and only one card was returned from the Chatham Islands, some 640 km east of New Zealand. Quinnat salmon, some maturing, have been caught by Japanese fishing vessels in waters about 56 km south-east of Timaru at depths of 18 m (Eggleston, 1972),

but no catches of salmon in the vicinity of the Chatham Islands appear to have been noted. I can find no records of any of the drift cards being returned from South America, Africa or India—or from the Falkland Islands. The general oceanic circulations around New Zealand are integrated, to some degree, with the West Wind Drift and the South Pacific Ocean, according to Heath (1973).

If the conclusion I reached as a result of the Falkland survey had any validity, it might be expected that suitable oceanic gyres would be present in the seas around New Zealand to account for the presence of substantial sea runs of quinnat in east coast rivers. During discussions with R. A. Heath at the time of my visit to New Zealand, he informed me that there is a small gyre in the Pegasus Bay area and thought that there is a circular water flow in the Canterbury Bight, inside the Southland Current. These gyres would probably extend about 200 km offshore of the South Island's east coast and could be the main reason, in my opinion, for the presence of sea-going quinnat salmon in rivers emptying into the Canterbury Bight and Pegasus Bay. I have marked the possible locations of these gyres, together with the approximate positions of the east coast rivers holding sea runs of quinnat, on the drawing supplied by Heath (Fig. 24). Heg and Van Hyming (1951) show that quinnat salmon at sea off Oregon eat mostly fish, including herrings and anchovies, and also euphausiids, and similar food organisms are abundant in the areas where salmon occur off the South Island (Eggleston, 1972).

In considering the causes of the failure of the attempts to establish sea runs of Atlantic salmon in the Falkland Islands despite the success achieved with runs of sea trout, *Salmo trutta*, account should be taken of the different behaviour of these two species in the sea. Whereas the majority of sea trout usually travel to feeding grounds in inshore coastal regions, Atlantic salmon may migrate thousands of kilometres to their oceanic feeding grounds; for example, it is now known that some salmon from the British Isles travel to feeding grounds off Greenland, an approximate distance of more than 3000 km. The reason for some salmon travelling such enormous distances to feeding grounds when it seems that most sea trout can feed successfully in coastal areas may lie in the stage of evolutionary development that has been reached by the respective species and/or the swimming capabilities of the immature fish migrating seawards.

Falkland rivers are capable of supporting salmonids, both in respect of food for immature fish and spawning areas. Whilst the rivers are small when compared to many salmon rivers in the Northern Hemisphere, my researches into flow requirements for the migration of

FIG. 24. Oceanic currents and convergences around the coastline of New Zealand's South Island. (After Heath, 1975.)

Atlantic salmon in certain estuaries and rivers of England and Northern Ireland (1972) show that this species can maintain itself in a small river providing that water velocity in the estuary is between 61 and 91 cm/s, which condition, in all probability, applies in the sea-washed lagoons of the Falkland Islands; a velocity requirement of 61 cm/s for quinnat, *Oncorhynchus tschawytscha*, and chum salmon, *O. keta* (Walbaum), has been found by laboratory investigations in the United States. It may be considered worthwhile to carry out further experiments to establish sea runs in the Falkland Islands, on a much more intensive scale, with Atlantic salmon or Pacific salmon species. Even if the hypothesis propounded on the possible effect of oceanic gyres and currents on salmon migration, with its implications concerning the results of the previous experiment in the Islands, is valid, there are always the possibilities that suitable gyres or currents, at present unknown, exist in the region or that the chosen salmon species would be able to take advantage of the sea feeding grounds of the Falkland sea trout—for instance, Sacramento and New Zealand quinnat do not travel far from their natal rivers and not all Atlantic salmon journey great distances to feeding grounds in the sea.

In selecting salmon species for any future experimentation in establishing sea runs there might be in the Falkland Islands, there are practical considerations as well as genetic factors to be taken into account. Because food supplies for immature salmonids are limited in Falkland rivers, those species such as chum and pink salmon, *O. gorbuscha* (Walbaum), and some populations of quinnat, where the young can go to sea after only a few days in freshwater, seem suitable in this respect. Quinnat ova from New Zealand's substantial salmon runs, the only ones established in the Southern Hemisphere, are an obvious choice for introduction into the Islands, especially as those fish are not thought to travel far to their feeding grounds in the sea; however, their young stay as long as 18 months in freshwater. Also, the New Zealand experiments demonstrated the value of "matching" salmon to rivers when attempting to establish sea runs, and Falkland rivers are vastly different in character from the New Zealand quinnat rivers. (Attempts made in Tasmania, also situated in the Southern Hemisphere, to establish sea-going populations of quinnat from ova imported from New Zealand met with failure, though whether this was due to conditions in the rivers or in the sea or both is not known to me. Davidson and Hutchinson (1938) attributed failure to unfavourable coastal water conditions.) It would be preferable, in my opinion, to obtain ova from the sea-going quinnat salmon population of a Northern Hemisphere river where conditions both in the river and offshore,

including temperatures and, in the latter case, salinity tolerances, are similar to those pertaining in the Falklands, and where the quinnat young only stay in freshwater for a few days. The same criteria, presumably, would need to be applied if any of the other Pacific salmon species were to be considered. Of these, pink and chum salmon have young which are able to migrate to sea after a few days in freshwater; pink salmon return after more than a year in the sea whilst the sea feeding periods of chum vary from half a year to four years. Rockwell (1956) shows that normal percentages of the ova of pink and chum salmon developed more freely when salinity, during fertilization, did not exceed 18‰, which may apply in zones in the lower tidal reaches of Falkland rivers. The fry of pink and chum salmon, when hatched in freshwater, show a marked preference for migration to the sea after four to six weeks and these species are known to spawn in intertidal gravel even when freshwater with suitable gravel is available to them—this is especially true in south-east Alaska (Helle *et al.*, 1964). The rivers and estuaries of south-east Alaska, very approximately, are situated between latitudes 55 °N. and 60° N., which may be compared with the position of the Falkland rivers and estuaries situated, again very approximately, between latitudes 51° S. and 53° S.—a factor of possible importance when "matching" fish to Falkland rivers, especially if, in the case of the pink salmon, ova from any late runs could be obtained and their development delayed to allow the fry to develop under similar conditions to the Falkland sea trout. Before any further experimentation to establish sea runs of salmon in the Islands takes place, however, consideration should be given to possible adverse effects on the existing runs of sea trout, which contain a proportion of fish comparable in size and weight to many salmon.

As can be seen, the establishment of sea-going runs of salmon is a complex matter and there have been several failures of acclimatization experiments in the Northern as well as in the Southern Hemisphere. The fish live in different environments at various stages of their life-cycle and, whilst much is now known about their movements in rivers and estuaries, very little has been discovered concerning their movements in the sea when journeying to and from their feeding grounds or even the location of many of these feeding grounds. The hypothesis given in this section that oceanic currents and gyres possibly influence salmon migration puts forward the concept that the factors affecting the movements of these fish in the sea are of a simple, physical nature.

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