

Siphonophore Biology

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I.	Introduction	98
II.	Body Form	99
	A. Development	100
	B. Coloniality	109
III.	Systematics and Evolution	110
	A. Systematics	110
	B. Evolution	121
IV.	Distribution and Migration	133
	A. Vertical distribution	133
	B. Geographical distribution	139
	C. Neritic siphonophores	151
	D. Benthic and pleustonic siphonophores	154
	E. Diel vertical migration	156
	F. Siphonophores and deep-scattering layers	164
	G. Seasonal changes in abundance	165
V.	Physiology and Behaviour	172
	A. Behaviour	172
	B. Coordination	182
	C. Autotomy	189
	D. Flotation	193
	E. Colour, luminescence, camouflage and mimicry	199
VI.	Nutrition and Ecology	203
	A. Associations	203
	B. Predators	208
	C. Nematocysts	209
	D. Feeding	223
	E. Nutrition	232
	F. Ecological importance	241
	Acknowledgements	244
	References	245
	Addendum	262

1. Introduction

What are siphonophores, and why do people study them? In answer to the first question, many biologists would agree with E. O. Wilson's capsule definition of them as 'bizarre creatures.... vaguely resembling jellyfish' (Wilson, 1975), but those who have made *in situ* observations of them may object to Mary Winsor's reference to their "tangled, confused mass of tentacles and appendages" (Winsor, 1976). Siphonophores are complex, highly polymorphic creatures, whose "colonies" are composed of many polypoid and medusoid "individuals", and yet they function physiologically as single individuals. Curiosity about the paradoxical nature of these animals prompted attention in the past, particularly during the latter half of the nineteenth century, when many researchers provided detailed descriptions of siphonophore anatomy from animals collected in their entirety at the surface of the oceans. These authors attempted to make sense of these complicated animals in terms of the polypoid or medusoid origins of their component "members", and their relations with other hydrozoans. They were interested in finding out how such composite organisms could function effectively, and compete on equal terms with unitary zooplankton forms.

Much of our knowledge of siphonophore morphology and life cycles, also dates from that time, and the early years of the present century. However, during this period little attention was paid to the ecology of siphonophores, and it was not until the introduction of the "quantitative approach" to marine biology (Hensen, 1891) that the large-scale distributional patterns of many groups of pelagic organisms began to be investigated. Siphonophores, probably because of their fragility, generally were ignored in such studies and this is reflected in the dearth of literature on them for the first half of this century. Only a few major taxonomic monographs (e.g. Bigelow, 1911; Moser, 1925) and occasional papers on their quantitative distribution (e.g. Bigelow and Sears, 1937; and several papers by E. Leloup) marked that period.

In recent years, the introduction of *in situ* techniques, such as SCUBA diving and submersibles, has demonstrated the great importance of siphonophores and other gelatinous organisms in the marine ecosystem, and a plethora of works on, for instance, their physiology, behaviour and ecological impact have resulted. Many of these organisms are very common and are easily observed, yet they, including a whole subset of siphonophore species, rarely, if ever, are collected by nets. Harbison (1983) has succinctly summarized this dilemma and has pointed out that, at present, no one sampling technique can give a complete picture of life in the oceans.

Today, thanks to both *in situ* observations and to improved net sampling techniques, we have a better appreciation of the importance of siphono-

phores in the marine environment. Siphonophores occur at the surface; on the bottom; and at all levels in between, often in numbers that make them one of the dominant groups of marine predators (Pugh, 1984). This growing understanding of the group's importance highlights the need for an up-to-date treatment of siphonophore biology, and that is our goal for the present review. The one constraint to this endeavour is the existence of a substantial chapter on "Siphonophora" by Claude and Danièle Carré for the *Traité de Zoologie*, that has been *in press* for several years. These authors kindly have allowed us to see the manuscript, and this has enabled us to plan the present review so as to complement their treatment and to avoid overlap. The Carrés have emphasized the basic morphology, development and life history of the siphonophores, so we have stressed the ecological and physiological aspects. In this context we have deferred from giving yet another account of the complicated and unique terminology that is used to describe siphonophores. Such definitions will appear in Carré and Carré (1987), and can be found in standard textbooks or in recent taxonomic works (e.g. Totton, 1965a; Kirkpatrick and Pugh, 1984). Nonetheless, if our review does no more than stimulate interest in this fascinating group of animals, we will feel that our efforts have been well rewarded.

II. Body Form

The basic details of morphology and development of Siphonophora, established during the nineteenth century and early years of the present century, may be found in standard textbooks. Morphology is well covered by Chun (1897a,b), Chun and Will (1902), Moser (1924), Hyman (1940), and Totton (1954, 1965a) while the chief facts of development, worked out by Metschnikoff, Chun, Lochmann, Fewkes, Woltereck and other pioneers can be found in summary form in treatises by Dawydoff (1928), Garstang (1946), Leloup (1954) and Totton (1965a). The treatment of development in this section will be restricted to a general overview of siphonophore embryology emphasizing recent contributions, especially the work of C. and D. Carré, and of G. Freeman, who have successfully raised several species through early larval development in the laboratory. Both development and morphology, including many details of histology and ultrastructure will be covered by Carré and Carré (1987).

The genera, families and sub-orders of the Siphonophora that are mentioned in this and subsequent sections are listed in Table 1, p. 112. Photographs of living siphonophores will be found on pp. 113–115, 224.

A. Development

1. Cytogenetics

Chromosomes have only been studied in one siphonophore, *Physalia*, and only in somatic tissues (Mackie, 1960b). *Physalia* has a diploid set of 20 chromosomes, which are simple rod-shaped structures seen in late prophase, three pairs being long (4.5 µm) and the remainder grading down from 3.0 µm–1.8 µm. No differences have been observed between chromosomes from left- and right-handed morphs. In certain tissues, binucleate and polyploid mononucleate cells occur. The latter probably arise from the former by combination of the two sets of chromosomes during prophase (endopolyploidy). The process can evidently take place repeatedly because $4n$, $8n$, $16n$, and $32n$ nuclei have been found. The frequency of polyploid cells is inversely related to polyploid number. Ploidy can be determined from measurements of nucleolar size in resting stage nuclei (Mackie, unpublished).

There have been no studies on the genetics of siphonophores.

2. Gametes

Most siphonophores whose development has been studied are believed to be dioecious, but *Physalia* is monoecious, as are the Rhodaliids and possibly a few other species. The gonads are located on the manubria of the gonophores, which are budded from the stem in orderly arrays, sometimes in clusters on gonodendra. The gonophores usually remain attached but in some species they are liberated as free-swimming medusoids, e.g. the female gonophores of *Nanomia bijuga* (Carré, 1969b). The diphyids and some other calycophores produce eudoxids (see p. 107). From these free-living, monogastric subcolonies there can arise a succession of gonophores which ripen one after the other. In *Chelophyses*, as many as eight are produced, and they alternate roughly between males and females (Carré and Carré, 1987).

The sex cells originate in the ectoderm of the gonophore bud prior to formation of the entocodon and reach their final destinations in the manubrial ectoderm indirectly after migrating through the endoderm (Heyne, 1916). In *Muggiaeae*, according to Benasso and Benasso Stroiazzo (1976) there is a regular over-production of oocytes, with only a small percentage surviving, but this may only happen under suboptimal conditions (Carré and Carré, 1987). Timing of gamete release is probably related to photoperiod as in many hydromedusae (Miller, 1979). The spermatozoa are of simple form having a conical nucleus, a middle piece with mitochondria and a single flagellum, as in many other cnidarians (Carré, 1979). An

unusual feature is a striated rod extending from the centriolar region to the anterior end of the nucleus. At fertilization, this rod forms part of the acrosomal process but it may be implicated earlier in bending the sperm head to one side during chemotaxis (Carré and Sardet, 1981). The eggs are moderately large, ranging from about 300 µm in diameter in *Nanomia* and *Muggiaeae* (Freeman, 1983) to 500 µm in *Abylopsis* (Carré, 1967). They have a pronounced centrolecithal organization with a distinct cortical zone of yolk-free ectoplasm. They are released from the gonophore following the second meiotic division, with polar bodies still attached.

Species-specific attraction of sperm to eggs was noted in *Muggiaeae* and *Nanomia* by Miller (1979). Carré and Sardet (1981) showed that the attractiveness is associated with a structure, the cupula, located close to the egg surface close to the female pronucleus. The attractant, a low molecular weight protein, causes the sperm to concentrate in the vicinity of the cupula, and fertilization always takes place at this point.

3. Development to planula

Cleavage has usually been described as total and equal, resulting in a compact cell mass with no central cavity (a morula), gastrulation being said to take place by secondary delamination. These conclusions, based for the most part on studies of whole eggs and embryos, require reassessment in the light of work by Carré (1971, 1975) using optical and electron microscopy of sectioned material (Fig. 1A-D). Carré finds that there is no true morula. Instead, from the 32 cell stage onward, cleavage is superficial and partial, and the larva becomes a periblastula. She further finds that gastrulation is by primary delamination. The early gastrula consists of an external layer of ectoderm cells, an inner anucleate mass of yolk and patches of endoderm cells on the inside of the ectoderm layer. Transformation to the planula stage involves multiplication of the endoderm cells to form a continuous inner lining layer and migration of cells into the interior.

4. Polarity, symmetry and determination

Freeman (1983) shows that the oral-aboral axis of the embryo is established by the plane of the first cleavage furrow and that the initiation point of this furrow corresponds to the future oral pole, the posterior end of the free-swimming planula. Subsequent development in both calycophores and physonects involves the development of thickened endoderm in a line along one side ("ventral") where organogenesis takes place (Fig. 1). Freeman's studies with *Muggiaeae* show that this thickening develops in a position corresponding to one side of the first cleavage furrow. The same is probably

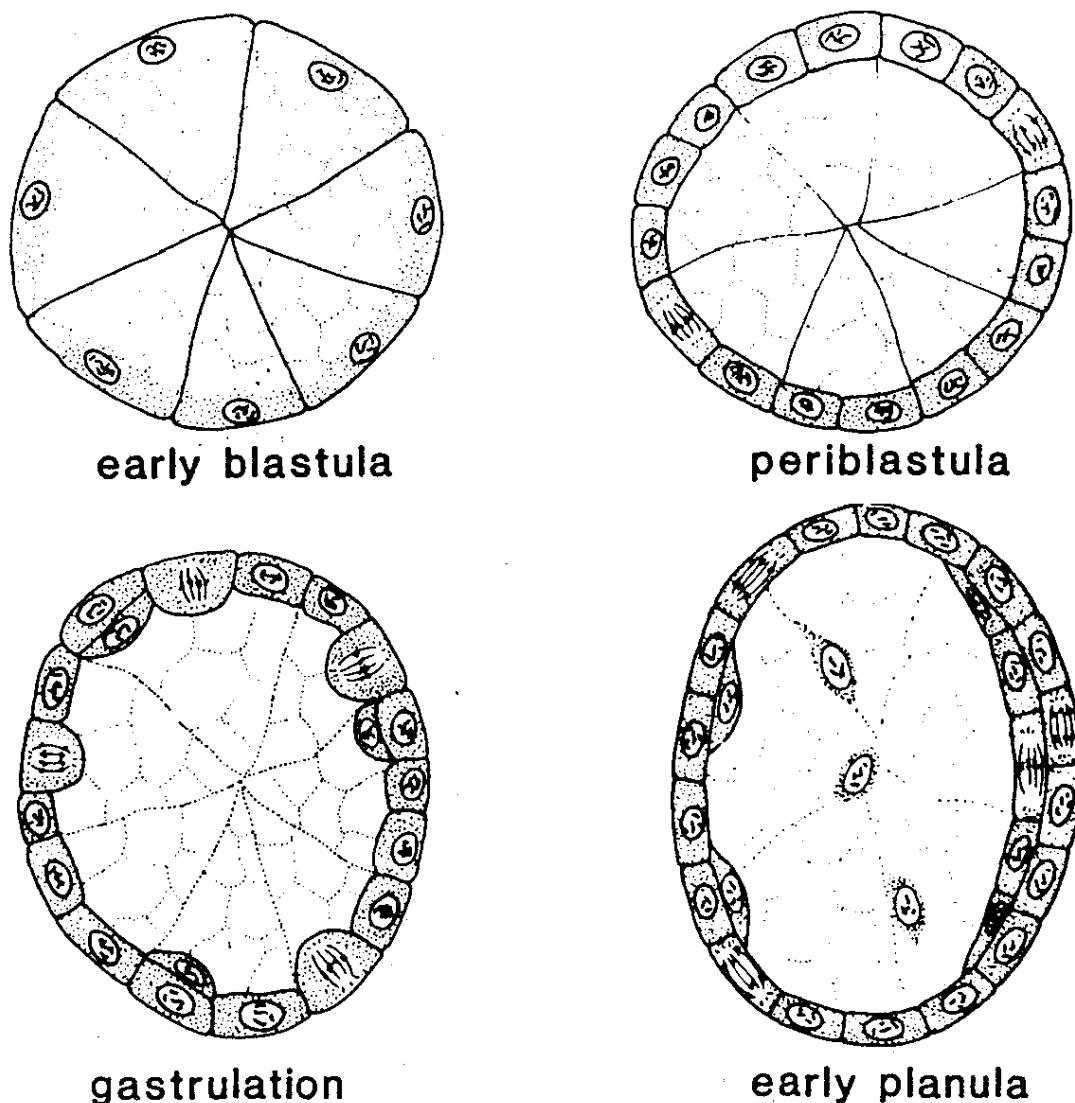


FIG. 1. Early developmental stages of siphonophores. After Carré (1975).

true in the case of *Nanomia*. Thus, the first cleavage establishes not only the primary longitudinal axis, but the oral and aboral poles as well as the plane of bilateral symmetry of the future larva. Freeman (1983) further finds that in both *Nanomia* and *Muggiaeae* there is an early determination of cell fate along the oral-aboral axis. Specification of mouth, tentacle and float-forming regions has already occurred at the eight-cell stage. Determinate development of this sort is unusual in hydrozoans but occurs in the rhopalonematid medusa *Aglantha digitale* where the planula develops directly to the medusa without passing through a hydroid stage. Freeman suggests that, both in *Aglantha* and in the siphonophores, complex structures have to be produced within a restricted time frame, before nutrient reserves are exhausted. Mapping out the parts in the egg and early embryo presumably saves time.

5. Post-planula development of physonects

Studies on *Nanomia* (Carré, 1969b; Freeman, 1983; Totton, 1954, 1965a) show that the planula transforms into a siphonula larva starting at 18–24 h

of development (Fig. 2). The endoderm along one side and at the anterior end starts to thicken. The ectoderm cells also enlarge at the anterior end and invaginate, forming the float rudiment (Fig. 2B). At the same time, a tentacle sprouts from the side. By the time the siphonula is a week old, gas secretion has begun in the float, and the tentacle has elongated and become recognizably part of the protozooid (first gastrozooid formed) (Fig. 2D). The protozooid forms directly in the oral end of the transforming planula, by hollowing out of the gut cavity, and appearance of a mouth. Its production less resembles a process of budding than transformation of pre-existing structure and it, therefore, appears better to regard it as part of the primary zooid derived from the egg (the oozooid) than as a new zooid budded from the latter. If we accept that the protozooid is a direct derivative of one end of the oozooid, we can represent siphonophore development as in Fig. 3, essentially as a process of elongation of the central part of the oozooid to form the stem, and with its oral end transformed into the protozooid, which is carried away distally further and further as the stem grows.

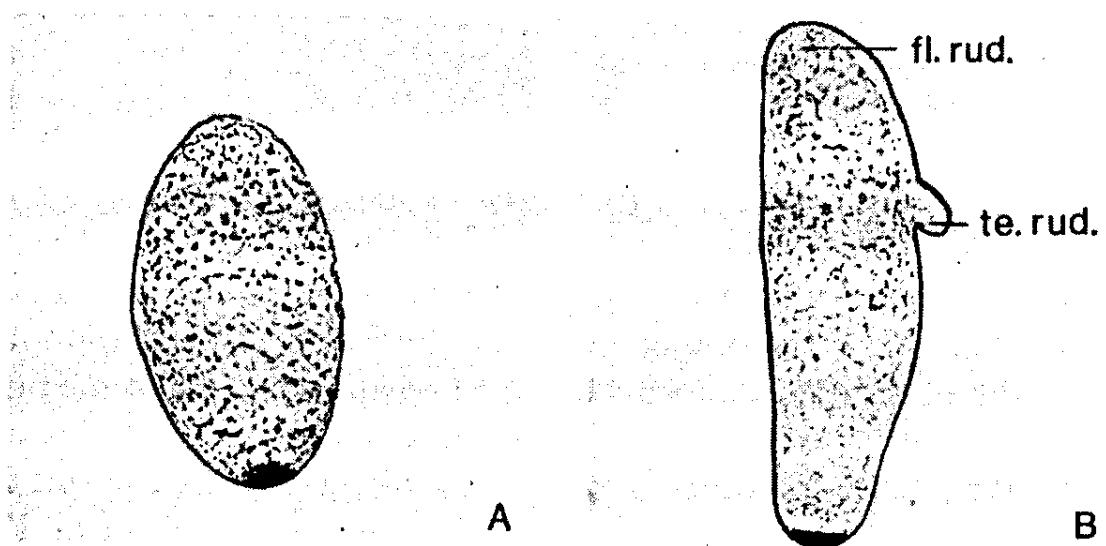
The float is also best regarded as part of the oozooid, having presumably arisen neomorphically in evolution rather than by modification of a medusa bud as some have suggested and a few (e.g. Campbell, 1974; Gould, 1984) still suppose. Siphonophore specialists have generally abandoned any attempt to homologize the float with a medusa, following the critiques of Garstang (1946) and Leloup (1954). Most important, however, have been the histological studies of Carré (1967, 1969b, 1971) which remove any basis for homologizing medusoid development with float development.

For Totton (1965a), then, as for the present authors

"It is essential to understand that the long axis of a fully grown physonect, even many metres long, carries at one end the original larval mouth of the oozooid and its invaginated aboral float at the other".

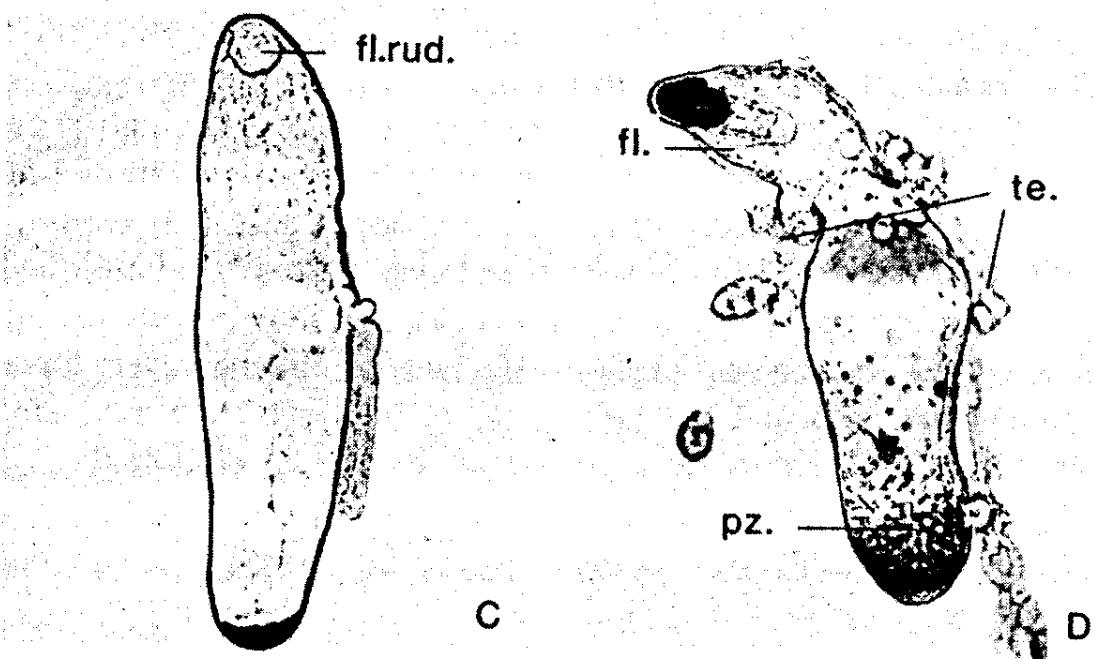
Budding of secondary zooids occurs from two budding zones, one just beneath the float for the nectophores and one lower down for the siphosomal appendages (gastrozooids, palpons, bracts, gonophores). As the buds form, the stem elongates. Thus, with elongation of the stem in the nectosomal region, the two budding zones move progressively apart. The nectophores and other zooids are budded in a highly patterned array and the buds arise "almost like the rudiments of organs" (Mergner, 1971).

Development of other physonects differs in certain respects from the process as described in *Nanomia*. In *Forskalia*, temporary larval bracts appear at 6–8 days, providing for flotation, and are later shed. The small float develops late, and appears not at the aboral pole but in the lateral thickening just anterior to the bracts (Carré, 1967). *Agalma elegans*, in contrast to *Forskalia*, retains its larval bracts (Totton, 1956). In *Halistemma rubrum*, large larval bracts develop (Woltereck, 1905) and are probably



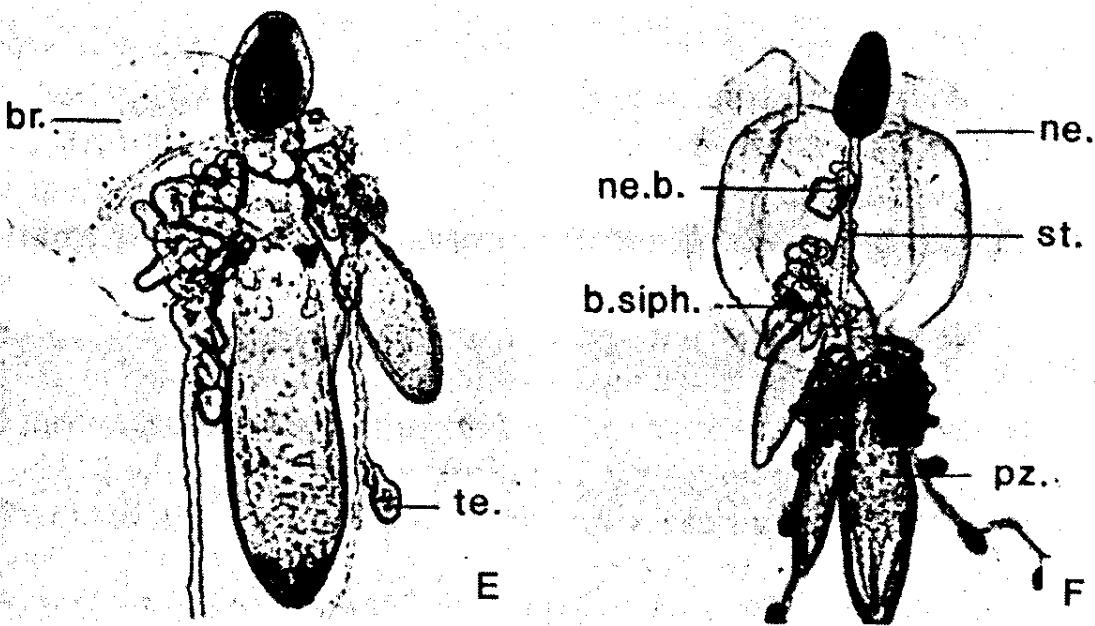
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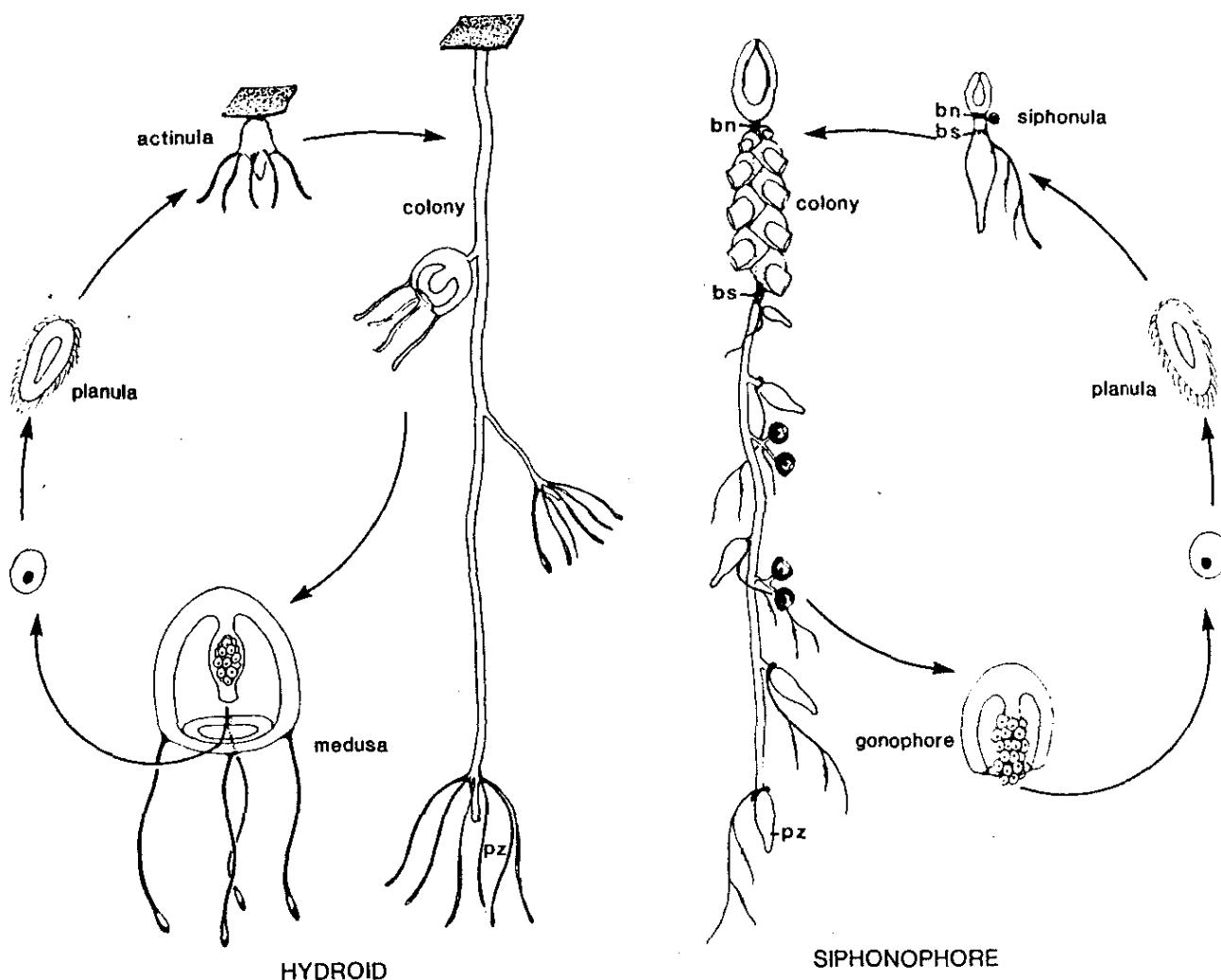
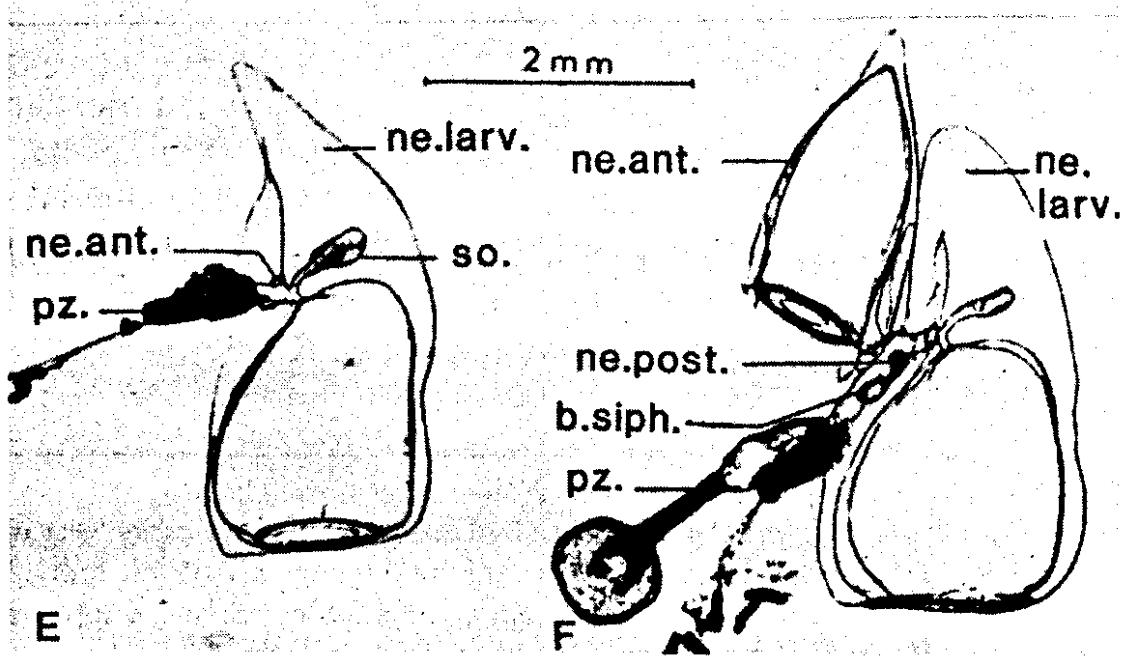
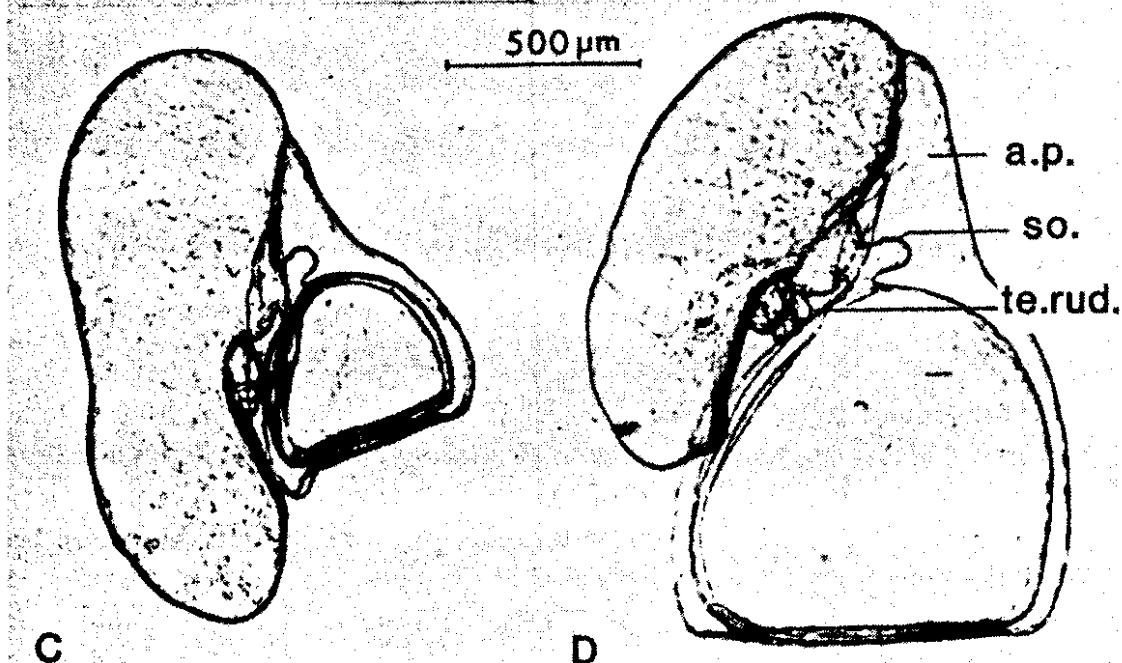
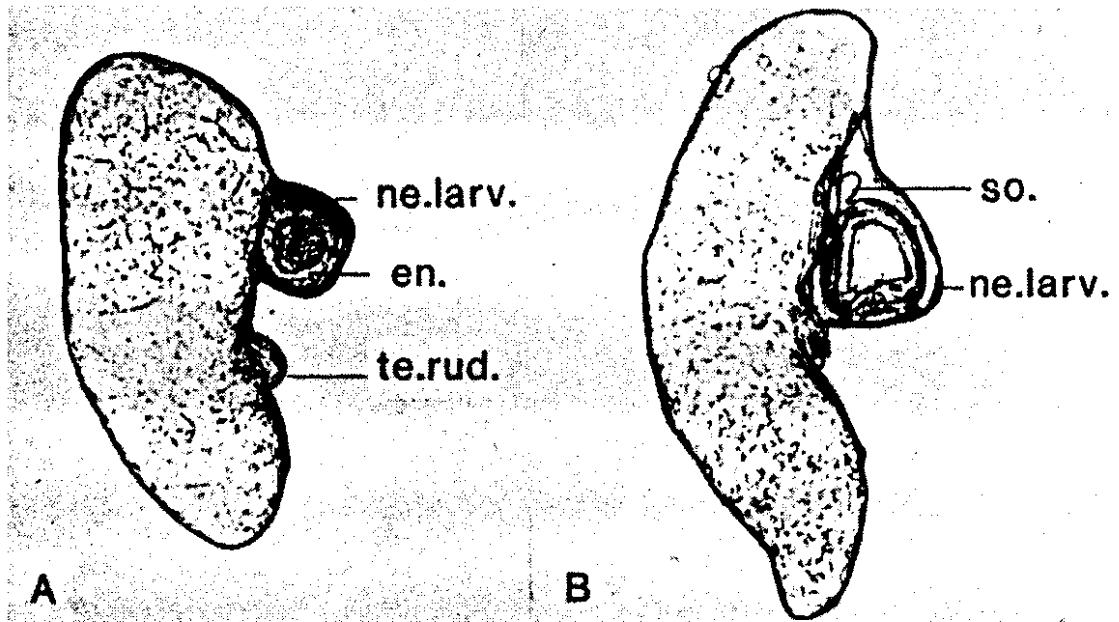


FIG. 3. Comparison of life cycles for a hydroid and a physonect siphonophore. In the hydroid, elongation of the basal region of the attached actinula larva carries the mouth and tentacles (protozooid, pz) away at the end of the growing stem. In the siphonula larva of the siphonophore the stem is created by a similar process, the elongation of the region below the float. Budding of secondary zooids is complicated in the siphonophore by the existence of two separate budding zones, one for the nectophores (bn) and one for the siphosomal appendages (bs). Redrawn from Mackie (1986).

retained; these are also the bracts of "*Nectalia loligo*", a postlarva of *Halistemma*. The first nectophore develops very early in *Halistemma*, probably again as a rotational device; it is later shed, like the caducous larval nectophores of many calycophorans (Carré, 1971). *Cordagalma cordiformis* has a single enormous larval bract which envelops most of the embryo and is shed only after several nectophores have developed (Carré, 1973).

FIG. 2. Postplanula development of *Nanomia bijuga*. After Carré (1969b).
A. planula, 36 h, 325 µm long. *B*. planula, 48 h. *C*. planula, 60 h. *D*. siphonula, one week, ca 550 µm long. *E*. siphonula, three weeks. *F*. young colony (no scale given). br. bract, b. siph. budding zone for siphosome appendages, fl. float, fl. rud. float rudiment, ne. nectophore, ne. b. nectophore bud, pz. protozooid, st. stem, te. tentacle, te. rud. tentacle rudiment.



6. Post-planula development of calycophores

The larval nectophore starts to bud within the lateral thickening after two days of development and is swimming within three (Carré, 1967). Its formation, as depicted by Carré (1967) for *Lensia* (Fig. 4) and by Carré (1967) for *Abylopsis*, follows the normal steps in medusan development. The first tentacle appears in *Lensia* just below the nectophore bud (Fig. 4A). The larva is now termed a calyconula. The aboral part of the calyconula shows no trace of a float rudiment at any stage but contains yolk reserves, most of which are used up during the first five or six days of development, after which the larva is self sustaining on the basis of its functional protozooid. Stem elongation and production of secondary zooids proceeds as in physonects.

In most calycophores the part of the planula containing the yolk mass becomes the protozooid and the first nectophore appears as a small organ on the outside of the embryo but in *Lilyopsis* and *Hippopodius* the yolk mass is enclosed in the somatocyst of the larval nectophore and the protozooid is the "appendage" (Carré and Carré, 1969).

In *Sphaeronectes*, the larval nectophore survives to become the definitive and only nectophore of the fully grown colony (Carré, 1969a). In the abyliids (e.g. *Abylopsis tetragona*) the larval nectophore becomes the definitive anterior nectophore and a second, much larger posterior nectophore arises behind it (Carré, 1967). This species also has a caducous larval bract, recalling *Cordagalma*. In *Lilyopsis* the larval nectophore is described as "semi-permanent" (Carré and Carré, 1969). In *Hippopodius* the larval nectophore is shed after two or three nectophores are formed (Carré, 1968). In the diphyids the larval nectophore is replaced by one or two definitive nectophores of elaborate form, the posterior one, where present, articulating with the back of the anterior one (Fig. 5). It is thought that the nectophores in prayids and hippopodiids are produced continually throughout life. The posterior nectophore of abyliids and both nectophores of certain diphyids can probably be replaced if lost (C. Carré, personal communication).

It is customary to speak of the "polygastric" stage of a calycophore, as distinct from the eudoxid stage. Eudoxids are produced in all groups except the Hippopodiidae, Prayidae and Sulculeolariinae. They consist of monogastric stem groups which detach from the distal end of the stem of the

FIG. 4. Postplanula development of *Lensia conoidea*, right lateral view of calyconula, after Carré (1967). A. 60 h larva, B. 3 d larva, C. 3.5 d, D. 4 d, E. 10 d, F. three weeks. a.p. apical process, b. siph. budding zone for stem appendages, en. entocodon, ne. ant. anterior nectophore, ne. larv. larval nectophore, ne. post. posterior nectophore, pz. protozooid, so. somatocyst, te. tentacle, te. rud. tentacle rudiment.

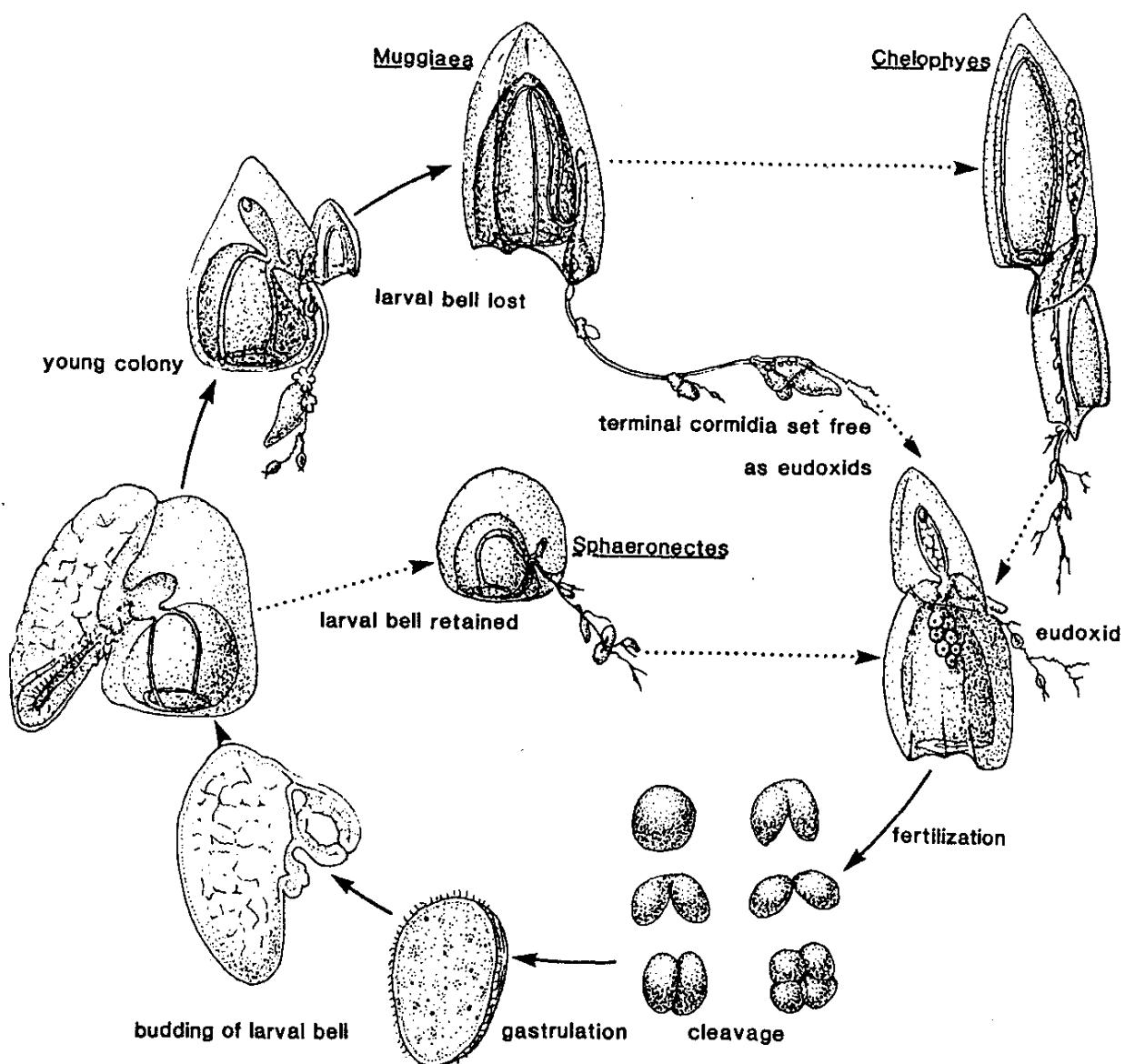


FIG. 5. Three calyphoran life cycles, to illustrate retention of the larval nectophore in *Sphaeronectes* and its replacement by one or two new nectophores in *Muggiaeae* and *Chelophyes* respectively. From an unpublished drawing kindly lent by Carré.

polygastric organism and lead a free existence, dispersing the gametes. Stem fragmentation occurs in prayids, but the fragments are usually polygastric, and should not be termed eudoxids.

7. Development of cystonects

The earliest stages are unknown and are believed to occur in deep water. *Physalia* larvae first appear at the surface with a float about 2 mm long. The protozooid with its developing tentacle lies toward one end of the float. No secondary zooids are present at this stage (Totton, 1960). When they form, they do so by budding from the lower side of the float. In *Rhizophysa* a stem forms with a budding zone below the float.

B. Coloniality

Study of the development and morphology shows that the siphonophore arises from a single egg and grows up to become a well-integrated organism, but at the same time is composed of parts which can only have originated in evolution from free-living individual polyps or medusae. Should the siphonophore then be regarded as a colony or an individual? "La question des Siphonophores a, de tout temps, préoccupé les savants les plus qualifiés", notes Leloup (1954) in discussing this peculiar paradox. Two distinguished contemporary biological theorists, E. O. Wilson and S. J. Gould, have contributed thoughtful essays on the same topic.

For Wilson (1975), "the resolution of the paradox is that siphonophores are both organisms and colonies. Structurally and embryonically they qualify as organisms. Phylogenetically they originated as colonies."

For Gould (1984), "the siphonophore paradox does have an answer of sorts, and a profound one at that. The answer is that we asked the wrong question Are siphonophores organisms or colonies? Both and neither; they lie in the middle of a continuum where one grades into the other."

For both Gould (1984) and Winsor (1976), T. H. Huxley is a key figure in "the great siphonophore debate". Almost alone in taking the position he did, he came to represent one whole side of the argument in the polyperson-polyorgan controversy. Huxley defined an individual as the sum of the products of a single ovum. Hence, the different manifestations of that individuality in any given life cycle, whether larvae, polyps or medusae, could not also be called individuals. Therefore, he termed them organs. The fact that these "organs" (e.g. medusae in many hydrozoan life cycles) detach and lead a free life did not alter Huxley's belief in the primacy of the egg-individual or oozooid. Many plant and animal community ecologists would today respond sympathetically to Huxley's views on coloniality. To workers in these fields, the primary object of interest is not the "individual" oozooid in a colony or clone, but the genetic individual (genet) to which the oozooids belong. The genet is the unit upon which selection acts. The zooids are merely expressions of an iterative growth process, the "modules" whereby the genet expands in time and space. A considerable literature has grown up on this topic, based almost entirely on plants, bryozoans, corals, hydroids and ascidians.

Siphonophores and other pelagic colonies can also be thought of as modular organisms but they differ from typical benthic colonies in several important respects (Mackie, 1986). Benthic colonies often show indeterminate growth, along with the potential for exponential increase in numbers of modules. Frequently, they undergo fragmentation, and the fragments regenerate to form new colonies, or fuse with one another, sometimes producing

chimaeric colonies. The genet may thus achieve widespread dispersal and extreme longevity. Colony form is often based on a branching pattern but may be highly variable. In some cases, the disposition of the different zooid types can be altered to conform to local variations in substrate. In times of hardship, modules regress and the colony shrinks, only to expand again when favourable conditions return.

Siphonophores, by contrast, in keeping with their ability to swim freely in the sea, are linear in form, with little branching, and are polarized, with a distinct anterior end. They are also bilaterally symmetrical. They grow by addition of modules at localized growth zones. The result is a high degree of determinancy of form. Isolated zooids cannot replicate or restore missing parts of the colony. Siphonophores cannot fuse, vary their shapes, shrink and re-expand, or switch their zooids around. Thus siphonophores, though modular, more closely resemble unitary organisms than do conventional (benthic) colonies. In an earlier discussion of this topic, Mackie (1963) expressed the view that siphonophores are the most advanced animal colonies, and the only ones to have fully exploited the physiological possibilities of coloniality.

"They have developed colonialism to the point where it has provided them with a means of escaping from the limitations of the diploblastic body plan. The higher animals escaped these limitations by becoming triploblastic and using the new layer, the mesoderm, to form organs. The siphonophores have reached the organ grade of construction by a different method—that of converting whole individuals into organs" (Mackie, 1963).

The achievement of the siphonophores can indeed be regarded "as one of the greatest in the history of evolution" (Wilson, 1975).

III. Systematics and Evolution

A. Systematics

As Totton (1965a) points out, the classification of siphonophores is based on the characters of the asexual stage, the larval nurse-carriers, and not on those of the sexual adult medusoids, which are much reduced. Nonetheless, the nomenclature of siphonophores became highly confused, particularly towards the end of the last century, possibly reaching a peak in Haeckel's (1888) *Challenger Monograph*. Bigelow (1911) strove to sort out much of this confusion, strictly applying the law of priority for species names, and attempting to relate descriptions of doubtful species with those of better known ones. Although he was for the most part successful in this venture,

unfortunately, in certain notable cases, he introduced further disorder. Totton (1954, 1965a), however, was able to correct these errors and in his detailed work, *A Synopsis of the Siphonophora*, he brought together descriptions of all the species of siphonophores that he considered to be valid. Totton's work represents the reference point for any discussion on the taxonomy and systematics of siphonophores, and it is unfortunate that some recent authors have not adopted Totton's (1965a) reasoned and considered nomenclatural system but have retained outmoded names. Totton (1965a) does not always give a full list of synonymies for each species but, to a large extent, such lists can be found in Daniel (1974), who follows Totton's nomenclature, for those species which have been found in the Indian Ocean. Stepanjants (1967) also has produced a Monograph on the Siphonophores of the North Pacific Ocean which, unfortunately, remains obscure to us as no English translation exists. Her classification is somewhat different from Totton's (1965a) and retains several specific names which Totton had reduced to junior synonyms of others.

The Order Siphonophora is split into three suborders based largely on the presence or absence of two basic structures; a pneumatophore, or gas-filled float, and an apical or sub-apical nectosome, consisting of one, two or a series of asexual medusoid swimming bells or nectophores. The members of the Suborder Cystonectae possess a pneumatophore but no nectosome; those of the Suborder Physonectae, with two notable exceptions, possess both; while the species of the Suborder Calcyophorae only have apical nectophores and no pneumatophore. Totton (1965a) list 134 species (several of which are *species inquirendae* (see below), plus one variety, and divides these amongst 54 genera and 15 families (Table 1). The reader is referred to Totton (1965a) for a list of all the relevant authorities.

Totton (1954) commented on the fact that there are relatively few species of siphonophores in the World's oceans. He conjectured that the widespread, panoceanic distribution of many of these species meant that, in effect, there was a single interbreeding population, such that the evolution of species by geographical isolation was inhibited. Phillips (1973) also concluded that the low-species diversity of holoplanktonic cnidarian groups was correlated with the relative slowness of major tectonic changes in geological history and the less frequent establishment of allopatric populations necessary for speciation.

The following notes are intended to update Totton (1965a) and include most of the relevant information which has been published on the systematics of siphonophores since then, classified in the same way (Table 1). It is doubtful whether all the new species will stand the test of time, but space does not allow a full discussion here of their relative merits.

TABLE 1. CLASSIFICATION OF THE ORDER SIPHONOPHORA (FROM TOTTON, 1965a)

	Family	Genus
Suborder Cystonectae		
	1. Physaliidae	<i>Physalia</i>
	2. Rhizophysidae	<i>Rhizophysa</i> , <i>Bathyphysa</i> , <i>Epibulia</i> .
Suborder Physonectae		
	3. Apolemiidae	<i>Apolemia</i>
	4. Agalmidae	<i>Agalma</i> , <i>Halistemma</i> , <i>Cordagalma</i> , <i>Marrus</i> , <i>Moseria</i> , <i>Nanomia</i> , <i>Lychnagalma</i> , <i>Erenna</i> . <i>Pyrostephos</i> , <i>Bargmannia</i> .
	5. Pyrostephidae	<i>Pyrostephos</i>
	6. Physophoridae	<i>Physophora</i>
	7. Athorybiidae	<i>Athorybia</i> , <i>Melophysa</i> .
	8. Rhodaliidae	<i>Rhodalia</i> , <i>Stephalia</i> , <i>Angelopsis</i> , <i>Archangelopsis</i> , <i>Dromalia</i> .
	9. Forskaliidae	<i>Forskalia</i>
Suborder Calycophorae		
	10. Prayidae	
	Amphicaryoninae	<i>Amphicaryon</i> , <i>Maresearsia</i> ,
	Prayinae	<i>Rosacea</i> , <i>Praya</i> , <i>Prayoides</i> , <i>Lilyopsis</i> , <i>Desmophyes</i> , <i>Stephanophyes</i> .
	Nectopyramidinae	<i>Nectopyramis</i>
	11. Hippopodiidae	<i>Hippopodium</i> , <i>Vogtia</i> .
	12. Diphyidae	
	Sulculeolariinae	<i>Sulculeolaria</i>
	Diphyinae	<i>Diphyes</i> , <i>Lensia</i> , <i>Muggiae</i> , <i>Dimophyes</i> , <i>Chelophyes</i> , <i>Eodoxoides</i> , <i>Eodoxia</i> .
	13. Clausophyidae	<i>Clausophyes</i> , <i>Chuniphyes</i> , <i>Crystallophyes</i> , <i>Heteropyramis</i> , <i>Thalassophyes</i> .
	14. Sphaeronectidae	<i>Sphaeronectes</i>
	15. Abylidiae	
	Abylinae	<i>Ceratocymba</i> , <i>Abyla</i> .
	Abylopsinae	<i>Abylopsis</i> , <i>Bassia</i> , <i>Enneagonum</i> .

1. Suborder Cystonectae

Family 2. Rhizophysidae

Totton (1965a) mentioned three species *inquirendae*, namely *Bathyphysa japonica*, *Epibulia chamissonis* and *E. ritteriana*. Totton (1965a) suggested that *B. japonica*, which was described as having stem branches, was most

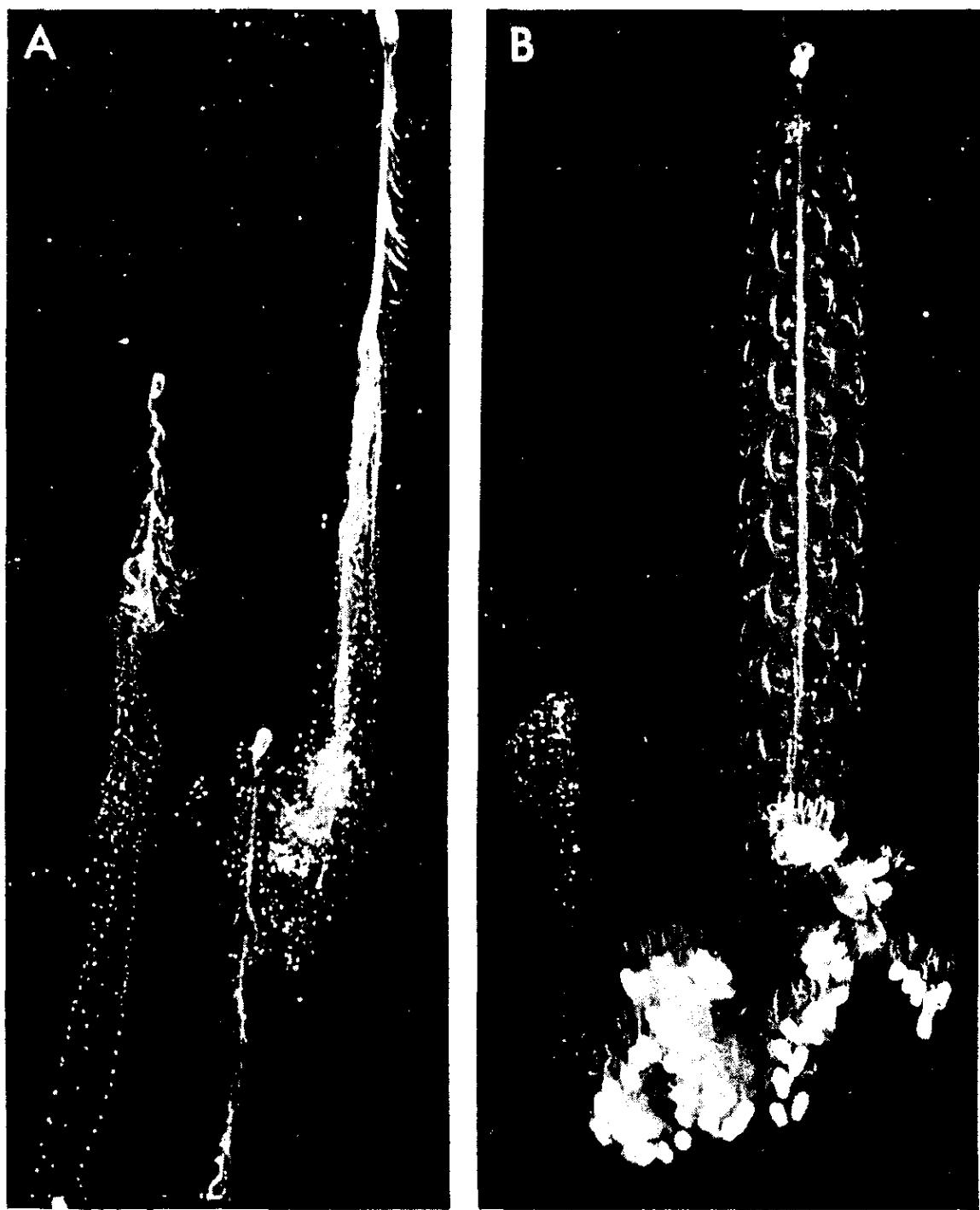
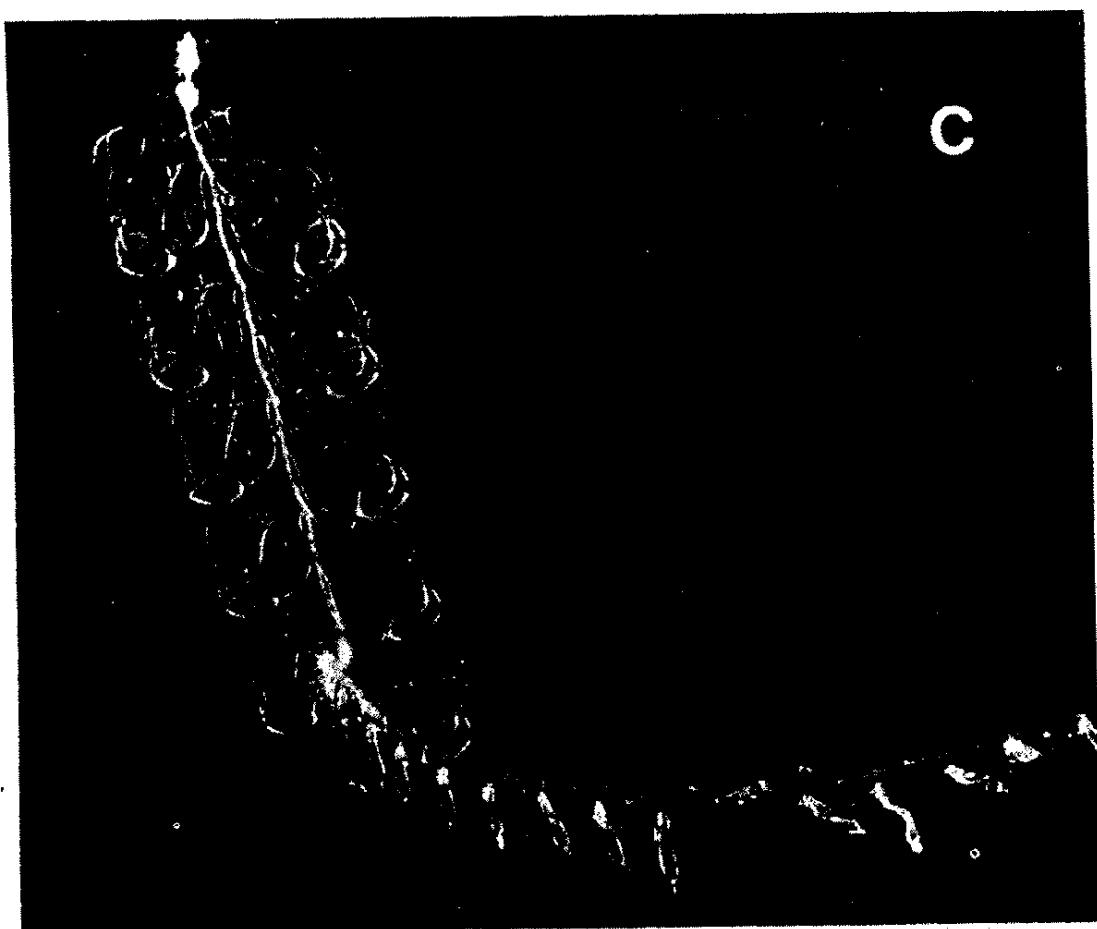


FIG. 6. Photographs of live specimens of Siphonophores. *A*. *Bathyphysa sibogae* (photograph reproduced by kind permission of L. P. Madin). *B*. *Lychnagalma utricularia* (photograph reproduced by kind permission of R. W. Gilmer).

likely a synonym of *B. conifera*. Alvariño (1972a) redescribed *E. ritteriana*, but we believe that her specimen is, most probably, a highly contracted specimen of a *Rhizophysa* species. The colouration of the various components and the presence of hypocystic villi in the pneumatophore are characters which apply equally to a well established species, *R. eysenhardti*, as does the presence of simple, filiform tentilla on the tentacles. Only the ring



C



D

FIG. 6. *cont.*

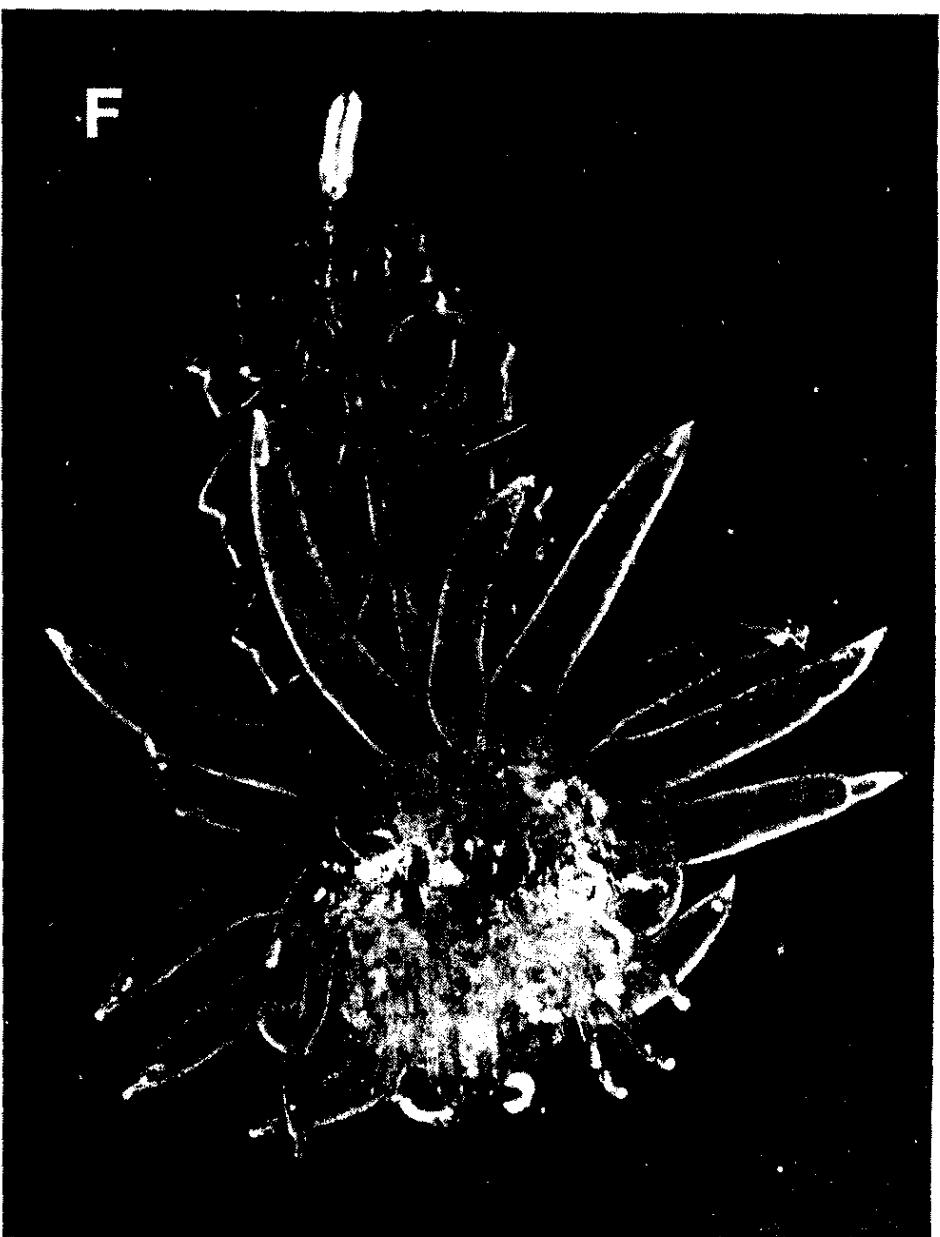
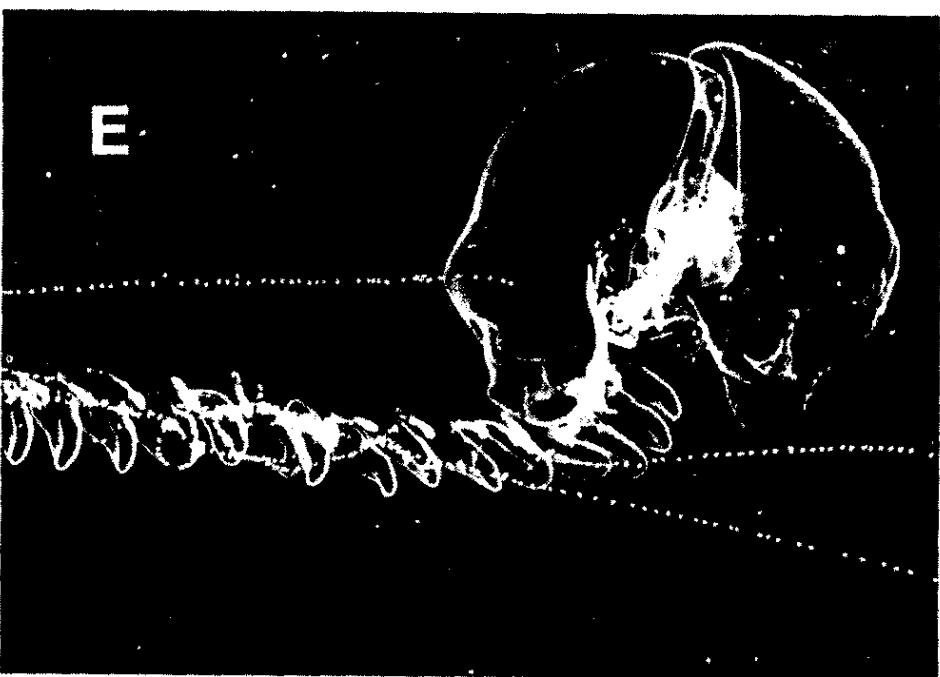


FIG. 6. *cont.*

of palpons surrounding the pneumatophore in Alvariño's specimen appears to be a unique character as palpons *per se* are not present in cystonect siphonophores. However, young gastrozooids, that have not yet developed tentacles at their bases, are found towards the apex of the stem both in *Rhizophysa* and *Bathyphysa* spp., and on contraction of the stem these young gastrozooids frequently appear to form a corona around the pneumatophore (Pugh and Purcell, personal observations). Even Alvariño (1972a) suggests that the crown of palpons might indeed be young gastrozooids.

Our knowledge of one other species, *Bathyphysa sibogae* (Fig. 6A), which was known from only two specimens taken during the Siboga Expedition, has been enhanced by a redescription, with several new records, by Biggs and Harbison (1976).

In his introduction to the genus *Bathyphysa*, Totton (1965a) states that specimens of this genus are distinguished from those of the other genus, *Rhizophysa*, by the presence of ptera on the walls of the gastrozooids and the absence of hypocystic villi at the base of the pneumatophore. The latter fact is, however, not true as hypocystic villi are present in the pneumatophore of both *B. conifera* and *B. sibogae*, although these villi do tend to be smaller than those seen in *Rhizophysa* species.

2. Suborder Physonectae

Family 3. Apolemiidae

Two new species have been described, *Ramosia vitiasi* Stepanjants, 1967, and *Tottonia contorta* Margulis, 1976b. *T. contorta* was redescribed by Margulis (1980a). Several specimens of giant apolemids, at least 10 m long, have been collected by the submersibles "Alvin" (Harbison, personal communication) and Johnson-Sea-Link (Pugh, unpublished data). These specimens are extremely fragile and many parts disintegrate on preservation. It is clear, however, that the whole family Apolemiidae is in need of revision.

Family 4. Agalmidae

Several new species and subspecies have been described since Totton (1965a). These are *Frillagalma vitiasi* Daniel, 1966; *Marrus antarcticus pacifica* Stepanjants, 1967; *Sphaeragalma rotunda* Margulis, 1976b; *Paragalma birsteini* Margulis, 1976b; *Moseria similis*, Margulis, 1977b; *Rudjakovia plicata* Margulis, 1982a; *Stepanjantsia polymorpha* Margulis, 1982b; and *Mica micula* Margulis, 1982b.

g. *Agalma*. Totton (1965a) considered the description of *Agalma haeckeli* as inadequate, and had grave doubts as to the distinctiveness of *A. clausi*. These two species are probably synonymous. There are now many records for specimens of *A. clausi* caught in the Atlantic Ocean by SCUBA divers (e.g. Biggs, 1977a; Harbison *et al.*, 1977; Harbison and Pugh, unpublished data).

g. *Halistemma*. It has yet to be established, but extremely likely, that the large *Halistemma* sp. mentioned by Totton (1936, 1965a) and frequently encountered in the *Discovery* Collections (Pugh, unpublished data) is the same as Totton's (1965a) "Indeterminate species" *H. amphytridis*.

Several recent authors (e.g. Alvariño, 1981; Zhang, 1980) still refer to the existence of the species *Nectalia loligo*. Totton (1954) remarked that this species should be treated with some caution and considered that the specimens were probably young-stages of a long-stemmed physonect, in which context he mentions *Halistemma (Stephanomia) amphytridis*. However, he noted that the specimen of *N. loligo* described by Haeckel (1888) had a very peculiar tentillum. Although this tentillum is not like that found on adult specimens of *Halistemma* species, it does bear a striking resemblance to the larval tentillum of *H. rubrum*, whose development was described by Carré (1971). Thus, as Pugh (1983) concluded, there can be little doubt that *N. loligo* is in fact the *nectalia* post-larval stage of *Halistemma* species.

g. *Cordagalma*. Totton's (1932) description of *C. cordiformis* was based solely on the small, characteristically heart-shaped nectophores. A detailed account of the whole animal has now been given by Carré (1968a), and of its development by Carré (1973).

g. *Marrus*. Andersen (1981) gave a detailed account of some excellent specimens of *M. orthocanna*, previously known only from the nectophores and a single bract. A subspecies *M. antarcticus pacifica* was described by Stepanjants (1967).

g. *Nanomia*. Carré (1969b) has described the development of *N. bijuga*, and Freeman (1983) has made studies on the embryogenesis of *N. cara*.

g. *Erenna*. Margulis (1977a) redescribed *E. richardi* and resurrected the species *E. bedoti*, which Totton (1965a) has synonymized with *E. richardi*.

g. *Lychnagalma*. Pugh and Harbison (1986) reviewed this genus and redescribed *L. utricularia* from specimens collected by the submersible, Johnson-Sea-Link II (Fig. 6B).

g. *Frillagalma*. A new genus, established by Daniel (1966), to include a single species *F. vitiazi*. *F. vitiazi* has been found extensively in the warmer waters of the North Atlantic Ocean (Pugh, unpublished data) and is the so-called Physonect C referred to by Pugh (1974, 1975). The bract which Totton (1965a, Fig. 6A) referred possibly to *Forskalia cuneata* most probably belongs to this species, despite the fact that Totton (1954) stated that nectophores of a *Forskalia* species were found in the same sample.

Family 5. Pyrostephidae

The systematic position of this whole family is uncertain. The family was erected by Moser (1925) to include a single species, *Pyrostephos vanhoeffeni*. Totton (1965a) criticised the necessity of erecting such a family, yet he retained it and added to it an additional monotypic genus, *Bargmannia*

Totton, 1954. However, the diagnosis of the family given by Totton is based solely on the characters of *P. vanhoeffeni* and perhaps only one of these applies to *Bargmannia*. Indeed, the only unique characters that Totton gives in his long list are that the dorsal canal of the nectophore is not straight, and questionably the shape of the bracts. Whether these characters are sufficient to warrant the retention of a separate family is debatable, and Stepanjants (1967) clearly thought that they were not as she placed both species in the family Agalmidae.

g. *Bargmannia*. There are undoubtedly several species in this genus (Pugh, in preparation) (Fig. 6C).

Family 7. Athorybiidae

Biggs (1978) described a new species, *Athorybia lucida*.

Family 8. Rhodaliidae

Pugh (1983) has reviewed the whole family and has established that, uniquely amongst the siphonophores, the members of this family are benthic in habit. Systematically, Pugh (1983) made several changes to Totton's (1965a) classification and he described two new species, namely *Angelopsis euryale* and *Thermopalia taraxaca* (Fig. 6D), the latter being the so-called "dandelions" found around the thermal vents in the Galapagos region. Two species, which Totton (1965a) had synonymized with *Stephalia corona* were resurrected, namely *Sagamalia hinomaru* and *Stephalia (Stephonia) bathyphysa*, and Bigelow's (1911) *Angelopsis dilata* also was moved into the genus *Stephalia*. New records for several species were given.

Family 9. Forskaliidae

Totton (1965a) considered that only two of the six species he mentioned were easily recognizable, namely *Forskalia edwardsi* and *F. leuckarti*. He considered *F. tholoides* Haeckel, 1888 to be a "doubtful species based on a beautiful idealized figure". However, there are now many records for this species, specimens of which have been collected by SCUBA divers (Biggs, 1977a; Harbison *et al.*, 1977; Purcell, 1980, 1983). Also in appearance it looks almost exactly as Haeckel (1888, pl. VIII) figured it (Pugh and Purcell, personal observations). Specimens of two other species of *Forskalia* were collected by the Johnson-Sea-Link II in 1984 (Pugh, personal observation).

The development of *Forskalia edwardsi* was studied by Carré (1967).

3. Suborder Calycophorae

Family 10. Prayidae

Several new species have been described since Totton (1965a) namely, *Maresearsia sphaera* (Stepanjants, 1967), *Rosacea villafrancae* (Carré,

1969a), *Prayola tottoni* (Carré, 1969b), *Amphicaryon intermedia* (Daniel, 1970); *R. flaccida* (Biggs *et al.*, 1978) (Fig. 6E), *Nectocarmen antonioi* (Alvariño, 1983). In addition, three new prayine species have been described by Pugh and Harbison (1987).

g. *Lilyopsis*. Carré (1969c) has shown that the two species mentioned by Totton (1965a), although the latter author doubted that two species existed, are in fact one and the same, and he retained the name *L. rosea*. Carré and Carré (1969) described in detail the development of this species. Totton (1966) also briefly described the eudoxid stage.

One of Totton's (1965a) rare siphonophores, *Stephanophyes superba*, recently has been collected on several occasions by SCUBA divers (e.g. Biggs, 1977a; Harbison *et al.*, 1977; Purcell, 1983; Harbison and Pugh, unpublished data).

Family 11. Hippopodiidae

Alvariño (1967a) has described a new species, *Vogtia kuruae*, and Carré (1968) gave a detailed description of the post larval development of *Hippopodius*.

Family 12. Diphyidae

Numerous new species and sub-species have been described recently, namely: *Sulculeolaria brintoni* (Alvariño, 1968), *S. pacifica* (Stepanjants, 1973) (as *Galette pacifica*); *S. tropica* (Zhang, 1980), *Lensia gnanamuthui* (Daniel and Daniel, 1963), *L. baryl* (Totton, 1965b), *L. cordata* (Totton, 1965b), *L. conoides pacifica* (Stepanjants, 1967), *L. achilles bigelowi* (Stepanjants, 1967), *L. asymmetrica* (Stepanjants, 1970), *L. peresi* (Patriti, 1970), *L. minuta* (Patriti, 1970), *L. roonwali* (Daniel, 1970), *L. panikkari* (Daniel, 1970), *L. nagabhushanami* (Daniel, 1970), *L. tiwarii* (Daniel, 1970), *L. zenkevitchi* (Margulis, 1970), *L. multilobata* (Rengarajan, 1973), *L. canopusi* (Stepanjants, 1977), *L. eltanin* (Alvariño and Wojtan, 1984), *L. eugenioi* (Alvariño and Wojtan, 1984), *L. landrumae* (Alvariño and Wojtan, 1984), *L. campanella elongata* (Margulis, 1984a), *L. campanella petrovskyi* (Alekseev, 1984), *L. lebedevi* (Alekseev, 1984), *L. patritii* (Alekseev, 1984), *Muggiae cantabrica* (Alcazar, 1982). Also several eudoxid stages have been described under separate names, e.g. *Eudoxia vasconiensis* (Patriti, 1965), *E. tenuis* (Patriti, 1965), *E. dohrni* (Gamulin, 1966).

g. *Sulculeolaria*. There have been two recent reviews of the genus *Sulculeolaria*. Stepanjants (1973) considered that the species could be divided amongst two genera depending on whether their nectophores possessed basal teeth on the ostium (g. *Sulculeolaria*) or whether these teeth were absent (g. *Galette*). However, Carré (1979) made a detailed study of the continual replacement of both anterior and posterior nectophores in three Mediterranean species and noted that there were considerable changes in the

structure of successive nectophores, not least in the degree of development or loss of the basal teeth. He concluded that all species belonged to a single genus, *Sulculeolaria*. Further, because of these structural changes in replacement nectophores, he concluded that *S. angusta* was a synonym of *S. turgida* as, probably, was *S. bigelowi*; and *S. brintoni* (Alvariño, 1968) was a probable synonym of *S. quadrivalvis*. *S. tropica* (Zhang, 1980) probably is a synonym of *S. turgida*. Carré (1979) retained six species, namely *S. chuni*, *S. quadrivalvis*, *S. monoica*, *S. biloba*, *S. turgida* and *S. pacifica*.

g. *Lensia*. In addition to the large number of new species which have been described recently (see above), Carré (1967) has described the larval development of *L. conoidea* and Carré (1968b) described the eudoxid stage of *L. campanella*. The eudoxid of *L. multicristata* was described by Gamulin (1966) under the name *Eodoxia dohrni*, and this author also described the eudoxid and posterior nectophore of *L. fowleri*. This eudoxid corresponds with that mentioned by Patriti (1965) under the name *E. vasconiensis*. The eudoxids ascribed to *L. lelouveteau* and *L. reticulata* were described by Alvariño and Wojtan (1984).

Stepanjants (1967) moved *Lensia havock* into the genus *Muggiaeae* on the basis of the absence of a posterior nectophore and the relative depth of the hydroecium. However, as Pugh (1974) discussed, the posterior nectophores of a large number of *Lensia* species have not been described and it is difficult to establish whether these nectophores are not developed, as in the genus *Muggiaeae*, or simply have not been found. Pugh (1974) further points out that there are distinct differences between the anterior nectophore of *L. havock* and that of species of the genus *Muggiaeae*, not least in the number and arrangement of the ridges and the organization of the hydroecium.

Recently, Margulis (1984a) and Alekseev (1984) have described some new subspecies of *Lensia campanella*, that basically differ in the configuration of their somatocysts. These authors also have reduced the status of *L. cossack* to yet another subspecies of *L. campanella*, namely *L. campanella cossack*.

Totton (1965a) described 22 species of *Lensia*, with one variety, and added another two species later that year (Totton, 1965b). Daniel (1974), whilst retaining all of Totton's species, including *L. havock*, added a further five species that she had described, but did not mention the five species (see above) that had been described by other authors prior to that date. Since that time a further six species of *Lensia* have been described bringing the grand total to 40. The whole genus recently has been reviewed by Margulis and Alekseev (1985). They recognized 32 species, including eight subspecies and one variety and considered all the species described to date, except those of Alvariño and Wojtan (1984) (three species) and Rengarajan (1973) (one species). On the other hand Alvariño and Wojtan (1984) apparently were unaware of any further descriptions of *Lensia* species since Totton (1965a,b).

Margulis and Alekseev (1985) followed Stepanjants (1967) in placing *L. havock* in the genus *Muggiaeae*, and considered, as above, that *L. cossack* was a subspecies of *L. campanella*. Further, *L. roonwali* was considered a junior synonym of *L. campanella campanella*, and *L. peresi* a junior synonym of *L. hotspur*. The genus still remains a cumbersome one, encompassing a large number of species whose characteristics, basically, are those not found in other diphyid genera.

g. *Muggiaeae*. Gamulin and Rottini (1966) considered that the gonophore described under the name *Ersea elongata* (Will, 1844) belonged to *M. kochi*. Freeman (1983) studied the embryogenesis of *M. atlantica* and Carré (1972) studied the development of the cnidocyst on the tentilla of *M. kochi*.

Family 13. Clausophyidae

Patriti (1969) described a new species *Clausophyes massiliiana*, which has been found occasionally in the North Atlantic Ocean (Pugh, 1975; Kirkpatrick and Pugh, 1984; and unpublished data). Two other new species, *Heteropyramis alcala* and *Thalassophyes ferrarii*, have been described by Alvariño and Frankwick (1983).

Family 14. Sphaeronectidae

Four new species have been described, namely *Sphaeronectes gamulini* (Carré, 1966), *S. bougisi* (Carré, 1968c), *S. fragilis* (Carré, 1968d) and *Monophyes japonica* (Stepanjants, 1967). The development of two other species, *S. gracilis* and *S. irregularis* has been described by Carré (1969a), and the status of the g. *Sphaeronectes* has been reviewed by Carré (1968e).

Family 15. Abylidæ

Two new species, *Ceratocymba indica* (Daniel, 1970) and *Enneagonum searsae* (Alvariño, 1968) have been described since Totton (1965a). The nectophores of many species are very variable in form and many aberrant forms exist (cf Sears, 1953) such that it is likely that the whole family is in need of further review. The larval development of *Abylopsis tetragona* was described by Carré (1967).

B. Evolution

The evolution of the whole phylum Cnidaria has aroused much discussion and controversy in the past and, indeed, the debate still continues. The numerous gaps in the palaeontological record hamper any attempt to establish a phylogeny and in the case of siphonophores it is debatable whether any fossil record has been found (Scrutton, 1979). Recourse has

been made to careful investigations of the morphology and life histories of the recent groups in order to infer the structure of their ancestors. However, as Werner (1973) points out, such information can be interpreted in different ways and any evidence can be taken to support totally different theories. Scrutton (1979) discussed such cases when reviewing two of the opposing theories on the origin of the Cnidaria, which are based on whether the earliest adult form was either a radially-symmetrical, planktonic medusoid, or a bilaterally-symmetrical, benthonic polyp.

The phylogeny of the class Hydrozoa has been recently revised by Petersen (1979), who introduced a new taxonomic division of the Cnidaria into two subphyla, Anthozoa and Medusozoa. He considered that the ancestral cnidarian was a solitary, sessile, tetramerous polyp, but later, in the Medusozoa, a medusa had become the normal, sexual adult and the polyp could be regarded as a larval stage. Amongst the Hydrozoa, he, like many other authors before (e.g. Totton, 1954), considered the trachyline forms to be the most primitive, although the reasoning behind such a conclusion has not always been the same. Freeman (1983) recently noted the similarities between the embryogenesis of trachyline hydrozoans, siphonophores and ctenophores. He suggested that this developmental parallelism could be explained on the basis of common descent, whilst noting that all three groups underwent direct development, which Petersen (1979), for instance, considered to be an adaptation to the oceanic, holoplanktonic way of life.

As with the general evolution of the phylum Cnidaria, the phylogeny of the siphonophores has produced several diametrically opposed theories in the past and the earlier, nineteenth century controversies have been reviewed by Winsor (1971/1972). Much of the more recent discussion has been summarized by Garstang (1946), Leloup (1954) and Totton (1954, 1965a), and will not be considered in detail here. These three authors have reached a measure of agreement amongst themselves on this subject, but this contrasts with the views expressed above as they seek to draw comparisons between the siphonophores and certain athecate hydroids. They considered that the original larva of the siphonophore ancestor was an actinula and not a planula. The planuloid appearance of the present-day larva is explained by the occurrence of precocious budding before the typical actinuloid characters were developed. It should be noted, as Totton (1960) points out, that this supposed ancestral, tentaculate, actinuloid larva should not be confused with the actinuloid organism that has been suggested as the ancestral cnidarian form.

Totton (1954) noted that many groups of hydrozoans possess an actinuloid larval stage, e.g. Narcomedusae, Trachymedusae and various capitate Athecata (Anthomedusae), which led him to suggest that all these groups had a common ancestor. He concluded that siphonophores, and several

other hydrozoan groups, arose as part of a comparatively recent radiation after the neotenic actinula had evolved from the larva of some protohydroid. However, actinuloid larvae may have been developed as a means of prolonging the pelagic way of life, and could have been followed by direct development into a medusa, as in some trachyline hydrozoans. Thus, as Phillips (1973) considered, evolution towards an oceanic, holoplanktonic life from neritic ancestors may have occurred on several independent occasions, such that similarities in developmental processes represent convergent evolution and do not necessarily demonstrate a common ancestry.

Garstang (1946) and Leloup (1954), in their reviews of the phylogeny of the siphonophores, concluded that the passage from the ancestral, benthic, sessile way of life to the free-swimming planktonic one could only have occurred during the larval period. Thus, by tachygenesis, they thought the siphonophore stock could be derived from the ancestral polypoid form, the actinula. Indeed there are close similarities between the actinula and the adult hydranth in recent tubulariid athecates. Totton (1954), however, suggested that the adult ancestor of the siphonophores, and indeed the Metazoa, had been planktonic at all times and that attachment to a substrate did not take place until much later in phylogeny. He based his arguments on the direct developmental processes in trachyline hydrozoans but, as discussed above, such evidence has been used to argue exactly the opposite point of view. Garstang (1946), in contrast, considered that the original function of the newly evolved actinula larva was as an organ of dispersion, swimming by means of its tentacles, before fixation and metamorphosis into the adult benthic form occurred. Further phylogenetic stages resulted in the postponement of fixation and precocious larval budding occurred on the free-swimming organism. Finally, in the case of siphonophores, fixation was abandoned, metamorphosis abbreviated and a nondescript oozoid nurse carrier of secondary larvae was produced on which the adult medusoids developed. Totton (1960) called this oozoid, the asexual carrier of the gonozooid offspring, a paedophore. He considered that further adaptive radiation of this paedophore would lead not only to the siphonophores, but to the velellids and certain free-swimming margelopsine athecates. In other cases, where fixation was not entirely suppressed, the loosely attached myriotheline and corymorphine athecates would result.

1. Phylogeny of the siphonophores

The phylogenetic relations of the present day siphonophores are difficult to establish. Totton (1965a) points out that many aspects of the organization of the species within the various suborders appear to represent reductions from a predicted ancestral form such that is difficult to decide whether a particular

group is primitive or derivative. Siphonophores are highly polymorphic animals, a fact which Stepanjants (1967) considered to be an inevitable consequence of the adoption of a pelagic life-style. Thus the individuality of the zooids became suppressed and each came to fulfil a specific function. She considered that the evolutionary pathways within the Siphonophora followed lines of oligomerization, whereby there was a reduction both in the number of types and in the actual number of zooids. Thus the most simply organized siphonophore is considered to be amongst the most advanced. Other authors, although agreeing with the basic principle of oligomerization, have come to different conclusions as to the phylogeny of the three siphonophore sub-orders.

2. Suborder Cystonectae

Many authors regard this suborder, whose constituent species possess a pneumatophore, but no nectosome, as having an early phylogenetic origin and to represent an early offshoot from the main evolutionary pathway leading to the physonects and calycophorans. The simple apparent organization of these animals might testify to this, but Stepanjants (1967) took this to represent an extreme case of oligomerization and thus considered this suborder to be relatively advanced. She derived all three suborders from an "Archiphysophore", which possessed large numbers of nectophores, bracts, palpons, etc., and even might have had several pneumatophores. This latter seems extremely unlikely, but derives from Stepanjant's misinterpretation of the pneumatophore as a zooid, of medusoid origin. In contrast, Totton (1954) suggested that the physonects did not pass through a "cystonect" stage, since the cystonects do not possess a nectosome, bracts, or asexual stem palpons, with palpacles. In addition the tentacles of cystonects are, in general, much simpler and possess fewer types of nematocysts (see p. 215). It would appear, therefore, that the cystonects and physonects diverged from each other at a relatively early stage and it is difficult to imagine the former as having arisen, by extreme oligomerization, from the latter.

The holopelagic rhizophysids (four species) usually are considered to be closer to the ancestral cystonect stock as they possess a relatively small pneumatophore and a long siphosome, on which the simple cormidial groups, each with a single gastrozooid and gonodendron, are arranged linearly. The extreme enlargement of the pneumatophore in the physaliid, *Physalia physalis*, would appear to be a secondary feature resulting from the adoption of the pleustonic way of life. Totton (1960) considered that *Physalia* might have arisen as a result of neoteny, and indeed in his other

publications he drew attention to the probable neotenic origin of several siphonophore species.

3. Suborder Physonectae

Most authors would agree that the Physonectae are more primitive than and gave rise to the Calycophorae. Garstang (1946), for instance, drew attention to the atrophy of the anterior part of the calycophoran larva, which could be equated to the elimination of the ancestral pneumatophore. However, many of Garstang's arguments, e.g. with relation to the evolution of the calycophoran larval nectophores and the positioning of the physonect larval bract, are not consistent with more recent information, and his whole recapitulationist approach to the evolution of siphonophores needs careful reconsideration. Stepanjants (1967) drew attention to other characters of the physonects that could be considered ancestral, e.g. the presence, in some species, of: (a) unmasked metagenesis (true alteration of generations); (b) a great diversity of zooids and the least oligomerization of parts; (c) irregularities in the arrangement of siphosomal cormidia; and (d) insufficient colonial integration to allow for a secondary alteration of colonial generations, i.e. no eudoxid stages were produced. However, Totton (1954) noted that not every feature of a physonect could be considered as primitive. For instance, he considered the reduced gonophores, borne on specialized gonostyles (cf cystonects) as more advanced than the gonophores of calycophoran species, which arise directly from the base of the gastrozooids.

The phylogenetic relations between the various physonect families have also been a source of much discussion and disagreement in the past. The schematic phylogenetic arrangements for the physonect families that have been produced by three recent authors are shown in Fig. 7. In order to consider these schematics it is convenient, first of all, to split the various families into two groups: (a) the three or four families whose species are short-stemmed (brachystele); and (b) the long-stemmed (macrostele) species belonging to the other three or four families.

4. Brachystele families

These families are the Physophoridae, Athorybiidae, Rhodaliidae and Nectaliidae. The Nectaliidae (in the schematic of Leloup, 1954) can be eliminated immediately as its single representative, *Nectalia loligo*, is the postlarval stage of a long-stemmed agalmid, *Halistemma*, as noted above. Although recent authors consider most, or all, of the remaining families to be derived from long-stemmed forms, this has not always been the case. For instance, Garstang (1946) argued, on the basis of ontogeny recapitulating

phylogeny, that the macrostele forms had been derived from the brachystele ones. His conclusion appears to be based on the striking resemblance of certain short-stemmed species, particularly of the family Athorybiidae and Physophoridae, to stages in the development of long-stemmed physonects of the family Agalmidae. Thus *Athorybia rosacea*, which does not develop nectophores, resembles the early larval (*athorybia*) stage of *Agalma* spp. (see Totton, 1956); *Melophysa melo*, with a rudimentary nectosome, is reminiscent of the later postlarval (*melophysa*) stage of the same agalmids; and *Physophora hydrostatica* (Fig. 6F), with a nectosome but laterally expanded siphosome, can be likened to the postlarval, *nectalia*-stage of *Halistemma* spp.

Totton (1954) appears, on the basis of the systematic order he presented, to have accepted Garstang's ideas, although he did suggest that brachystele forms could have arisen by neoteny; a point of view that would appear to be diametrically opposed to and irreconcilable with that of Garstang (1946). Later, Totton (1960, 1965a) rejected Garstang's ideas and proposed his paedophore theory to account for the evolution of certain siphonophore species and, as a result, rearranged his earlier systematic order so that the brachystele forms were placed after their projected macrostele, agalmid ancestors (Fig. 7). Stepanjants (1967) also believed that the Athorybiidae and Physophoridae arose by neoteny, but considered that they had branched off from the evolutionary pathway leading to the agalmids, rather than having been derived from the latter. Leloup (1954) considered the brachystele forms did not arise by neoteny but by an initial shortening of the siphosome and an enlargement of the pneumatophore. Thus the Physophoridae arose first and then, by secondary, horizontal expansion, these forms gave rise to: (a) the athorybiids, with reduced or non-existent nectosome; and (b) the rhodaliids, with their enormous pneumatophore and aurophore (Fig. 7).

Pugh (1983) pointed out that much of the discussion on the phylogeny of siphonophores had been based on the assumption that they were all holoplanktonic animals, with the exception of *Physalia physalis*. However, he established beyond doubt that the species of the family Rhodaliidae were benthic, attaching themselves to the substratum by means of their tentacles, whilst the main body floated above the bottom like a tethered air balloon. The origin of such a way of life could only be a secondary adaptation and, thus, the rhodaliid ancestors must have been pelagic organisms. The growth pattern of certain rhodaliid species indicated that their ancestors were long-stemmed forms, and the variations in this pattern suggested that the group as a whole might have had a di- or even polyphyletic origin. Similarities between the organization of the siphosome in the rhodaliids and in *Physophora hydrostatica* also were noted. Pugh (1983) conjectured that the

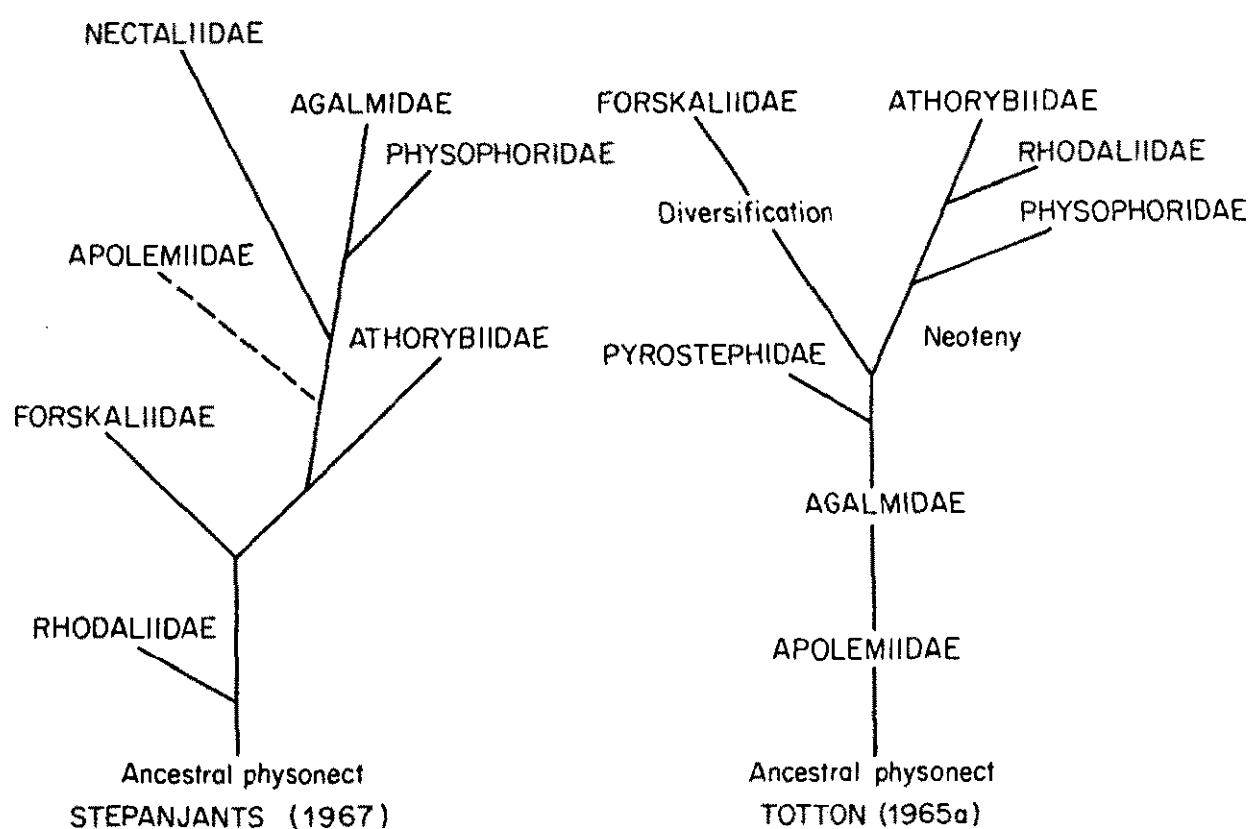
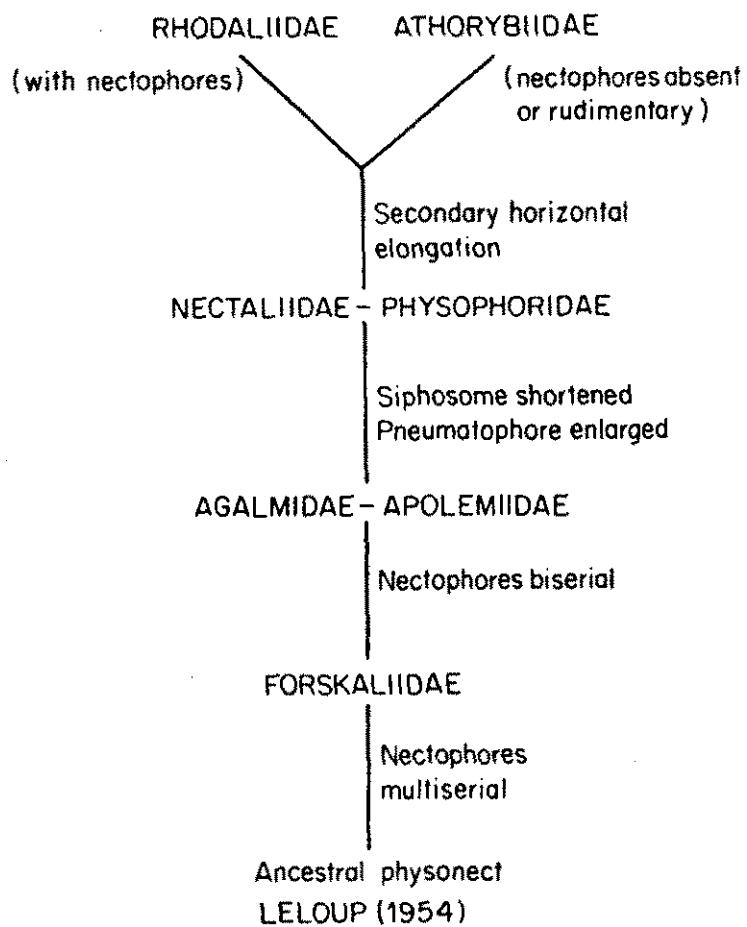


FIG 7. Schematics for the possible phylogeny of the families within the suborder Physonecta. Based on Leloup (1954), Stepanjants (1967) and Totton (1965a). The schematic attributed to Totton is a reasoned re-construction from his discussion.

ancestors of the latter species might have passed through a brief benthic (*rhodalia*) stage, before returning to a pelagic way of life. Thus the rhodaliids, and possibly physophorids, could not be considered as neotenic forms.

5. Macrostele families

These families include the Apolemiidae, Agalmidae, Pyrostephidae and Forskaliidae. The doubtful systematic position of the Pyrostephidae has been discussed earlier, and it is probable that its species should be included with the Agalmidae. However, the systematic relations of the agalmid species are uncertain, and it is probable that the whole group is polyphyletic. Totton (1965a) considered the Apolemiidae as the most primitive physonect family on the basis that bunches of larval tentacles, comparable with the aboral tentacles of the projected actinuloid ancestor, were developed between the nectophores on the nectosome. The simplicity of the gastrozooidal tentacles, and the release of free cormidial groups also were considered to be primitive characters. However, the latter could be considered as secondary, bearing no relation to the metagenic characteristics of an ancestral form. In this context Mackie (1985) has drawn attention to the frequent observations of stem fragments, probably representing several cormidia, of the agalmid physonect *Cordagalma cordiformis* floating free in the water column (see page 191). However, most physonect species do not release free cormidial groups.

True metagenesis, i.e. the release of the sexual medusoid (gonophore) from the siphosomal stem, is known to occur in several species of the family Agalmidae (e.g. Metschnikoff, 1870; Carré, 1969b) and so this family also might be considered as primitive. Indeed, Totton (1965a) placed it immediately after the Apolemiidae in his systematic order. However, Leloup (1954) and Stepanjants (1967) considered both families to be more advanced. These authors placed the Forskaliidae at or towards the base of their genealogical trees, while Totton (1965a) placed it at the top (Fig. 7). The reasoning behind both points of view is the same; namely the possession, by the forskaliids, of a multiserial arrangement of nectophores in the nectosome and of complex, pedunculate cormidia on the siphosome. Whereas Leloup and Stepanjants believed that evolution had followed lines of oligomerization, such that the complex organization of the forskaliids was primitive, Totton suggested that diversification had taken place, although he did not discuss this point in any detail. However, Totton (1954) believed that there was a fundamental difference in the development of forskaliids and agalmids, in that in the former the budding zones of both the nectosome and the siphosome appeared on the same, ventral, side of the larva, while in the

latter they were developed on either side of the pneumatophore. The exact significance of this difference is not clear and it remains to be verified. Thus, at the moment, it does not seem possible to resolve the systematic position of these physonect families.

6. Suborder Calycophorae

The phylogeny of the calycophoran families of siphonophores has created just as much discussion, and alternative hypotheses, as with the physonects. However, it is generally agreed that the calycophores arose from a physonect stock after the loss of the pneumatophore, such that the morphological summit of the larva then became occupied by a larval nectophore. There are, however, many fundamental differences between the two suborders, not least of which is the arrangement of the nectosomal and siphosomal budding zones. Nevertheless, Totton (1954) was able to postulate a means by which the budding pattern in the calycophoran family, Hippopodiidae, could be derived from the physonect one.

It is convenient to split the families of the suborder Calycophorae into the prayomorph and diphyomorph groupings of Leloup (1954). The phylogenetic schematics of Leloup (1954) and Stepanjants (1967) are shown in Fig. 8, while Totton's (1965a) thoughts are discussed in the text.

7. Prayomorph Calycophores

These calycophores can be taken to comprise the families Prayidae and Hippopodiidae, although Leloup (1954) and Stepanjants (1967) recognize other families (e.g. Amphicaryonidae, Desmophyidae, Nectopyramidae and Stephanophyidae) (Fig. 8), all of which Totton (1965a) placed in the Prayidae. These animals are characterized by having an opposed pair, or pairs, of identical, usually rounded, nectophores. The family Sphaeronectidae, whose species possess only a single larval nectophore, also can be included here.

Almost all authors agree, basically, that evolution within the Calycophorae has resulted in a reduction in the number and kind of stem appendages, by the process of oligomerization, and has led to a release of the simplified cormidial groups as free-swimming eudoxids (secondary metagenesis). Both Leloup (1954) and Stepanjants (1967) consider the family Hippopodiidae to be the most primitive (Fig. 8) as its representatives possess the largest number of nectophores, while eudoxids are not produced. However, as Totton (1965a) pointed out, their cormidia are very simple in structure and lack bracts, both of which could be considered as advanced characters. He concluded that the Prayidae were more primitive whilst

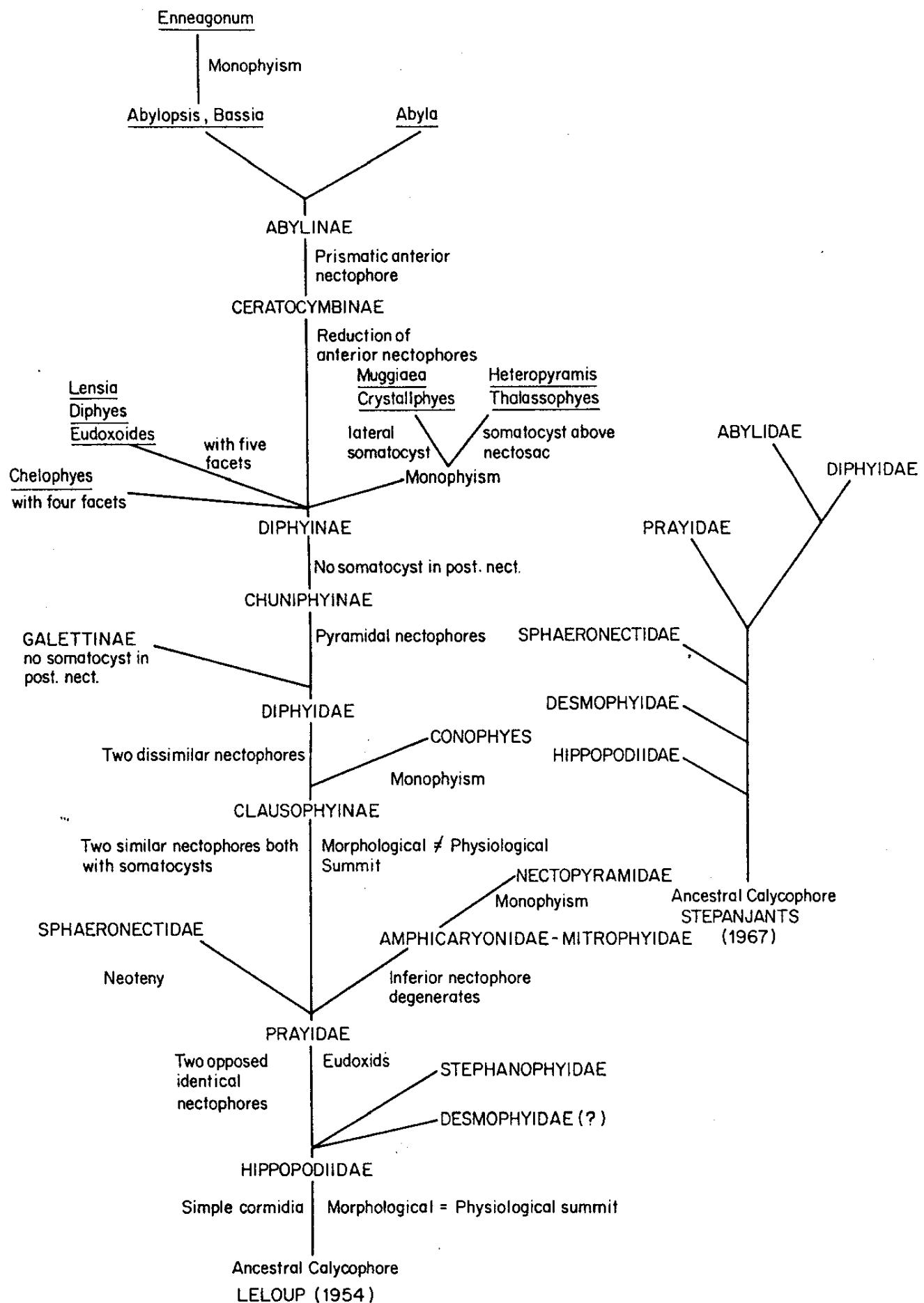


FIG. 8. Schematics for the possible phylogeny of the families within the suborder Calyco-phorae, according to Leloup (1954) and Stepanjants (1967).

noting the close similarity between the larval nectophores of both families. Within the family Prayidae there appear to have been several evolutionary pathways leading towards the present-day species, which are grouped into three subfamilies (Totton, 1965a).

Totton (1954) had used the recapitulationist approach to suggest that Sphaeronectidae were the ancestral calycophoran type, because of the simple larval nectophore. However, Totton (1965a) relocated this family between the diphyomorph families, Clausophyidae and Abylidiae, as he considered that they were descended, by the process of neoteny, from the precursors of the abyliids. Nevertheless, there are similarities between the larval nectophores of the sphaeronectids and those of prayids and hippopodiids and so it is also possible, as Leloup (1954) and Stepanjants (1967) suggested, that the sphaeronectids represent a neotenic offshoot from a prayid stock (Fig. 8).

8. Diphyomorph families

The diphyomorphs are distinguished from the prayomorphs by the presence of two streamlined, heteromorphic, nectophores superimposed one above the other. The families included are the Diphyidae, Clausophyidae and Abylidiae. Both Leloup (1954) and Stepanjants (1967) include the Clausophyidae as one or two subfamilies of the Diphyidae. According to Stepanjants, the diphyomorph families are a totally separate branch of the genealogical tree from that leading to the Prayidae, but Leloup (1954) derived them directly from the prayids (Fig. 8).

It is difficult to establish the exact relations of the three main diphyomorph families. Most authors have suggested that the presence of a somatocyst in the posterior nectophore of clausophyid species, whereas it is absent from such nectophores in the other two families, is a primitive character since such a structure is present in all prayomorph nectophores. Totton (1954, 1965a) considered that the evolutionary pathways of the diphyomorphs had diverged early, with one branch leading to the Diphyidae, and the other by way of the Clausophyidae to the Abylidiae. Leloup (1954), however, placed the clausophyids (Clausophyinae and Chuniophyinae, see Fig. 8) at the base of his diphyomorph genealogy, with the Abylidiae considered as the most advanced forms (Fig. 8).

It is of interest to note, that Totton (1954, 1965a) also conjectured that the clausophyid posterior nectophore, with its somatocyst, might be the first definitive nectophore, and that the anterior nectophore was the larval one retained, through neoteny, in the adult. Although not considered by Totton, such an interpretation would appear to suggest, on the basis of the paedophore theory, that the clausophyids represent an evolutionary advance

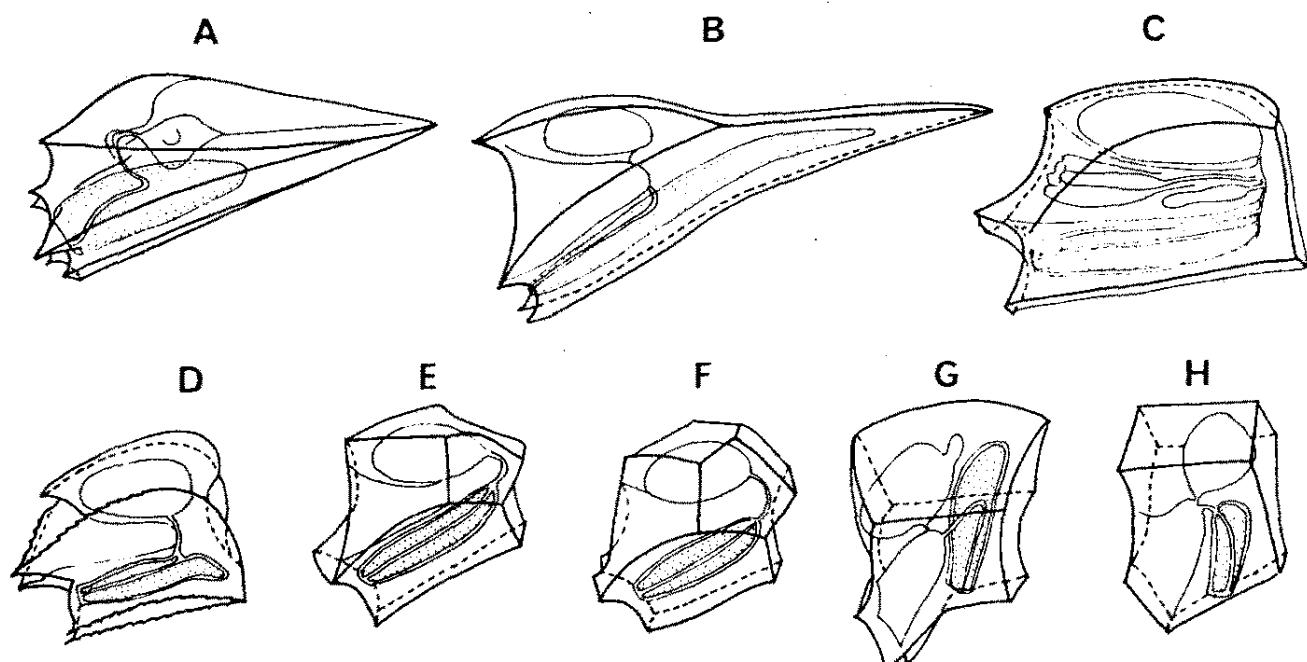


FIG. 9. Phylogeny of the Clausophyidae and Abylididae; anterior nectophores arranged in sequence of possible evolutionary trend. A, *Chuniphyes multidentata*; B, *Ceratocymba sagittata*; C, *C. leuckarti*; D, *C. dentata*; E, *Abyla trigona*; F, *A. haeckeli*; G, *Abylopsis tetragona*; H, *Bassia bassensis*. Redrawn from Totton (1954).

over the Diphyidae in which, as in most prayomorph species, the larval nectophore is caducous. Totton's supposition, without any developmental studies to prove it, was based on his conclusion that there was a close evolutionary link between the structure of the anterior nectophore in the Clausophyidae and Abylididae, and he drew up a tentative phylogenetic sequence based on present-day species (Fig. 9). Totton (1954) noted that it was difficult to decide in which direction evolution had proceeded. However, he conjectured that if the anterior nectophore of the abyloid species was the larval one retained in the adult then not only must this be the case in the clausophyids, but also (ontogeny recapitulating phylogeny) that the *Bassia*-like abyloid form (Fig. 9) would represent an initial rather than a later evolutionary stage. Nonetheless, Totton (1954, 1965a) chose to consider the clausophyids as protoabyloids. Certainly, it is easier to imagine an evolutionary pathway resulting in the loss of the somatocyst from the posterior nectophore, as in abyloids, rather than one requiring this structure to be developed anew. However, it is difficult to clarify the position of the *Diphyes* spp. (Diphyidae), which Totton conjectured might also be protoabyloids and, thereby, have retained their larval nectophores as the anterior ones.

Carré (1967) clearly established that the first nectophore to be developed by the abyloid, *Abylopsis tetragona*, was retained in the adult as the anterior nectophore. This would suggest that the family has arisen through neoteny, as Totton suggested. However, prior to the appearance of this nectophore, the larvae of *A. tetragona* develop a larval bract, which subsequently is dropped from the stem. This is extremely unusual amongst the calycophores,

for normally only a larval nectophore is budded off, but it does bear a striking resemblance to the development of some physonect siphonophores (see p. 105). Thus is the abyloid anterior nectophore a larval or definitive one? This raises many interesting questions, which unfortunately cannot be considered in detail here, but exemplifies the necessity for an expert in phylogeny to carry out a new review of the siphonophores.

Within the family Diphyidae, there is general agreement that the subfamily Sulculeolariinae (Galettinae) is the closest to the ancestral stock, particularly as the ability to replace both the anterior and posterior nectophores (see Carré, 1979) is considered to be a primitive character. However, there is evidence to suggest that other diphyids have this ability (see p. 107). Leloup's (1954) positioning of this subfamily as an offshoot between his Clausophyinae and Chuniphyinae (both with a somatocyst in their posterior nectophores) is difficult to comprehend, despite the simple, ridgeless appearance of the nectophores. The evolutionary pathway towards the absence of a somatocyst in the second definitive nectophore is not clear.

One feature in the evolution of certain species, in all the calycophoran families except the hippopodiids, is a trend towards monophyism (retention of a single nectophore). Stepanjants (1967) considered that true monophyism occurred when the larval nectophore was *not* developed, but was replaced by the first definitive nectophore, and when no further nectophores were budded off. This could be the case in the abyloid, *Enneagonum*, with the remaining abyloids representing an intermediate stage, as discussed above. However, Stepanjants also considered monophyism to have arisen, through neoteny, at other developmental stages, such as with the retention of the larval nectophore, and failure to develop any further nectophores, in the Sphaeronectidae. In the Diphyidae, monophyism manifests itself as a failure to develop a posterior nectophore, i.e. the second definitive one, as in *Eudoxoides spiralis* and *Muggiaeae* spp. An intermediate state is found in *Dimophyes arctica*, whose posterior nectophore is of a reduced size. Thus monophyism can arise either by neoteny or by tachygenesis, and since it has occurred on several, completely independent occasions, any grouping of such species together, as several early researchers had done, is artificial. There is also no reason to consider monophyism as ancestral (Totton, 1932).

IV. Distribution and Migration

A. Vertical Distribution

The classical view of the vertical distribution of siphonophores (e.g. Vinogradov, 1970) is that most species are found over considerable depth ranges, usually from the surface to thousands of metres. However, much of the earlier information is based on samples from nonclosing net systems and

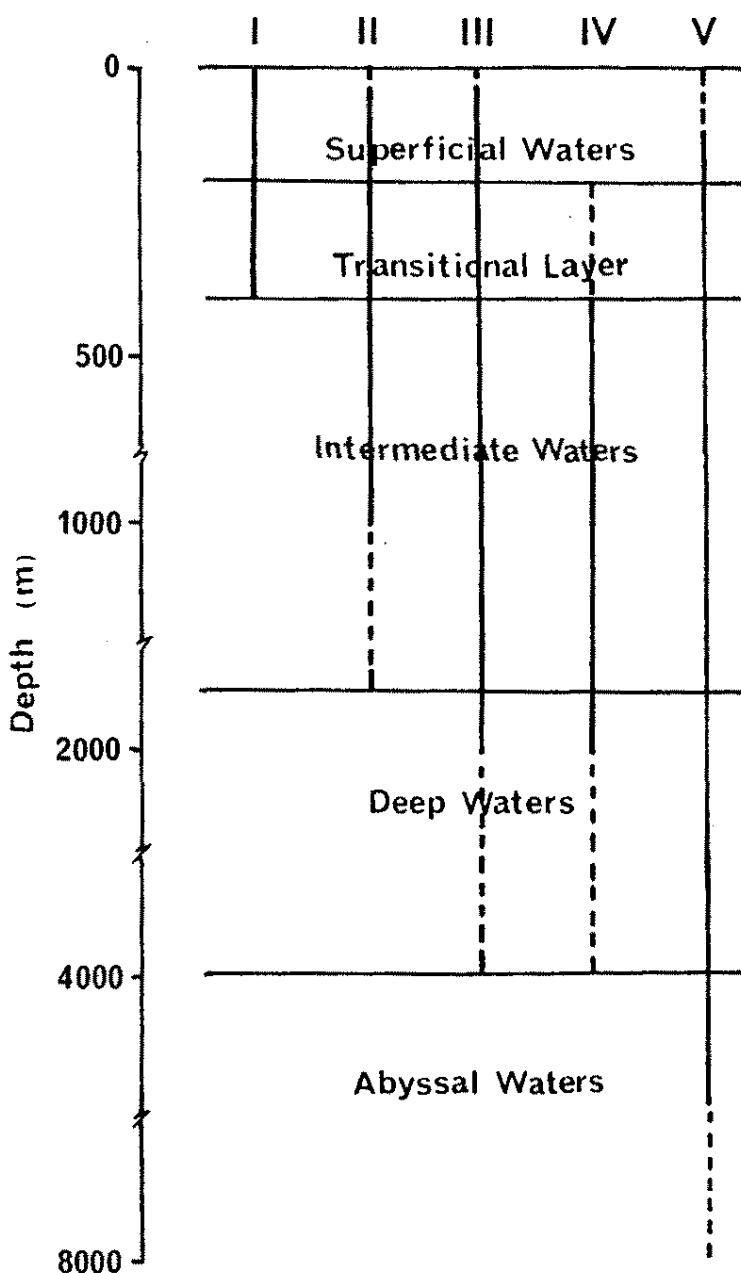


FIG. 10. Schematic for the vertical distribution of various groups (I-V) of siphonophores. Redrawn from Margulis (1980b). The number of species attributed to each group were I-6; II-20; III-27; IV-12; V-2.

there are inherent difficulties in interpreting such data (Bigelow and Sears, 1937). In addition, contamination can be a considerable problem and can cause the extended distributional "tails" that many authors have noted for normally epipelagic animals. The concept of the total depth range for an individual species also may be misleading as it is nonquantitative and ignores the actual numerical vertical distribution of the animals. However, Margulis (1980b, 1984b), while acknowledging this problem, chose that concept to divide the vertical distribution patterns of 67 siphonophore species into five groups, and to relate these to the known hydrographical structure of the water column (Fig. 10). Only six species (Group I) were considered to be totally epipelagic in their depth distribution, but it is

probable that many of the species in three of the other groups (49 spp. *in toto*), whose distributions extend up into the 0–200 m depth range, might also be mainly epipelagic, with long distributional tails. Thus, Michel and Foyo (1976) found that although the total depth range for seven epipelagic species could be very extensive, e.g. 0–2500 m for *Chelophyses appendiculata*, about 97% of the total catch of these animals came from the top 100 m of the water column.

Pugh (1974) reviewed many of the earlier attempts to study the quantitative vertical distribution of siphonophores, including those of Moore (1949, 1953), who studied the diel (see p. 156) and seasonal (see p. 165) variations in depth distribution of epipelagic species (0–300 m) in the Bermuda and Florida Current regions. Although Moore used open nets he established that, in contrast to Margulis (1980b), there was a large number of epipelagic siphonophore species. Pugh (1974), who used an opening/closing net system to make quantitative studies on the siphonophores in the top 1000 m near to the Canary Islands, concluded that about half of the 50 calycophoran species present were epipelagic (0–200 m). These epipelagic species also were the most abundant, forming over 80% of the total numbers caught, with one species, *Chelophyses appendiculata*, making up about 60%. There was also an indication of a separation in the depth ranges of certain congeneric or closely related species, particularly amongst the mesopelagic forms, e.g. the species of the genus *Nectopyramis* and those of the families Clausophyidae and Hippopodiidae (Fig. 11). Twelve of the 13 *Lensia* species also showed some depth stratification and had fairly narrow population spreads. Five species occurred within the top 150 m, while in the 150–400 m depth range only the upper population of *L. meteori* was found in addition to the eurybathic *L. multicristata*. Below 400 m the depth stratification of the species was even clearer, i.e. 400–410 m *L. grimaldi* (90% of total population); 410–450 m *L. exeter* (67%); 500–625 m *L. achilles* (62%); 580–660 m *L. havock* (100%) plus the deeper population of *L. meteori* (62%); 800–960 m *L. hostile* (100%); and 900–950 m *L. lelouveteau* (62%). Musayeva (1976) also noted that many congeneric, or closely related, epipelagic siphonophore species had mutually exclusive depth distribution ranges.

More recent studies on the vertical distribution of siphonophores, in various regions of the World's oceans, have been made by Patriti (1965), Alvariño (1967b), Stepanjants (1970, 1975), and Casanova (1980). However, in many cases the information is nonquantitative. Quantitative studies in the eastern Indian Ocean were made by Musayeva (1976), but only to a depth of 500 m. She noted that the great majority of the 60 siphonophore species identified had population maxima in the top 100 m of the water column, with some undergoing a diel vertical migration within this zone (see p. 162). In accord with Moore's (1949) conclusions, Musayeva found that the lower

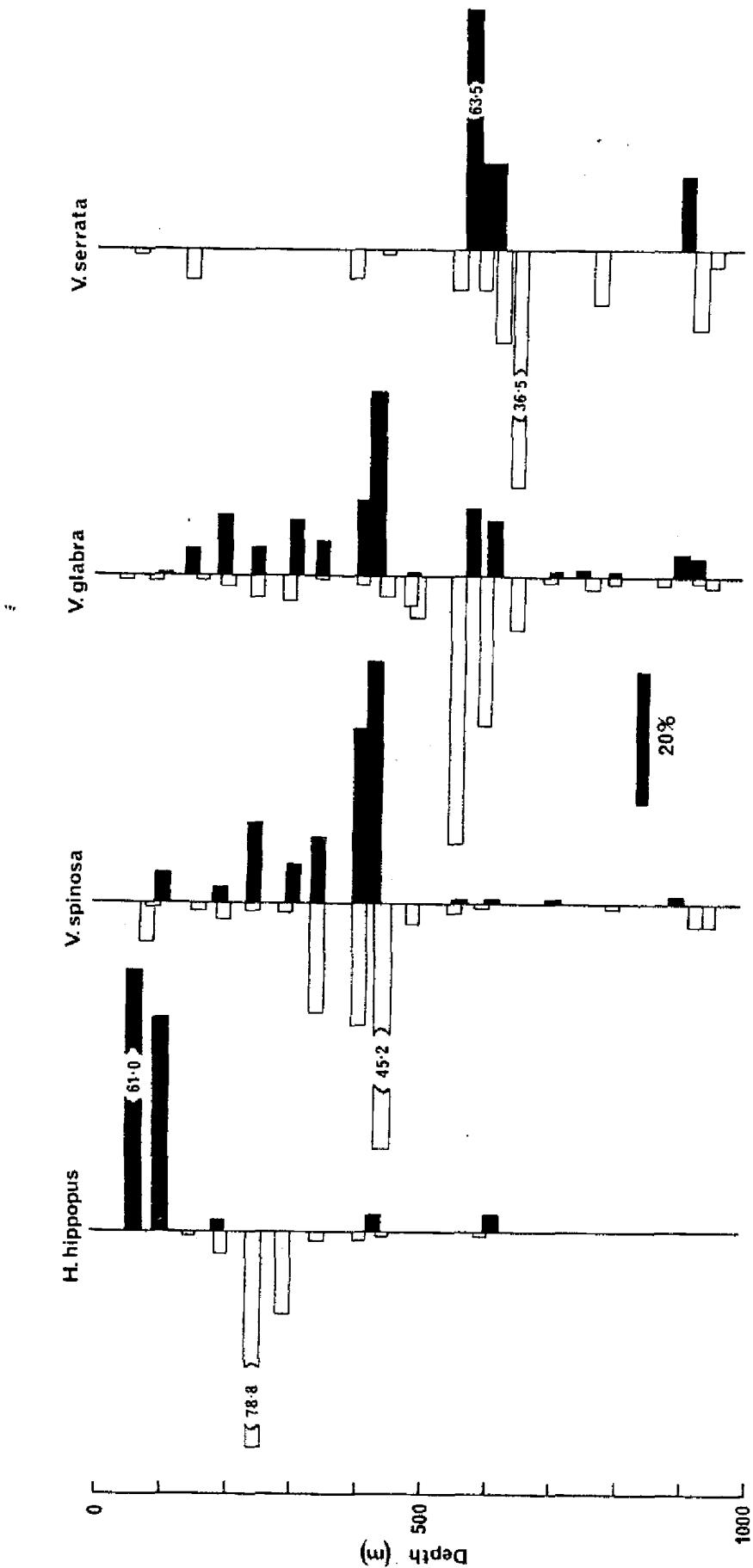


FIG. 11. The depth distribution of species of the family Hippopodiidae in the vicinity of the Canary Islands. Percentage of total catch, by day and night (black), found in each haul. Redrawn from Pugh (1974). The data are for the IKMT hauls only, except for *Vogtia serrata* where both the IKMT and NI 13 data have been combined.

TABLE 2. DEPTH RANGE (M) OF POPULATION NUCLEI (25-75% LEVELS) FOR VARIOUS SIPHONOPHORE SPECIES IN DIFFERENT REGIONS OF THE EASTERN INDIAN OCEAN, BY DAY (D) AND BY NIGHT (N). (ESTIMATED FROM TABLE 2, AND FIGURES 17 AND 19 OF MUSAYEVA, 1976)

	North			Equatorial			S. Tropical			Javan			Australian		
	D	N	D	N	D	N	D	N	D	N	D	N	D	N	
<i>Diphyes dispar</i>	17-37	10-25	20-57	11-36	29-60	22-49	55-109	49-77	21-41	18-32					
<i>Diphyes bojani</i>	32-68	30-51	34-76	32-78	57-116	58-99	33-86	31-71	33-53	20-48					
<i>Chelophys appendiculata</i>	41-84	38-76	48-78	43-64	61-128	39-79	38-90	30-47	45-100	27-40					
<i>Chelophys contorta</i>	32-72	23-51	35-83	27-59	66-133	43-87	39-97	32-80	-	35-70					
<i>Endoxoides mitra</i>	77-153	64-128	71-141	64-129	71-147	62-111	76-122	55-92	52-104	38-80					
<i>Endoxoides spiralis</i>	32-75	24-59	41-85	24-55	46-109	32-88	37-91	30-67	30-64	21-54					
<i>Ahydopsis tetragona</i>	88-148	71-125	102-162	70-111	123-173	68-105	95-149	69-112	44-71	42-79					
<i>Ahydopsis eschscholtzii</i>	30-95	28-91	40-104	39-101	62-146	60-140	32-83	29-94	33-73	23-65					
<i>Bassia bussensis</i>	37-98	35-100	40-84	39-80	58-108	57-111	38-85	26-69	30-67	23-57					

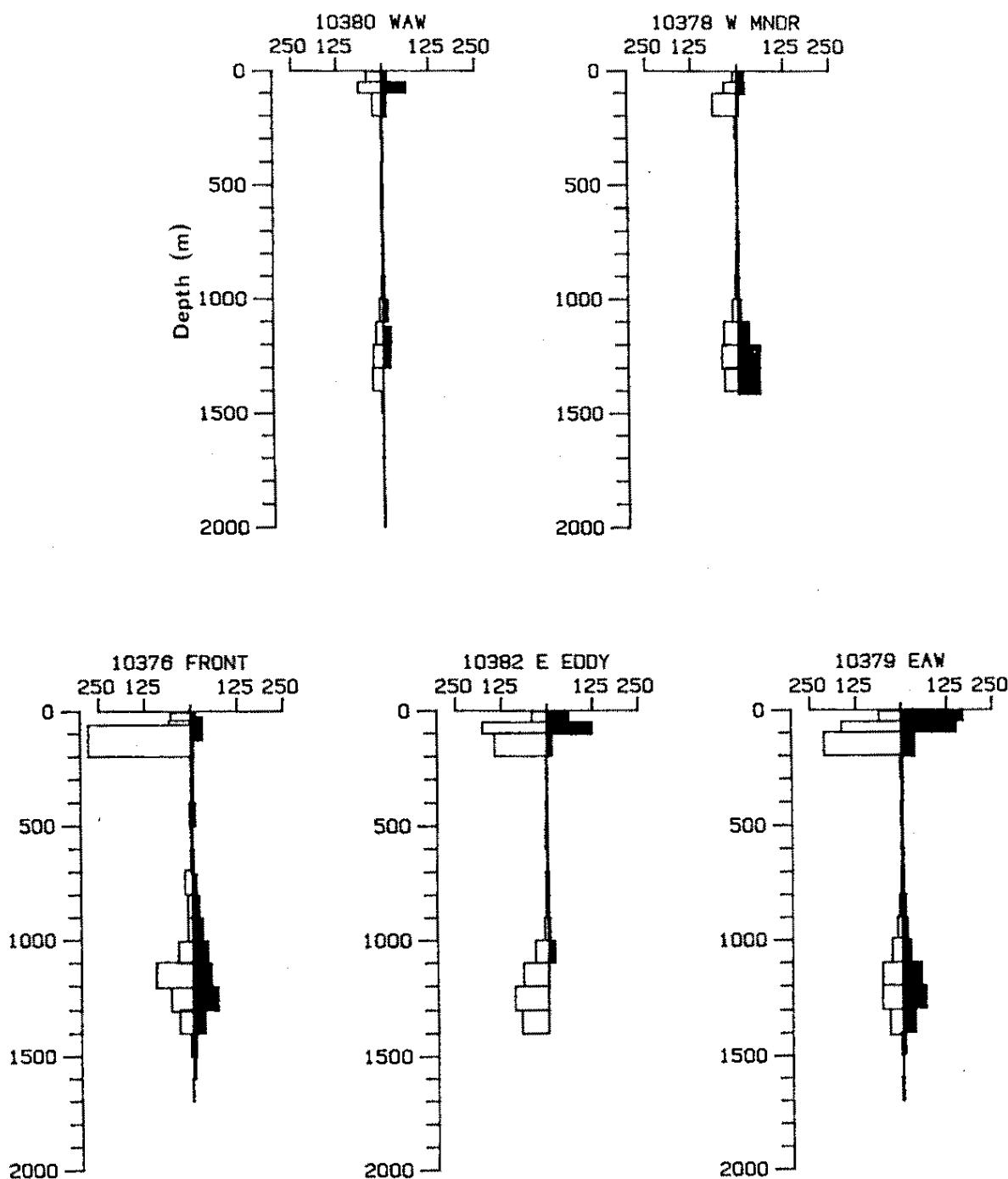


FIG. 12. Vertical distribution of *Eudoxoides spiralis* (nos/ 10^4 m^{-3}), by day and night (black), at five stations in the vicinity of the Azores Front ($\text{ca } 32^\circ\text{ N}, 32^\circ\text{ W}$). The headings refer to the *Discovery* station numbers; WAW—Western Atlantic Water; W MDR—Western Meander; E EDDY—Eastern Eddy; EAW—Eastern Atlantic Water.

limits of the population nuclei, for many common species, largely were determined by temperature, despite considerable changes in the isotherm depths over the study area, and were usually associated with the thermocline. In general, she found that in the regions where the epipelagic species had deeper depth distributions, then the greater was the depth range over which this population was spread (Table 2). There is evidence (Pugh, 1974; and unpublished data) that this axiom also applies to several mesopelagic species.

Musayeva's (1976) data showed regional differences not only in the depth distribution of certain species, but also in the number of species present in the water column. This latter point is discussed in the following section, but it, and the information provided by the other recent studies mentioned above, shed light on general geographical trends in the depth distribution and abundance of certain siphonophore species. These trends are discussed by Pugh (1986), particularly with regard to his own extensive data for calycophoran siphonophores in the NE Atlantic. He did not consider physonect species because of the inherent difficulties in making quantitative estimates of their abundance (Pugh, 1984). However, Pugh concluded that the vast majority of epipelagic calycophoran species belonged to the families Diphyidae and Abylidiae. Amongst the Diphyidae, all the species of the genera *Sulculeolaria*, *Diphyes*, *Chelophyes*, and *Eudoxoides*, plus *Muggiaeae* (neritic) appeared to be epipelagic, as were many of the species of the genus *Lensia*. A partial exception to this rule appeared in the case of *E. spiralis* which, in some areas, had a secondary, deep-living population (Fig. 12). Within the family Abylidiae, all of the species were considered to be near-surface living forms, with the possible exception of *Enneagonum hyalinum*, and any records from deeper depths probably were due to contamination. *E. hyalinum* often occurred in the top 200 m of the water column, but usually had a deeper distribution. Other epipelagic calycophoran species included those of the genus *Amphicaryon* (family Prayidae), and *Hippopodius hippocampus* (family Hippopodiidae), whose stratified vertical distribution in relation to the closely related *Vogtia* species was noted earlier. In all, well over half of the calycophoran species for which there is sufficient data were considered to be epipelagic, and almost all live in the warmer waters of the World's oceans. The meso- and bathypelagic calycophoran population was largely dominated by species from the families Clausophyidae (all species), Prayidae (although the information on some species is inadequate), Hippopodiidae (genus *Vogtia*), and members of the diphyid genus *Lensia*. The possible significance of these differences in the geographical distribution of epi-, meso- and bathypelagic siphonophores is discussed below.

B. Geographical Distribution

Much of the earlier work on the geographical distribution of siphonophores has been concerned either with an areal division of the World's oceans into various zones that coincide with climatic regions and the major circulation patterns (e.g. Stepanjants, 1967), or with the identification of species that are "indicators" of the prevailing hydrographical conditions, particularly in neritic regions (e.g. Russell, 1934). Margulis (1976a) has summarized such

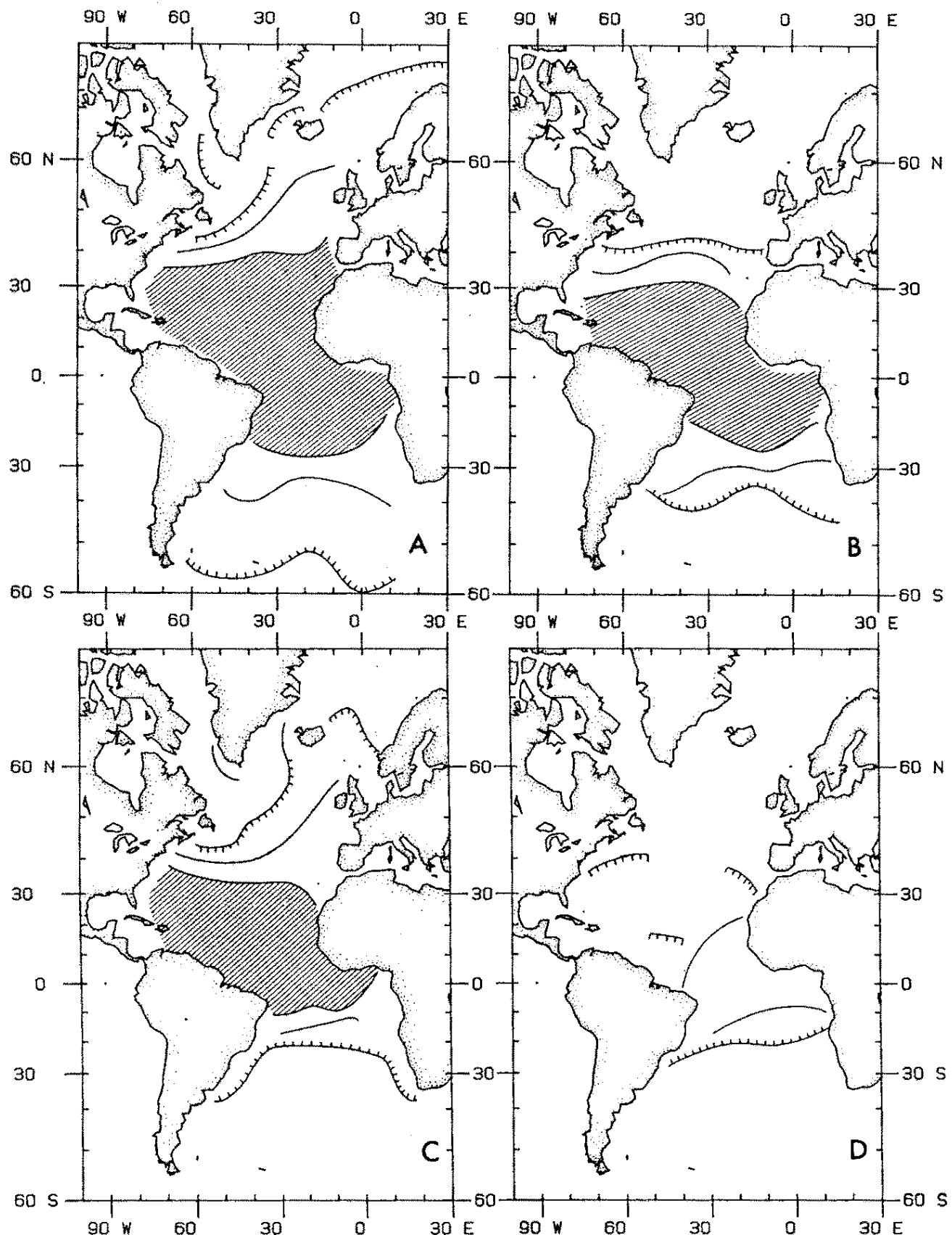


FIG. 13. Geographical distribution of Tropical siphonophore species in the Atlantic Ocean. Redrawn after Margulis (1976a).

- A. Group 5a—widespread species with extensive migration zones.
- B. Group 5b—widespread species with small migration zones.
- C. Group 5c—species with asymmetric latitudinal distribution.
- D. Group 5d—equatorial species.

data for the Atlantic Ocean and has drawn up distributional maps for the various species, based on their total ranges of occurrence. On the basis of these maps, she categorized the species into various groups, namely:

- (1) Arctic species. *Marrus orthocanna* was the only representative.
- (2) Northern Boreal species. Only *Nanomia cara* was included.
- (3) Antarctic species. Two species, *Diphyes antarcticus* and *Pyrostephos vanhoeffeni*, whose habitat bases lay in the West Wind Drift.
- (4) Bipolar species. Two species, *Muggiae bargmannae* and *Marrus antarcticus*; the latter occurring as a subspecies, *M. a. pacifica* in the North Pacific Ocean (Stepanjants, 1967).
- (5) Tropical species. This included most of the other species under study, and was subdivided into four sections as the distribution of the species was not uniform:
 - (a) Species with extensive emigration zones in both hemispheres (Fig. 13A). Temperature, or more specifically the depth of certain isotherms, was considered to be a possible regulatory factor, and was considered to account for the skewed distributions of many species in the NE Atlantic. Margulis (1972) discussed the possibility that the faunal assemblages in the north eastern sector might be affected by the presence of Lusitanian waters, originating in the Straits of Gibraltar, as suggested by Fraser (1967). She concluded that the concept of a "Lusitanian fauna" was neither very precise nor properly substantiated, and that it was more likely that the species were brought into this region by way of the North Atlantic Current. This does seem to be the more likely explanation.
 - (b) Species that avoid the transition/emigration zones (Fig. 13B). The northern boundary for these species was considered to be produced by peculiar hydrographical conditions, as the prevailing circulation system ought to carry the animals towards the north. Recent information, e.g. Gould (1985), indicates a major physical boundary in that region which probably represents the southern branch of the Gulf Stream recirculation. This frontal region has a marked effect on the composition of the siphonophore population (Pugh, unpublished) (Fig. 12).
 - (c) Species with an asymmetric latitudinal distribution (Fig. 13C).
 - (d) Equatorial species (Fig. 13D). Margulis found that the distributional boundaries for the five species in this group did not produce a consistent pattern. This is probably because the data were scant, as other information (Pugh, unpublished data) indicates that these species have much more extensive distributions in the N Atlantic and one, *Lensia hostile*, has been found at 60° N.

- (6) Peripheral species. Also referred to as distant neritic species as they are found mainly around the margins of the tropical and subtropical Atlantic. The peculiar distributional patterns of the three species again are thought to be the result of an inadequate data set.
- (7) Eurybiotic species. Species living in all biogeographical areas and over quite wide temperature ranges. The main species included in this category was *Dimophyes arctica*.
- (8) Neritic species. This group was not discussed in detail by Margulis (1976a), but the geographical distributions of some species show some interesting features which will be discussed later (see p. 151).

From these studies Margulis (1976a) established that the patterns of distribution for many, mainly epipelagic, species could be related to the major climatic regions of the World's oceans. She concluded that the controlling factors also could be associated either with water productivity or a particular combination of hydrographical conditions that characterized certain water masses. However, the major drawback with such studies is that they are concerned only with the absolute habitat boundaries for each species, based on first and last capture principles, and give no information on the quantitative geographical distribution of the animals, nor do they take into account specific patterns of vertical abundance.

Musayeva (1976) studied the quantitative geographical distribution of epipelagic siphonophores in the eastern Indian Ocean, and noted interesting regional differences not only in the total population (Fig. 14) but also in the relative abundance of the nine commonest species. She divided these species into five groups:

- (a) Those whose population maxima lay in the productive equatorial waters, e.g. *Abylopsis eschscholtzii*.
- (b) Those equally divided between equatorial and central waters, and associated with zones of convergence, e.g. *Bassia bassensis*.
- (c) Those absent from all central waters, e.g. *Diphyes dispar*.
- (d) Those that do not occur in the Bay of Bengal, e.g. *Chelophyes appendiculata*.
- (e) Those which reach peak numbers in the central, most oligotrophic waters, e.g. *Eudoxoides spiralis*.

Thus, although the geographical variations in abundance of the total siphonophore population corresponded with those of the entire zooplankton biomass, that was not necessarily the case for the individual species, particularly *E. spiralis*. Musayeva concluded that there were specific differences in the response to the peculiar hydrographical conditions in the Indian Ocean resulting from the monsoons.

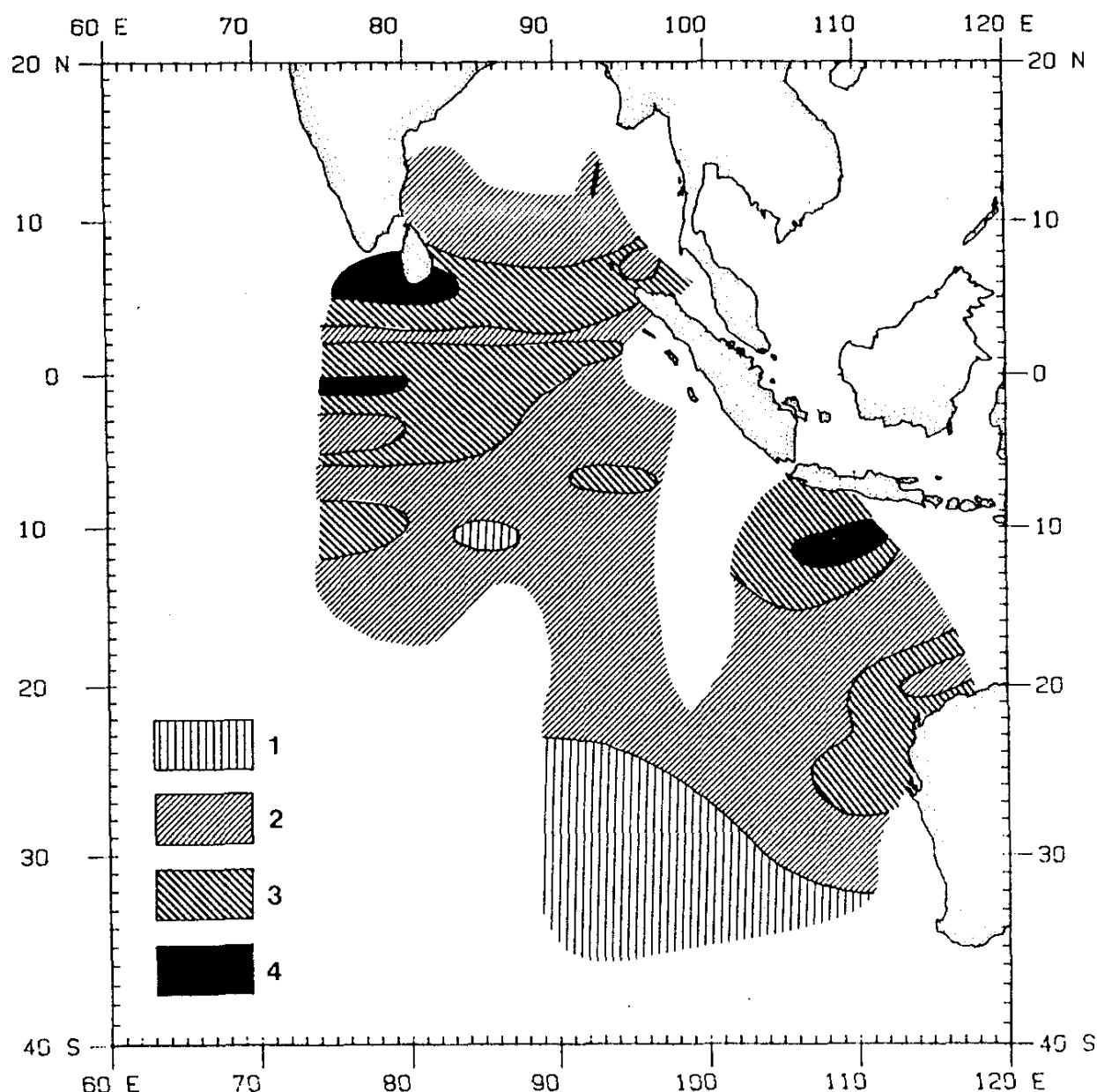


FIG. 14. Geographical distribution of siphonophores in the eastern Indian Ocean (Redrawn after Musayeva, 1976). Contour levels: 1. <100; 2. 100–300; 3. 300–1000; 4. >1000 individuals/m² (0–200 m depth range).

Pugh (1975) also reported marked differences in the quantitative distribution of siphonophore species across the N Atlantic at 32° N. Two main populations were found, one in the eastern central water mass and the other in the Sargasso Sea, and these bore a clear relationship with the different hydrographical conditions in these two regions. However, it was apparent that the reactions to the changes in hydrography were specifically variable. Unfortunately, these data were derived from oblique (0–1000 m) hauls and so it was not possible to analyse possible changes in the specific vertical distribution patterns.

Fasham and Angel (1975) clearly demonstrated that, in order to establish faunal zones and to study the geographical distribution patterns of any

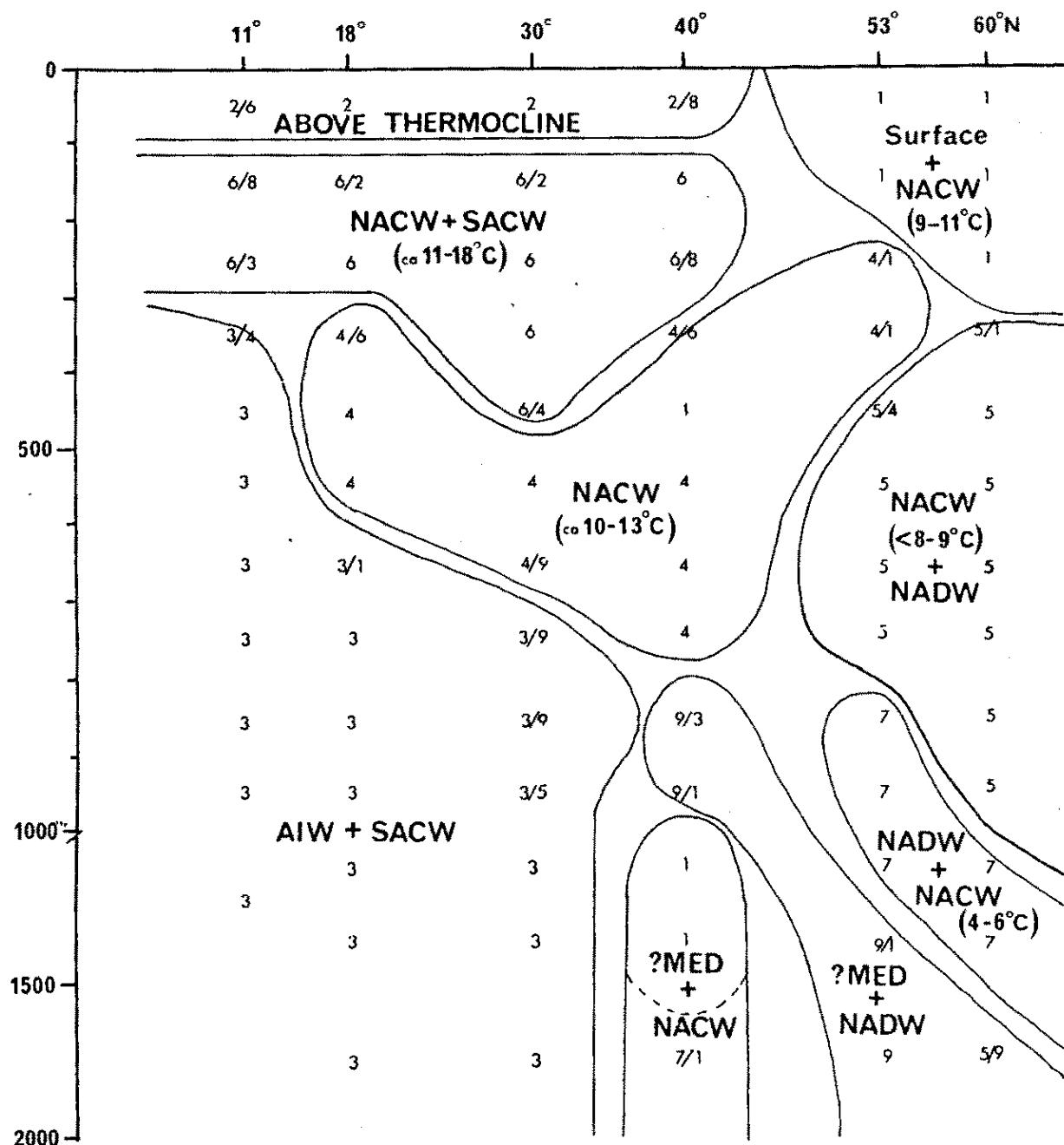


FIG. 15. The vertical and geographical distribution of the statistical factor groupings in the day-time hauls. See Fig. 17 and Pugh (1977) for station and other details. AIW = Antarctic Intermediate Water. SACW = South Atlantic Central Water. NACW = North Atlantic Central Water. NADW = North Atlantic Deep Water. MED = Mediterranean Water.

pelagic group of organisms, it was essential to consider all aspects of their regional, vertical and numerical distribution. Several faunal zones could be present in a single water column, and each zone was characterized by a particular assemblage of species, with typical and relative numerical abundances. It was unusual to find an individual species wholly confined to a single zone. Similarly, Pugh (1977) considered the vertical and latitudinal distribution of siphonophores in relation to the water masses in the warmer waters of the NE Atlantic. A fuller picture of the results from those statistical analyses is presented here, using information from two further stations, at 53 and 60° N (Fig. 15). As Pugh (1977) noted, there is good

correspondence with the results of Fasham and Angel (1975) for ostracods, and reference should be made to Pugh (1977) for a full discussion of the data from the more southerly stations (11–40° N). The main features of the statistical results are:

- (a) The siphonophore faunal zones broadly can be associated with the major hydrographical features that characterize the various water masses present in the NE Atlantic, as outlined by Fasham and Angel (1975). Fasham and Foxton (1979) used a predictive model to exemplify this correspondence in the case of the distribution of decapods.
- (b) There is a clearly defined, and very abundant, population of epipelagic siphonophore species above the permanent thermocline in the warm, southerly waters.
- (c) There is a marked discontinuity, at least in the top 1000 m of the water column, between the more southerly (11–40° N) and northerly (53–60° N) populations. The northern midwater population occurs in the region where there is mixing between cold (<8–9 °C) N Atlantic Central and Deep Waters (cf Fasham and Angel, 1975).
- (d) The faunal assemblage normally associated with superficial northerly waters also occurs below 1000 m at 40° N. This results from the presence of certain species, mainly *Lensia conoidea* and *Chuniphyes multidentata*, with similar relative abundances.
- (e) There are differences between the siphonophore and ostracod faunal zones below ca 700 m at the more northerly stations (30–60° N). It appears that a characteristic Mediterranean Water fauna of siphonophores is present at 30 and 40° N, while no such ostracod fauna could be defined (Fasham and Angel, 1975). At shallower depths at these stations, and at deeper ones farther to the north, there was a different assemblage of siphonophores, dominated by *Clausophyes ovata* and *Vogtia serrata*, and to a lesser extent *Lensia conoidea*.
- (f) The siphonophore faunal zone occupying the deeper waters at 53 and 60° N did not appear in the ostracod analyses. It represents a region of mixing between N Atlantic Central (4–6 °C) and deep waters, with a greater preponderance of the latter than in the zone above. It is characterized by the presence of relatively large numbers of *Lensia havock*, in association with *Apolemia* sp., *L. conoidea* and *Rosacea plicata*.
- (g) The above points demonstrate that one species, *Lensia conoidea*, made an important contribution to several of the more northerly faunal zones. This exemplifies the conclusion that it is not necessarily the total distribution ranges of certain species, whether by depth or latitude, that determine the faunal zones, but rather their relative abundances.

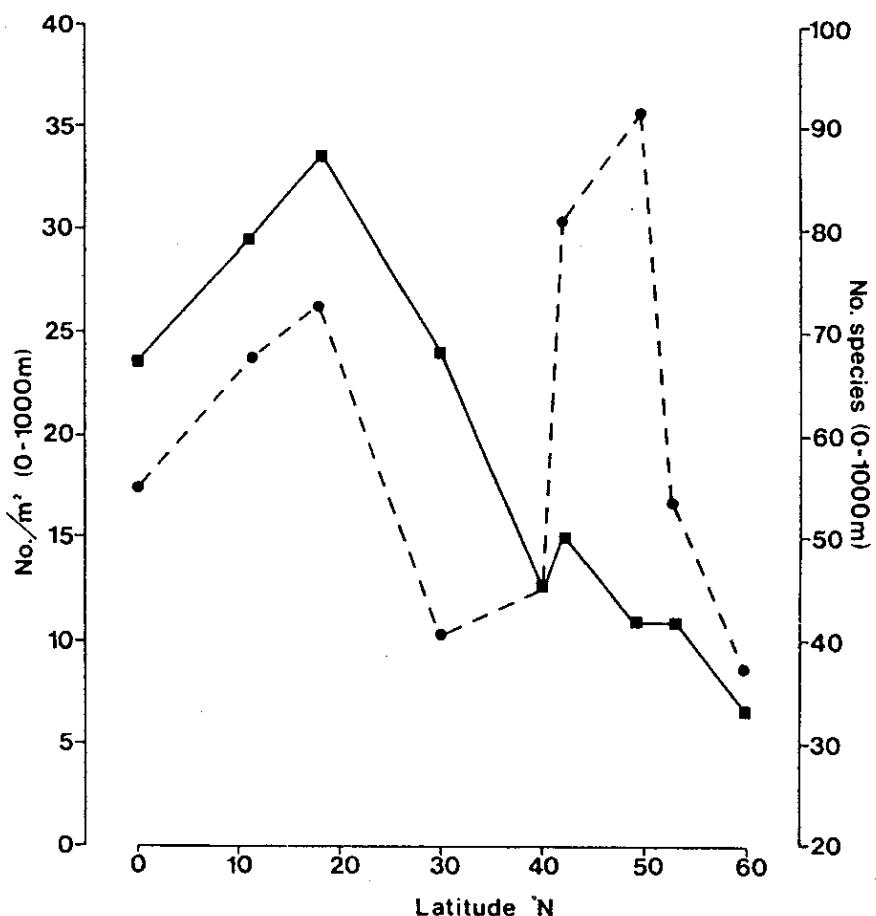


FIG. 16. Geographical distribution, in the NE Atlantic Ocean, of the total number of siphonophore species (squares) and the number of specimens/m² (21 commonest calycophoran species) (circles) present in the top 1000 m of the water column. See Fig. 17 for position of stations.

Pugh (1986) used a more extensive data set, based on ten stations ranging from the equator to 60° N, to draw some general conclusions on the geographical and vertical distribution of siphonophores in the NE Atlantic. He found that species diversity in the top 1000 m of the water column was greatest at the 18° N station (Fig. 16). There was a small decline in species numbers towards the equator, as has been noted for other groups of pelagic animals, but the decline was far more dramatic towards the more northerly stations. At even higher latitudes the number of species would be expected to decrease even further as Zelickman (1972) found only three in the Barents Sea. This latitudinal distribution of species number would appear to be in accord with the generalized theory that species diversity, in the pelagic realm, is highest in the so-called "stable" environments. However, Musayeva (1976), who also noted a latitudinal change in the numbers of epipelagic siphonophore species in the eastern Indian Ocean, found that the greatest number occurred in the most productive, north-eastern region with lowest numbers in the oligotrophic, and so possibly more stable, subtropical region. The peculiar monsoonal conditions probably were a contributory factor. Nonetheless, further evidence for a latitudinal change in species

diversity in the N Atlantic comes from other sources. Stepanjants (1975) found 62 species in the Gulf of Mexico (depth range of sampling 0–3000 m); Pugh (1974) 63 spp. around the Canary Islands (0–960 m); Casanova (1980) 59 spp. at 30° 18' N, 29° 20' W (0–900 m); while Patriti (1965) found only 18 spp. in the Bay of Biscay (0–2000 m). Similarly, in the colder waters of the North Pacific (44° N, 150° E) (0–5240 m), Stepanjants (1970) found only 14 spp. Alvariño (1967b) reported on a relatively small number of species (36) off California (0–3040 m), but this may reflect the prevailing circulation pattern in that area, particularly as most of the typical warm-water, epipelagic species did not occur there.

It was noted earlier that in the warmer, tropical waters there are large numbers of numerically abundant epipelagic siphonophore species. Pugh (1986) noted that it was the disappearance of these species at higher latitudes that largely accounted for the reduction in species diversity there. The geographical distribution of *Eudoxoides spiralis* (Fig. 17A) typifies this point. Thus, in the top 100 m of the water column, 47 spp. were found at the 18° N station (representing ca 50% of the total number in the 0–1000 m depth range), while at 60° N only nine occurred (ca 30% of total), and of these only three, *Nanomia cara*, *Lensia conoidea* and *Dimophyes arctica*, could be considered as common. *L. conoidea* is largely confined to northerly latitudes in the NE Atlantic (Fig. 17B), and the deep population that appears ca 40° N may come from the Mediterranean, as discussed earlier. *N. cara* is a northern boreal species (Margulis, 1976a) and has an allopatric distribution with its congener *N. bijuga*, which is a widespread warm-water species. The distributional ranges of these two species overlap in the region of the UK, but the presence of each depends on the prevailing current pattern (Southward, 1962).

Pugh (1986) noted that neither the numerical abundance of the 21 commonest calycophoran species, nor the total siphonophore biomass (displacement volume) followed the same latitudinal trends as those noted for species diversity. Two peaks of numerical abundance were found (Fig. 16), one between 11 and 18° N and the other between 40 and 53° N. In contrast, biomass tended to increase with increasing latitude and, thereby, with decreasing species diversity. These differing trends were related to the depth and geographical distribution of the various calycophoran taxa, as noted above (see p. 139). Thus, the large number of actively swimming, but generally small epipelagic species (chiefly of the families Diphyidae and Abylidae) were the main component of the total biomass in warmer, southerly waters. To the north the larger, less active and deeper living species (family Prayidae, Hippopodiidae and Clausophyidae) tended to predominate. The species diversity of the meso- and bathypelagic population overall is less than the epipelagic one and, in addition, relatively few species tend to

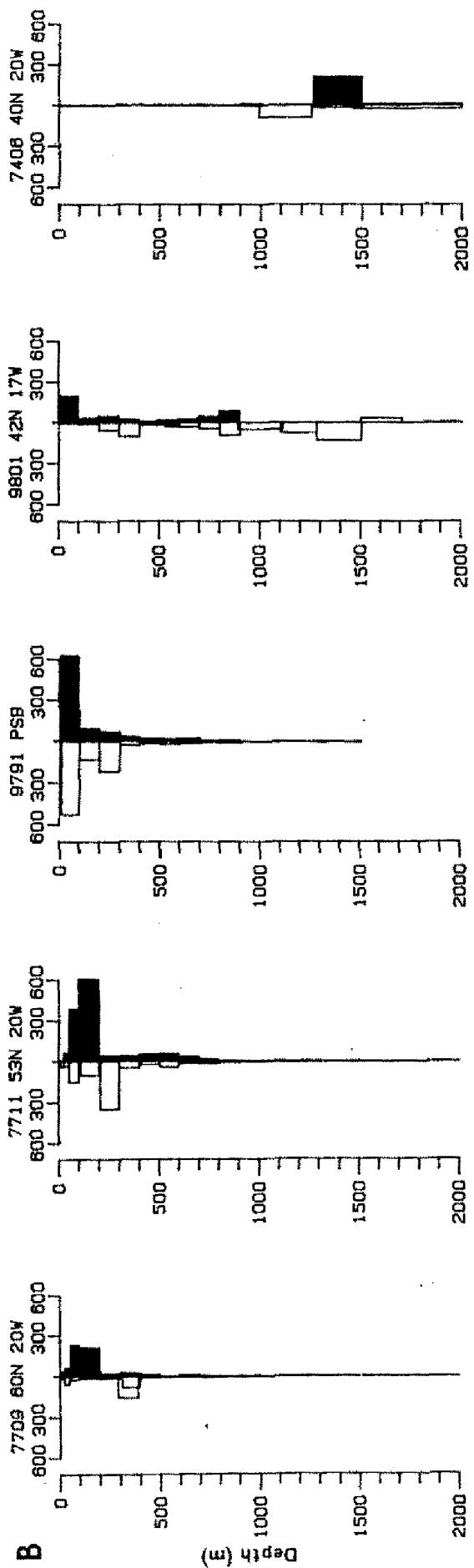
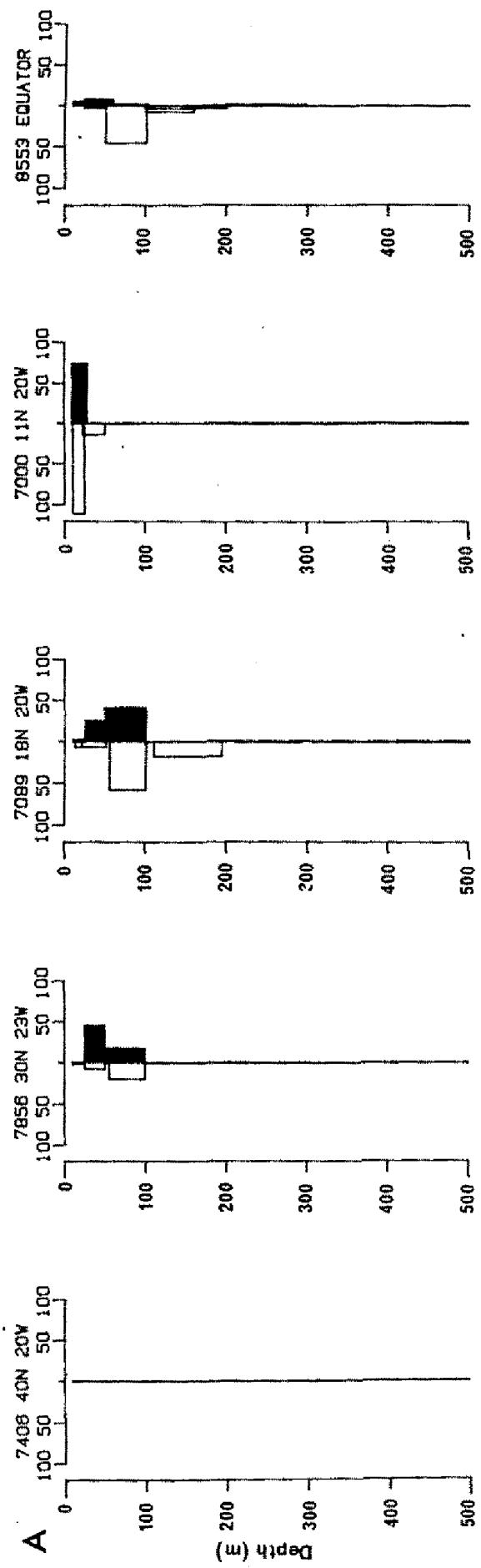


FIG. 17. Vertical distributions of *A* *Eudoxoides spiralis* and *B* *Lensia conoidea* (nos/10⁴m³), by day (white) and night (black), in the NE Atlantic Ocean. No specimens of *E. spiralis* were found north of 40° N, while occasional specimens of *L. conoidea* were found south of 40° N (never more than 3.6/10⁴m³). The headings refer to Discovery stations, except for St 7000 which is an amalgam of Discovery stns 6662 and 7824. PSB = Porcupine Seabight, ca 49°30' N, 14° W; Equator = 0° N, 22° W.

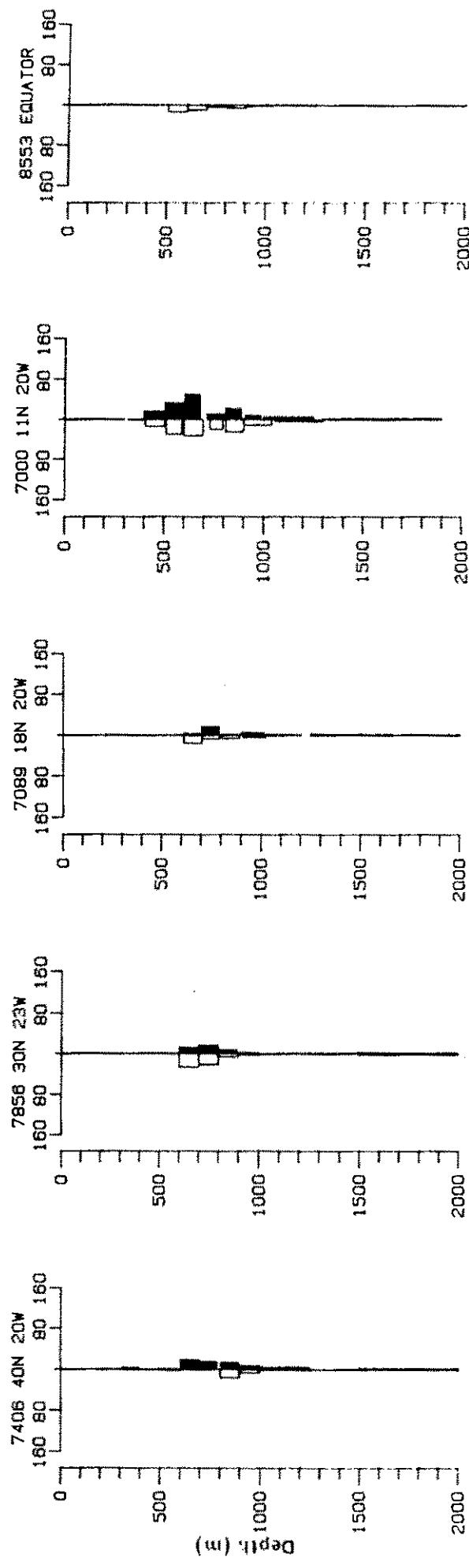
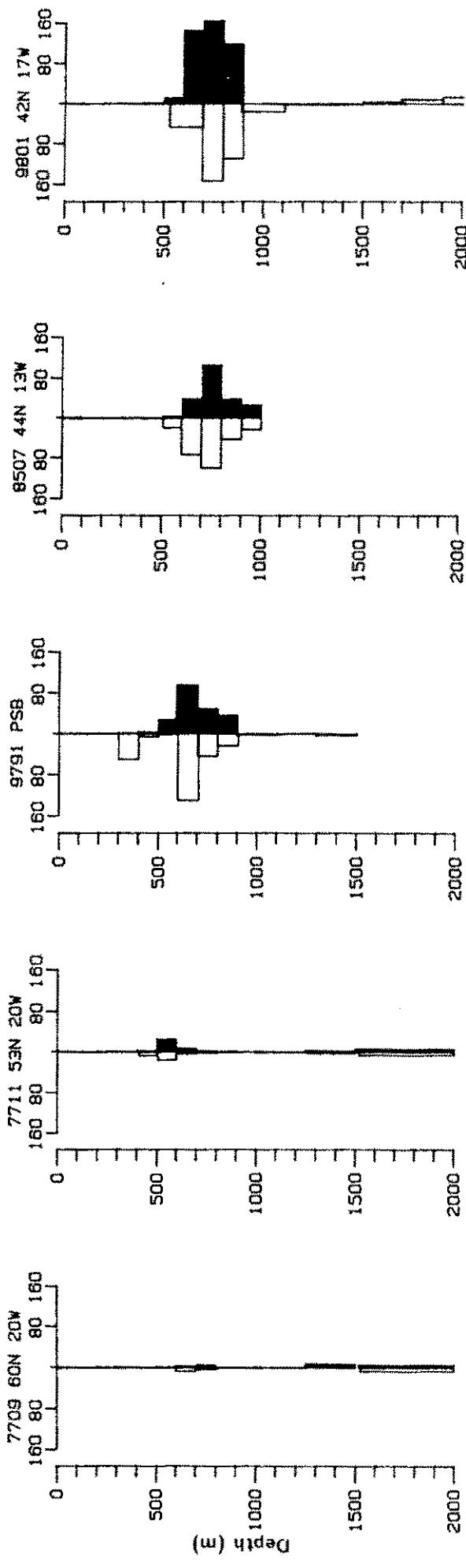


FIG. 18. Vertical distribution of *Clausophyes ovata* (nos./ 10^4m^3), by day (white) and night (black), in the NE Atlantic Ocean. See Fig. 17 for station details.

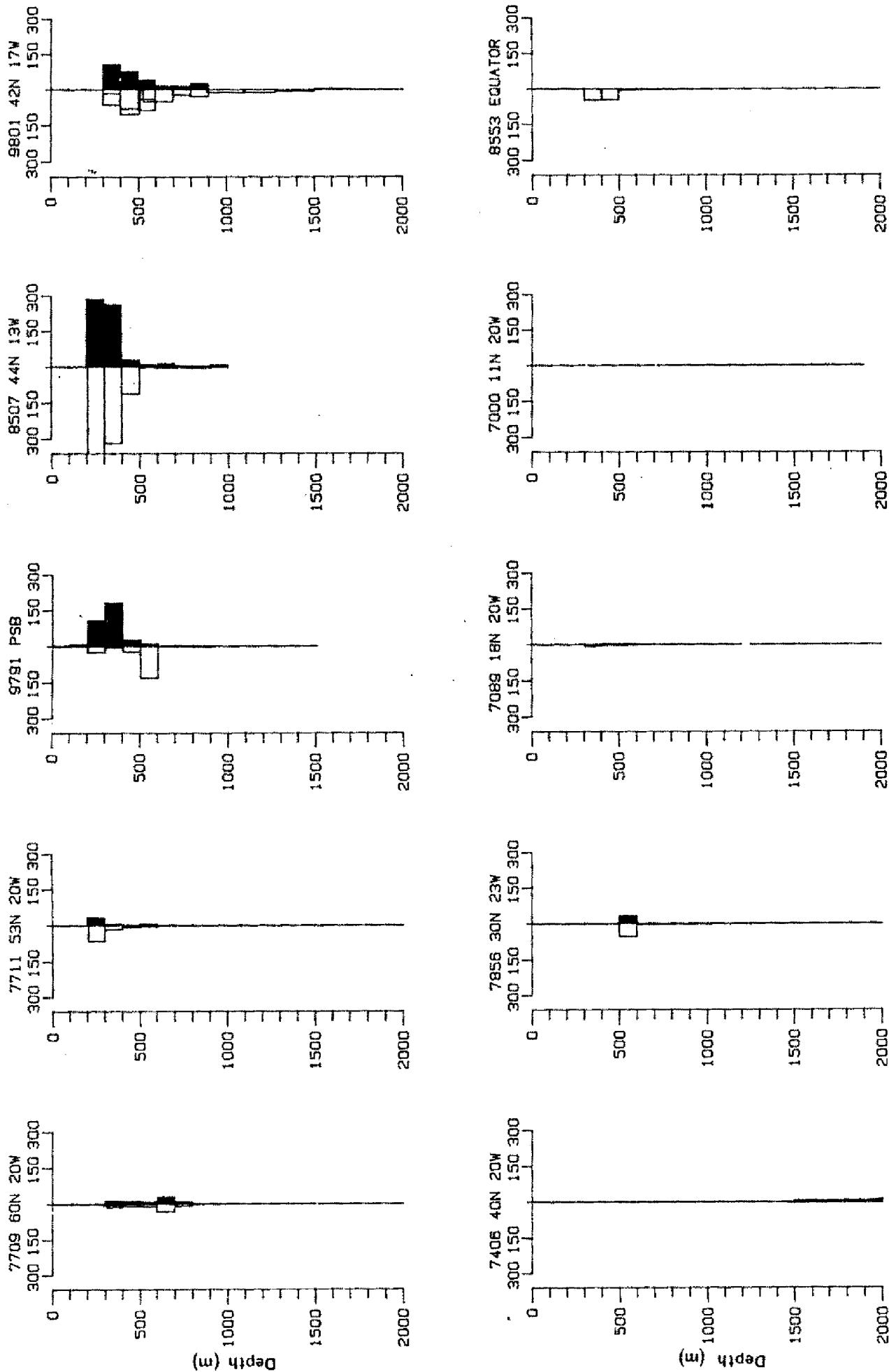


FIG. 19. Vertical distribution of *Chuniphyes multidentata* (nos/10⁴ m³), by day (white) and night (black), in the NE Atlantic Ocean. See Fig. 17 for station details.

dominate the deeper population. Although several of the deeper living species have a widespread geographical distribution, e.g. *Clausophyes ovata* (Fig. 18), others, e.g. *Rosacea* spp. (see Pugh, 1986), or *Chuniphyes multidentata* (Fig. 19) are generally more abundant at, or restricted to, higher latitudes. This latter species appears to have an allopatric distribution with its congener, *C. moserae* (Pugh, unpublished data). *C. moserae* is found mainly at stations to the south of 40° N, but where the two species do co-exist their population nuclei are spread over different depth zones, although there is some overlap in their total depth ranges.

Although these regional differences in the siphonophore faunal assemblage could be associated with hydrographical features, Pugh (1986) considered that a more immediate controlling factor might be the distribution of the preferred prey items. (The dietary preferences and feeding behaviour of the various groups of siphonophores are discussed in Section VID of this paper.) He noted that available data indicated a preponderance of small prey items, such as copepods and ostracods, in near surface warm waters and that this would accord with the presence there of large numbers of small epipelagic siphonophores. On the other hand, the greater size of the potential prey items at higher latitudes or deeper depths would suit the larger, less active species. Pugh concluded, therefore, that the size distribution and abundance of the potential prey population at any one position and depth plays an important role in determining the specific siphonophore assemblage associated with it. Thus, as Haedrich and Judkins (1979) surmised, although it is relatively easy to establish correlations between faunal zones and hydrographical features, it is probable that some other, underlying factor has a more immediate controlling effect on the distribution of siphonophore species.

C. Neritic Siphonophores

Only a few species of siphonophores are neritic, confined almost exclusively to near-shore waters. Chief amongst these are three of the four species of the calcyophoran genus *Muggiaeae*. Alvariño (1972b) also suggested that the fourth species, *M. bargmannae*, was a cold-water neritic form, but Margulis (1976a) classified it as a boreal-bipolar species. The information on the geographical distribution of the other *Muggiaeae* species shows that they rarely co-occur, although their ranges may overlap. *M. delsmani* occurs along the coastal regions of the Indian Ocean from Zanzibar to Singapore, and also in the Java and South China Seas (Totton, 1954; Rees and White, 1966; Rengarajan, 1973). In contrast, there are no reliable records for the presence of *M. kochi* in the Indian Ocean, but *M. atlantica* has been found

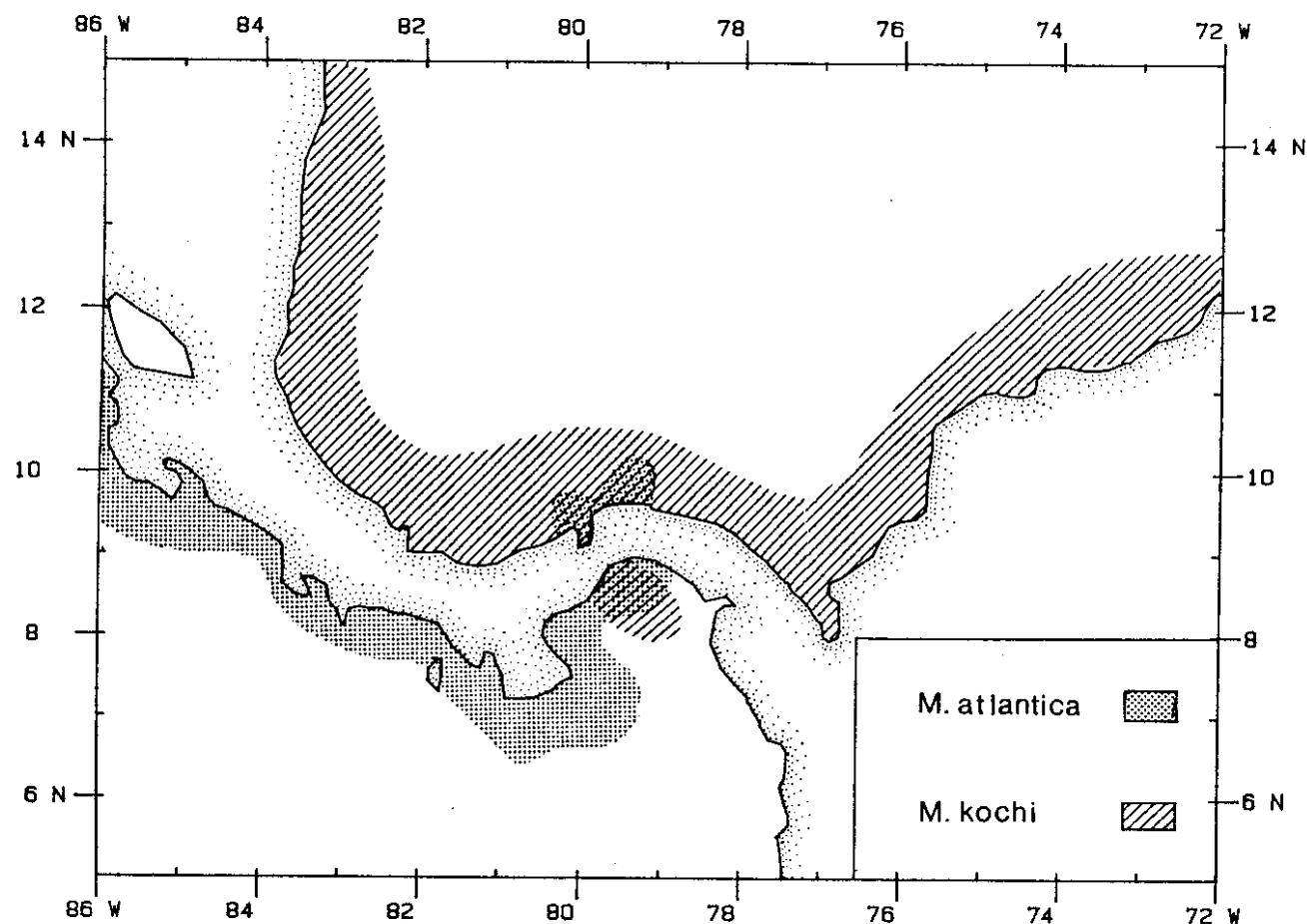


FIG. 20. Distribution of *Muggiaea atlantica* and *M. kochi* in the regions adjacent to the Panama Canal. Redrawn from Alvariño (1974).

occasionally in the Red Sea, Gulf of Aden and associated Arabian coastal regions (Totton, 1954; Daniel, 1974). Possibly this is a relict fauna isolated after the closure of the Tethys Sea, although *M. atlantica* appears to be absent from the eastern Mediterranean (Alvariño, 1974).

Muggiaea atlantica and *M. kochi* have been found at various localities throughout the Atlantic Ocean, but they rarely co-occur. For instance, Russell (1934), who studied the presence of these species in the English Channel over a 23-year period, found that between 1913 and 1924 only *M. atlantica* was present, while from 1925 to 1934 it was replaced completely by *M. kochi*. A similar alternation in the abundance of these two species was noted by Bigelow and Sears (1939) off the NE coast of America. Along the NW African coastline, *M. atlantica* is abundant whereas there are few records for *M. kochi* (Furnestin, 1957). However, during a seasonal study in the Gulf of Guinea, Neto and de Paiva (1966) found both species in reasonable numbers, but again rarely did they co-occur. On the other side of the Atlantic there appears to be a major population of *M. kochi* in the coastal waters of the Gulf of Mexico (Alvariño, 1974) (Fig. 20). In the western Mediterranean, the situation is more complex as these two species do co-occur, although it is usual for one species, more often *M. kochi*, to

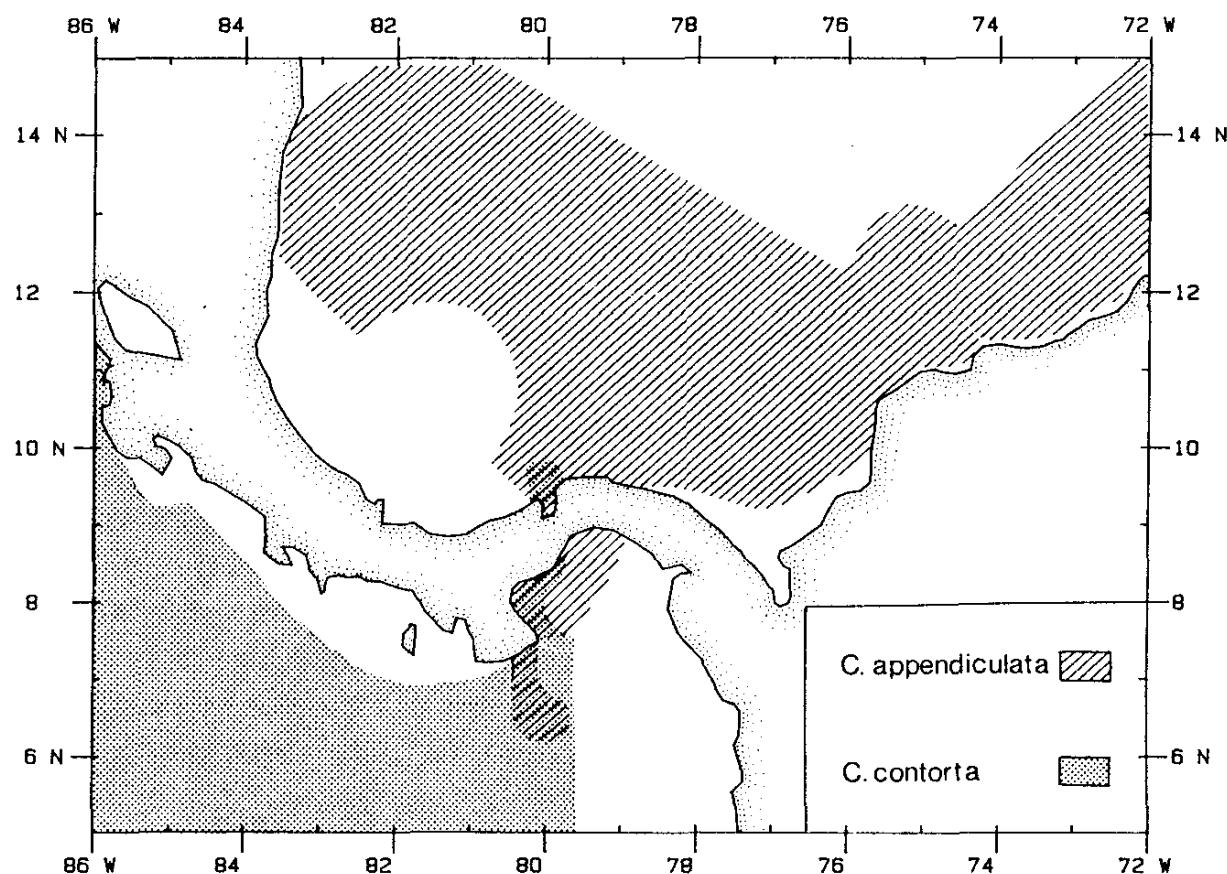


FIG. 21. Distribution of *Chelophyses appendiculata* and *C. contorta* in the regions adjacent to the Panama Canal. Redrawn from Alvariño (1974).

predominate (see p. 169). However, Carré (personal communication) has found both species to be present in similar numbers in that region, particularly in the Ligurian Sea. It is possible that changes in the hydrological conditions are controlling the appearance of these two species at the various localities.

In the Pacific Ocean, there are only a few records for the occurrence of *Muggiae kochi*, while *M. atlantica* occurs along the coastline of America and in the north eastern region (Alvariño, 1971; Zhang and Xu, 1980). Alvariño's (1974) data also demonstrate the allopatric distributions of these two species in the Central American region as *M. atlantica* was found to predominate along the Pacific coastline and *M. kochi* in the Gulf of Mexico (Fig. 20), although some intermixing was noted in the regions on either side of the Panama Canal. Another pair of species, *Chelophyses appendiculata* and *C. contorta*, had a similar allopatric distribution in the Central American region (Fig. 21), but Rengarajan (1975) found these two very common species to be sympatric along the western coast of India. *C. appendiculata* usually is an open water species, while *C. contorta* normally is neritic.

At times of peak abundance, *Muggiae atlantica* totally dominates the neritic siphonophore population off the NW African Coast (Furnestin, 1957;

Pugh and Boxshall, 1984), whereas *M. delsmani* appears to be sympatric with two other neritic diphyid species, *Diphyes chamissonis* and *Lensia subtiloides*, in the Indian Ocean (Rengarajan, 1973, 1975). The latter two species also co-occur at several localities as far round as the coast of Japan (Alvariño, 1971), beyond the geographical range of *M. delsmani*, and they were the predominant species within the Great Barrier Reef (Totton, 1932).

Species of the genus *Sphaeronectes* probably are neritic, although few are well known, while many other species appear to have inshore or neritic distributions, particularly in the Mediterranean, but elsewhere are found to be widespread epipelagic oceanic forms, e.g. *Lensia subtilis*, *L. meteori*, *L. campanella*, *Eudoxoides mitra*, and possibly *Chelophyes contorta*.

D. Benthic and Pleustonic Siphonophores

The discussion so far has referred to the distribution of holopelagic siphonophores, which make up the vast majority of the known species. However, there are two groups of siphonophores that have adopted another way of life, living in the two-dimensional realm on the top or at the bottom of the ocean. First, there are species of the physonect family Rhodaliidae which have reattached themselves to the bottom substrate, using their tentacles, and have become benthic organisms, as Pugh (1983) has shown. There are very few records for these unusual siphonophores, but Pugh noted that the geographical and depth distributions (Table 3) of the ten species he recognized were relatively restricted, although geographical isolation was used as a criterion for establishing certain poorly known forms as separate species. With regard to depth distribution, the species could be divided into three groups (Table 3). Pugh (1983) suggested that the papilliform processes present only on the aurophores (enlarged gas secreting organs) of the two shallowest living species might allow greater buoyancy control if the animals became detached from the substrate. He also reported possible observations of the Galapagos dandelions, *Thermopalia taraxaca*, or a related species, in the Juan de Fuca Ridge region, but more recent information does not confirm this.

The second group of nonholopelagic siphonophores is represented by a single cystonect species, *Physalia physalis*, the Portuguese Man-of-War. This peculiar siphonophore, with its enormous gas-filled pneumatophore topped by an erectile crest, floats at the surface of the oceans and does not propel itself about. It is transported by surface currents and sails with the prevailing winds. The species is dimorphic, being either right- or left-handed depending on which side of the pneumatophore the cormidia are attached. The dynamics of this arrangement, as discussed by Savilov (1969), means that the

TABLE 3. DEPTH RANGES AND GEOGRAPHICAL DISTRIBUTION FOR BENTHIC RHODALIID SIPHONOPHORES

	Depth range (m)	No. of specimens	Locality
<i>Archangelopsis typica</i>	100–112†	3	ca 07°–09° S, 115°–126° E and 32°31' N, 128°33' E
<i>Dromalia alexandri</i>	64–725 (peak 150–300 m)	> 100*	ca 28°–34° N, 115°–120° W
<i>Sagamalia hinomaru</i>	450	1 (?)	35°10' N, 139°30' E
<i>Rhodalia miranda</i>	455–1098	16	37°17' S, 53°52' W and 46°–53° S, 56°–59° W
<i>Stephalia bathyphysa</i>	503	1	38°50' S, 169°20' E
<i>Stephalia corona</i>	945–1658	11	ca 60° N, 17° W and 23°–29° N, 12°–17° W
<i>Stephalia dilata</i>	1158	1	01°34' S, 89°30' W
<i>Thermopalia taraxaca</i>	2500–2600	> 100*	ca 0°–1° N, 86° W†
<i>Angelopsis globosa</i>	2553	2 (?)	37°50' N, 73°04' W
<i>Angelopsis euryale</i>	3089–3109	3	20°50' N, 18°56' W

* Numerous observations from submersibles.

† See Pugh (1983) for discussion.

animals tack at an angle of ca 40–50 °C to the wind direction. Rather confusingly, the left-handed forms tack to the right and vice versa. Because of this arrangement some researchers have sought to prove that, because of the generalized oceanic and atmospheric circulation patterns, one form would predominate in the northern hemisphere and the other in the southern. However, the evidence discussed by Totton (1960) and Savilov (1969) clearly shows that this is not the case. *Physalia* is thermophilic and is widely distributed in the tropical and subtropical regions of the World's oceans, although because its distribution is greatly dependent on circulation patterns, specimens are frequently found at higher latitudes. Thus, in the N Atlantic its distribution is generally restricted to south of 45° N, but the Gulf Stream and the prevailing wind often carries specimens much further to the north. There are many records from the British Isles (Wilson, 1947; Kirkpatrick and Pugh, 1984). Although the two dimorphic forms are found in both hemispheres in the Atlantic and Pacific Oceans, Savilov (1969) noted that there was a definite trend for the concentration of one particular form in certain regions. It is not known what factor controls the dimorphism. Totton (1960) believed that the orientation was determined randomly, shortly after the larvae appeared at the sea surface, but Savilov (1969) considered that it might be determined genetically, as has been suggested for the velellids. Maynard Smith (personal communication) suggests that dimorphism may develop by individual selection, as an example of frequency-dependent fitness, and that all specimens may be genetically similar, with an even chance of being right- or left-handed.

TABLE 4. THE DAY-NIGHT DEPTH CHANGES, AND PERCENTAGE RATIOS OF THE TOTAL DAY AND NIGHT (0–250 m) POPULATIONS FOR VARIOUS SPECIES FOUND IN THE FLORIDA CURRENT (2 DATA SETS) AND IN THE VICINITY OF BERMUDA (FROM MOORE, 1949, 1953)

Species	Day-night Ranges (m)		D : N (%)	
	Florida	Bermuda	Florida	Bermuda
	1	2	1	2
<i>Amphicaryon acaule</i>	.	.	-77	0
<i>Hippopodius hippopus</i>	-50	.	NM	28
<i>Diphyes dispar</i>	-38	+49	.	9
<i>D. bojani</i>	-59	-16	NM	18
<i>Lensia campanella</i>	.	.	NM	.
<i>L. fowleri</i>	-32	.	NM	3
<i>L. subtilis</i>	.	.	Slight	.
<i>Chelophyes appendiculata</i>	-48	-5	-87	29
<i>Eudoxoides mitra</i>	-50	-44	Slight	12
<i>E. spiralis</i>	-33	-30	-47	40
<i>Ceratocymba leuckarti</i>	-92	.	A	6
<i>Abylopsis tetragona</i>	-70	-80	-89	8
<i>A. eschscholtzi</i>	-6	-48	NM	29
<i>Bassia bassensis</i>	-28	-41	NM	12
<i>Enneagonum hyalinum</i>	-19	.	A	28

NM, non migrant; A, absent from collections; . no data given.

E. Diel Vertical Migration

Only a few detailed studies on the diel vertical migration (DVM) patterns of siphonophores have been carried out. There are many problems associated with the interpretation of the results from such studies, and these can be exemplified as follows.

1. Total depth distribution range of migrating species not sampled.

Some of the earliest studies on the DVM patterns of siphonophores were made in the Bermuda (Moore, 1949) and Florida Current (Moore, 1953) regions of the NW Atlantic Ocean. In both regions sampling, over six depth intervals, was carried out from the surface to 250 m, on *ca* six occasions during an 18–24-h period. Moore (1949) considered that five of the 11 commonest species underwent a DVM, while Moore (1953) found that almost all such species migrated dielly (Table 4). An outward impression from the results, e.g. for *Eudoxoides spiralis* (Fig. 22), was that only the shallower part of a specific population migrated while the deeper part remained static. However, this was not necessarily the case for, at night, there was a considerable recruitment of individuals into the sampling zone

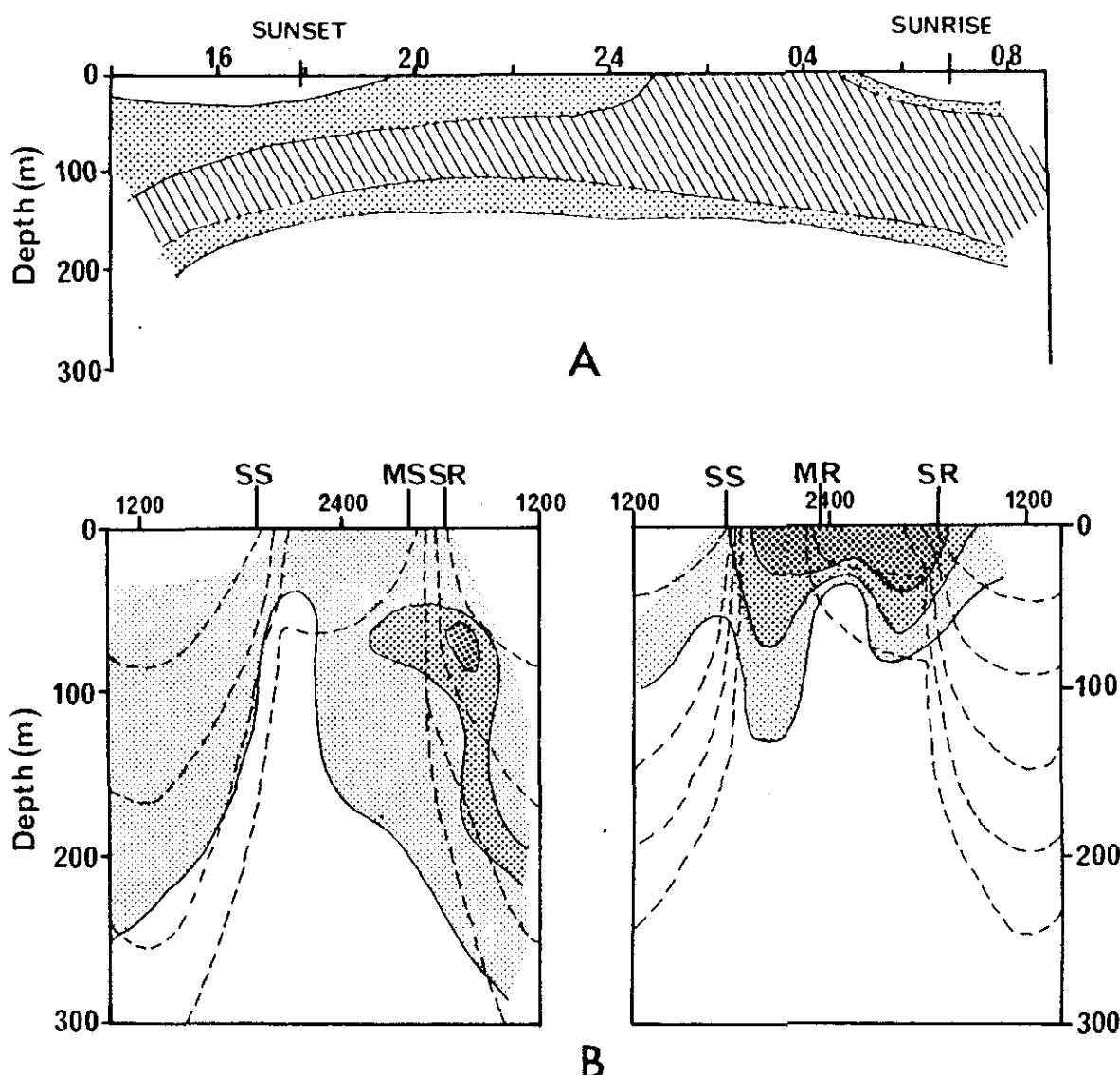


FIG. 22. Diel vertical migration patterns for *Eudoxoides spiralis*.

A Bermuda region. Redrawn from Moore (1949). B Florida Current region on two different occasions. Redrawn from Moore (1953). The contour levels are drawn at different levels in each Fig. In A at ca 70 and 120 specimens/haul; in B left-hand figure at 1, 10 and 100 specimens/haul; and right-hand figure at 100, 500 and 1000 specimens/haul.

from below 250 m, as shown by the day : night percentage ratios (Table 4). Thus, in the case of *Chelophysa appendiculata*, although the vertical range of DVM was found to vary between eight and 87 m in the Florida Current, Moore (1953) considered that, in the former case, there had been a 100% nighttime recruitment of animals. By inference, therefore, the actual depth range for the DVM must have been in excess of 200 m, and such a range could only be assessed if the total depth of the specific population had been sampled.

2. Sinusoidal patterns of DVM and sampling time.

One feature of Moore's (1949, 1953) results, as with those of Hure (1961) for the Adriatic Sea, is that there are few indications of a rapid crepuscular DVM. Instead many siphonophore species exhibit a fairly slow, undulating

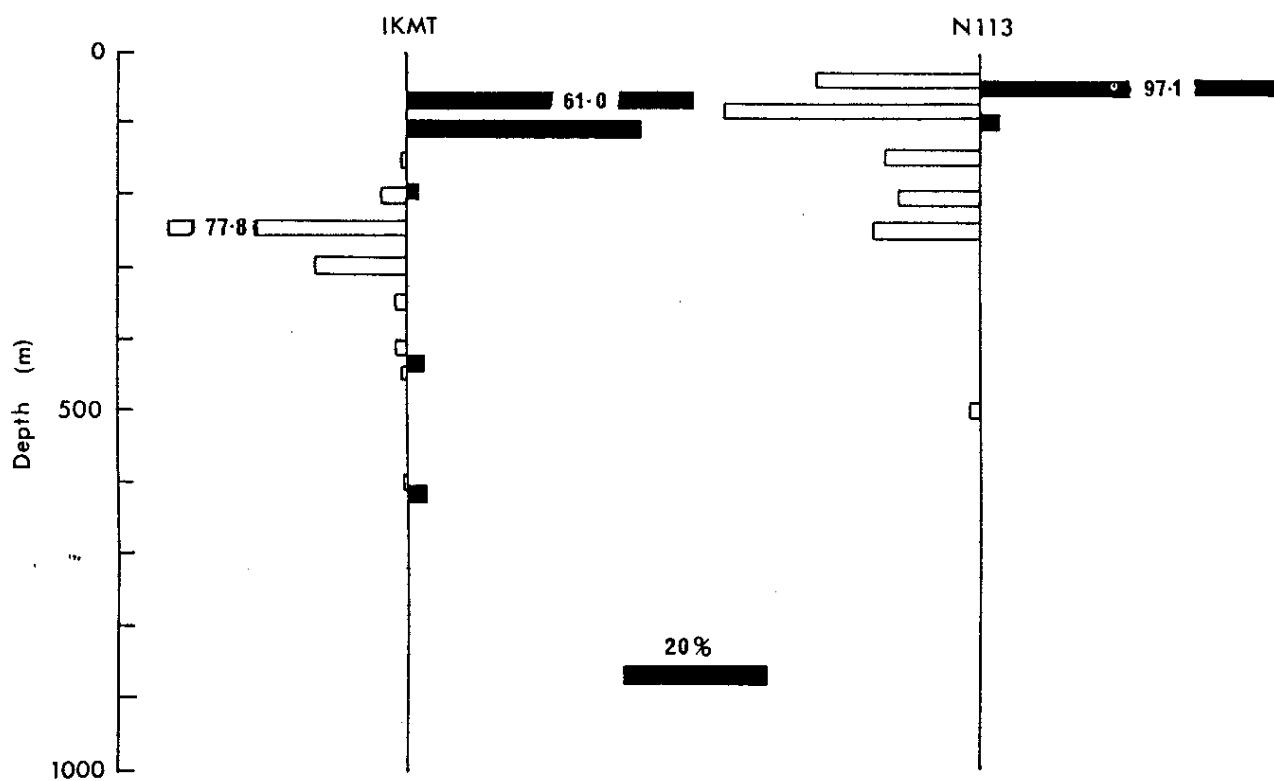


FIG. 23. The depth distribution of *Hippopodius hippocampus* as shown by two series of hauls, using different nets, in the vicinity of the Canary Islands. Percentage of total catch, by day and night (black), found in each haul. Redrawn from Pugh (1974).

pattern of depth change over a 24-h period. Evidence for such a cyclical, sinusoidal pattern of DVM was provided by Pugh (1977). He found that the population of all but one of the migrating species passed slowly through the sampling depth of 250 m, with only the eudoxid stage of *Ceratocymba sagittata* having a rapid, crepuscular DVM.

Such a sinusoidal pattern of DVM, where a single depth range is occupied only at certain times of the day or night, raises problems with the interpretation of the results from day/night series of hauls. In these, although the total depth range of a certain siphonophore species may be sampled, each depth horizon is sampled only once, by day and night, at a time of convenience. Thus Pugh (1974) found that, using two types of net fished at different times, the apparent day/night depth distributions and ranges of DVM for certain siphonophore species, e.g. *Hippopodius hippocampus* (Fig. 23), could vary considerably, particularly during the daytime. These differences can be explained if one assumes that the specific population is undergoing a slow, sinusoidal DVM. Such a pattern emerges if the depth distribution data are plotted according to the time of day at which sampling occurred (Fig. 24). The consistency of the pattern is apparent despite the fact that the nets were not fished over a single 24-h period but at intervals over 47 days.

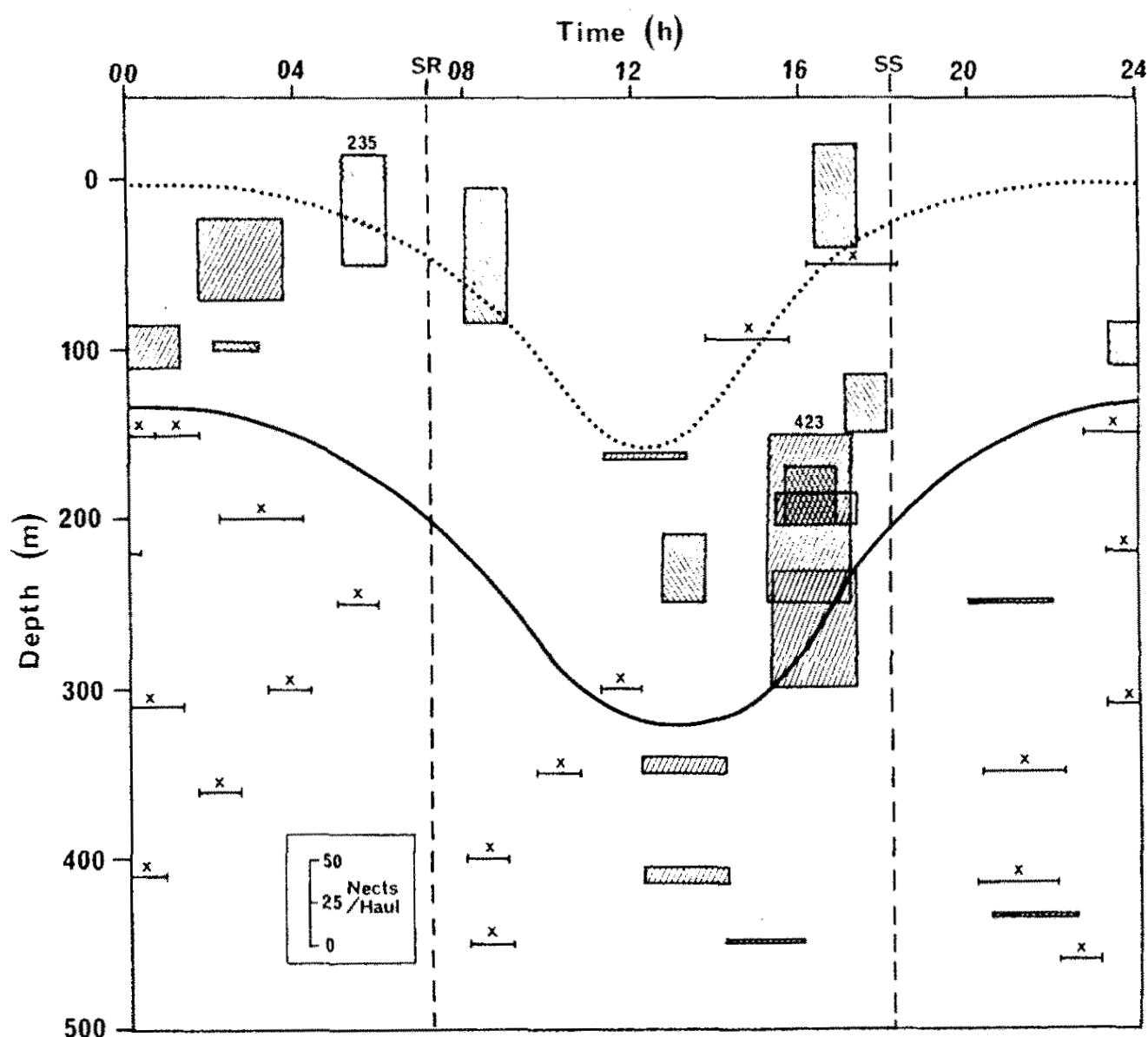


FIG. 24. Possible pattern of diel vertical migration for *Hippopodius hippopus* suggested by plotting data in Fig. 23 according to time at which hauls were made. IKMT N113 The N113 numbers/haul have been multiplied by a factor of 5.

3. Depth intervals of sampling too great

Although Pugh's (1977) results illustrate the sinusoidal pattern of DVM for many siphonophore species, the magnitude or direction of these migrations could not be assessed directly, as sampling was carried out only at a depth of 250 m. An associated day/night series of samples gave such information, but was subject both to the constraints of timing, as discussed above, and to the large depth ranges (100 m) of the sampling horizons. The extent of these horizons can mask any DVM patterns and caused Casanova (1980), for instance, to conclude that very few, if any, siphonophore species undertook such a migration. His data were based on six oblique hauls which subdivided the top 900 m of the water column, with no depth horizon being less than

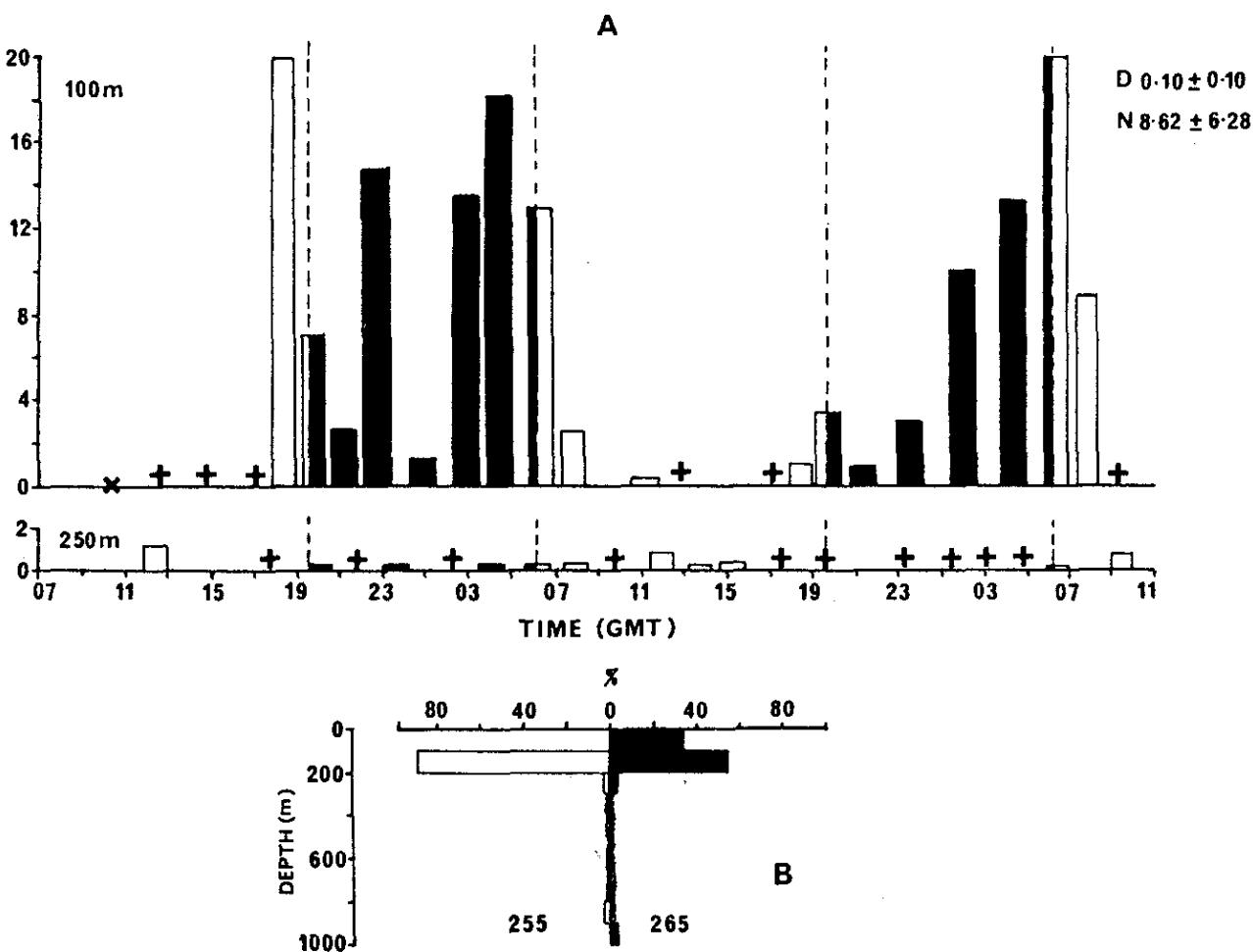


FIG. 25. A Changes in the abundance (nos/ 10^3 m^3) of *Lensia conoidea* at depths of 100 and 250 m during a series of hauls, over a 48-h period, at 44° N , 13° W . \times denotes absence; + denotes $<0.2/10^3\text{ m}^3$. The mean day (D) and night (N) nos/ 10^3 m^3 also are shown.

B The day and night (black) depth distribution of *L. conoidea* shown as percentages of the total numbers in the top 1000 m of the water column (from Pugh, 1984).

100 m. Pugh's (1974) data also indicate a dearth of migrating species, even though the sampling interval was *ca* 50 m, but in both cases the top 100 m was poorly sampled and it is within this range that most small-scale DVMs occur.

Pugh (1984) attempted to look in detail at both the patterns and ranges of DVM for various siphonophore species, as part of a detailed study of the mesopelagic community in the NE Atlantic Ocean at 44° N , 13° W (Roe *et al.*, 1984). Unfortunately the spacing of the four depth horizons (100, 250, 450, and 600 m), which were sampled repeatedly over four separate 48-h periods, was generally too great for such an analysis. Obvious patterns of DVM were noted for certain species, e.g. *Lensia conoidea* (Fig. 25A), but associated day/night series of hauls (Fig. 25B) appeared to show that only part of the population was migrating. The depth range of this migration could not be assessed. Another species, *Vogtia glabra*, had a pattern of

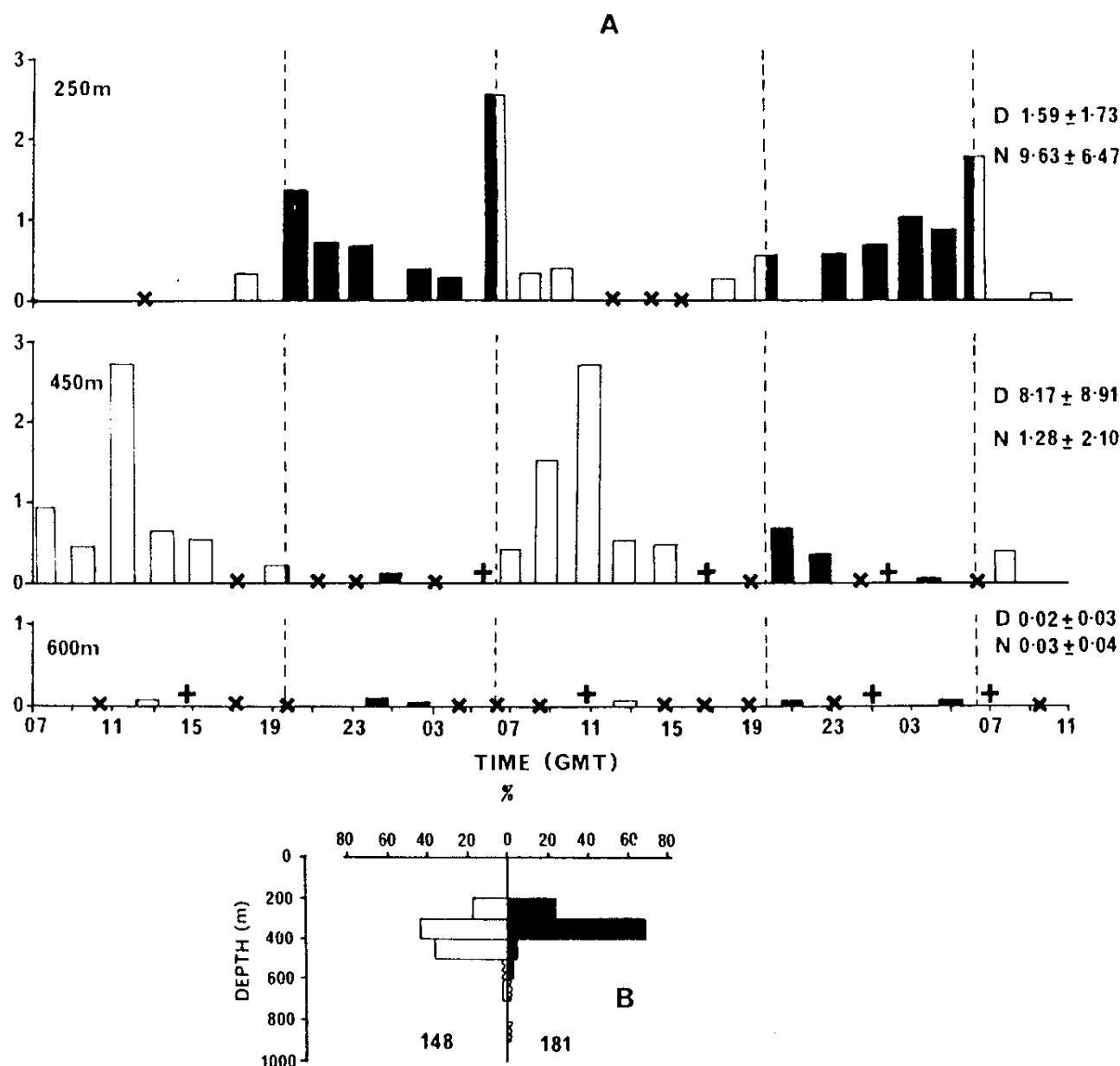


FIG. 26. A Changes in the abundance (nos/ 10^3m^3) of *Voglia glabra* at depths of 250, 450 and 600 m during a series of hauls, over a 48-h period, at 44°N , 13°W . \times denotes absence; + denotes $<0.05/10^3\text{m}^3$. The mean day (D) and night (N) nos/ 10^3m^3 also are shown. From Pugh (1984). B The day and night (black) depth distribution of *V. glabra* shown as percentages of the total numbers in the top 1000 m of the water column.

DVM that encompassed two of the depth horizons sampled (Fig. 26A). The shallower part of the population migrated up to 250 m at night, while the deeper part left the 450 m depth zone. The associated day/night series (Fig. 26B) also indicated an upward migration of the deeper part of the population, but there was little enhancement of the population in the 200–300 m depth range. The data indicate that the entire population of *V. glabra* probably was undergoing a DVM but the extent of this migration for each individual animal might be only of the order of tens of metres.

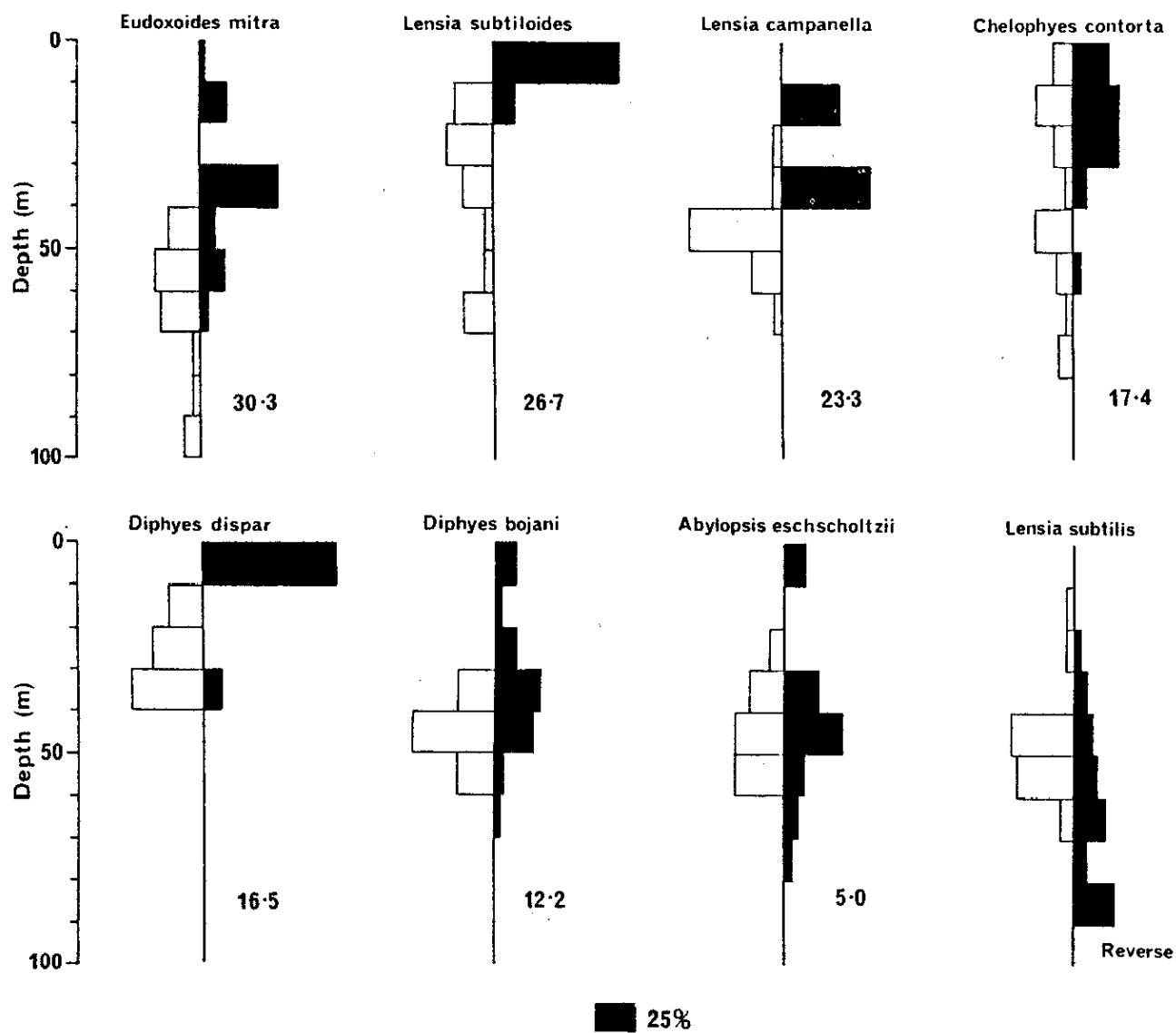


FIG. 27. Vertical distribution of certain siphonophore species in the Sulu Sea, by day (white) and night (black), expressed as percentages of the total numbers in the 0–500 m depth range. The species are arranged in order of their diel vertical migration intensity ($k_{100\%}$). Redrawn from Musayeva (1976).

4. Small-scale DVM patterns.

The above examples serve to illustrate the difficulties in studying the DVM patterns of siphonophores, particularly if such patterns are small-scale such that they become obscured by the sampling programme. Such patterns were shown to occur by Musayeva (1976) in the Sulu Sea. Nets were fished over 10 m depth intervals from the surface to 150 m, and at greater intervals down to 500 m. The problem of sampling time was largely overcome by fishing nets only around midnight and midday but, thereby, no indication of the pattern of DVM could be established. The results (Fig. 27) showed that the intensity of migration, i.e. that proportion of the total population that underwent a DVM, was specifically variable and that the range of the migration was not necessarily extensive, sometimes as little as 10–20 m.

5. Regional differences in DVM for specific siphonophore populations.

One important feature of Moore's (1949, 1953) work in the NW Atlantic Ocean, and Musayeva's (1976) in the Indian Ocean, was the observation that there were regional differences both in the depth distribution and DVM patterns of certain siphonophore species. These differences were correlated with the hydrographical conditions within the various water masses. Moore *et al.* (1953), Moore (1955) and Moore and Corwin (1956) extensively analysed their data and concluded that, for epipelagic siphonophores, there was a good correlation between the depth of the 15 °C isotherm and the lower daytime limit of a specific population. The upper limit of the population, however, was better correlated with the ambient light conditions. At night, Moore (1949) found that variations in depth distribution could be related to the phase of the moon. Musayeva (1976) similarly found that the lower limit of a population nucleus was related to the depth of certain isotherms within the thermocline, and noted that water clarity also was a determining factor. All these data indicated that the deeper the population nucleus the greater was the range over which it was spread (Table 2). The effects of these regional variations in depth distribution on the DVM patterns were specifically variable. For some species the range of DVM remained the same regardless of area, while for others, e.g. *Abylopsis tetragona*, it increased as the mean daytime depth of the population deepened (Table 2).

The temperature structure of the water column, and particularly the depth and intensity of the thermocline, clearly has a marked effect on the depth distribution of various epipelagic siphonophores. Daniel (1977), for instance, showed that only certain species migrated through the thermocline at night while others were restricted to greater depths. The effects of the thermocline varied regionally and this may reflect differences in the intensity of this discontinuity. Hansen (1951) also noted that, in a Norwegian fjord, the DVM pattern of *Lensia conoidea* was restricted to below a discontinuity layer. Although the rapid temperature change in this layer was thought to be responsible, it is more likely that the pronounced halocline, with salinity decreasing to *ca* 20‰ in the surface waters, was the determining factor as siphonophores do not survive in low salinity waters.

It is clear that several siphonophore species, particularly epipelagic ones, undergo some sort of a DVM. This raises the question as to what factors control these migrations and how are the animals able to accomplish them. Since the timing of the DVMs corresponds, generally, with the natural daily light cycle it appears that light is the proximate stimulus for these migrations; the light sensitivity of siphonophores is discussed on p. 173. It is most likely that these migrations are accomplished by active swimming,

but it has been suggested (e.g. Pugh, 1977) that some sort of buoyancy control might play a part. Bidigare and Biggs (1980) demonstrated, for several siphonophore species, that there was an active exclusion of heavy sulphate ions enabling neutral buoyancy to be achieved. However, Mills and Vogt (1984) could find no evidence for diel changes in the ionic composition of certain jellyfish which might have facilitated DVMs. Indeed, Mills (1984) showed that changes in the buoyancy of jellyfish, in response to alterations in the salinity of the medium, were brought about by passive osmotic accommodation, over periods of several hours, and not by active density regulation. She also pointed out that, during an upward migration, the decrease in density at a discontinuity might be of such magnitude that a jellyfish, or indeed a siphonophore, would be unable to swim through it, and would sink back down to where it was neutrally buoyant. It is, therefore, not surprising that the DVM of many gelatinous organisms is restricted by physical discontinuities, such as the thermocline.

F. Siphonophores and Deep-scattering Layers

Barham (1963) first drew attention to the association of physonect siphonophores with deep-scattering layers (DSL), whilst describing some direct observations from a submersible. The size of the gas bubble in the pneumatophore of these physonects, identified as *Nanomia bijuga*, was found to be within the range for a perfect resonator at 12 KHz. If these animals are to be major contributors to DSLs then clearly their DVM patterns must match those of the DSLs, with rapid depth changes over the crepuscular periods. Barham (1963, 1966) considered that *N. bijuga* met all such prerequisites as specimens exhibited a fast and directioned swimming behaviour, and any DVM also could be facilitated by regulation of the pneumatophoral gas volume. This might also be the case for rhizophysid cystonect siphonophores, which have no other means of locomotion. Expanding gas could be vented from the apical pore during upward migration.

Barham (1966), during a series of submersible dives over dawn and dusk periods, observed 108 specimens of three types of physonect siphonophore, of which 94 were associated with a DSL. It is unfortunate that specimens were not collected for identification as, in the present state of our knowledge, *Nanomia* spp. are the only physonects to possess an apical pore. Other species, lacking such a pore, might experience great difficulty in regulating their float volume during rapid DVMs (see Pugh, 1983). This may relate to the observations of Pickwell *et al.* (1970) that not all of the physonect population underwent a DVM in association with the DSL. However, they concluded that the energetics of gas secretion might be a controlling factor.

They associated the "fade-out" and "fade-in" of the sound scattering signals during the post dawn period with the compression of the pneumatophore during the descent phase and its subsequent expansion due to gas secretion.

Several authors, e.g. Voronina (1964), Alvariño (1967b), and Daniel *et al.* (1969), have noted, using nets, an increased biomass of siphonophores at the depths of certain DSLs. However, in the latter case at least, physonect siphonophores were rarely caught and so, as Kinzer (1969) pointed out, such an enhancement in biomass is not necessarily relevant unless it is reflected by an increase in the number of potential scatterers. Nonetheless, the fragility of physonect specimens means that they are poorly sampled by nets, and Pickwell *et al.* (1970) noted a marked disparity between the population of animals netted at the depth of or observed in a DSL.

McCartney (1976), amongst others, has calculated that a population of fish, with the right-sized swim-bladders, at densities of 1 per 10–10 000 m³ of water would produce sufficient acoustic scattering to generate a DSL. Since the pneumatophore is such a good resonator it is probable that the density of physonects need only be at the low end of this scale if they are to make a significant contribution to such a layer. Nonetheless, Barham (1963) noted concentrations of *Nanomia bijuga* as high as 0.3/m³, and Rogers, Biggs and Cooper (1978) found *N. cara* at densities up to 8/m³ in a dense scattering layer near the bottom of the Gulf of Maine. These animals repeatedly clogged trawl nets. In recent years siphonophores have received barely a mention in studies on DSLs, e.g. "Oceanic Sound Scattering Prediction" (Andersen and Zahuranec, 1977), despite their clear potential as significant contributors to such layers.

G. Seasonal Changes in Abundance

Most studies on the seasonal change in abundance of zooplankton, including siphonophores, have for logistic reasons been carried out at near-shore stations and investigations in the open ocean are rare. However, easy access to deep water enabled Moore (1949, 1953) to make detailed studies in the region of Bermuda and in the Florida Current, sampling the top 250 m of the water column up to 19 times in a year. Around Bermuda, Moore (1949) found that less than half of the siphonophore species present showed any seasonal change in abundance. Most of these species reached maximum numbers in winter, e.g. *Bassia bassensis* (Fig. 28), but some had maxima at other seasons depending on the year of sampling. Certain species, e.g. *Hippopodius hippopus* and *Eudoxoides spiralis*, also showed seasonal variations in their depth distribution. Despite the apparent stability of the area, Moore found considerable horizontal variability in the distribution of the

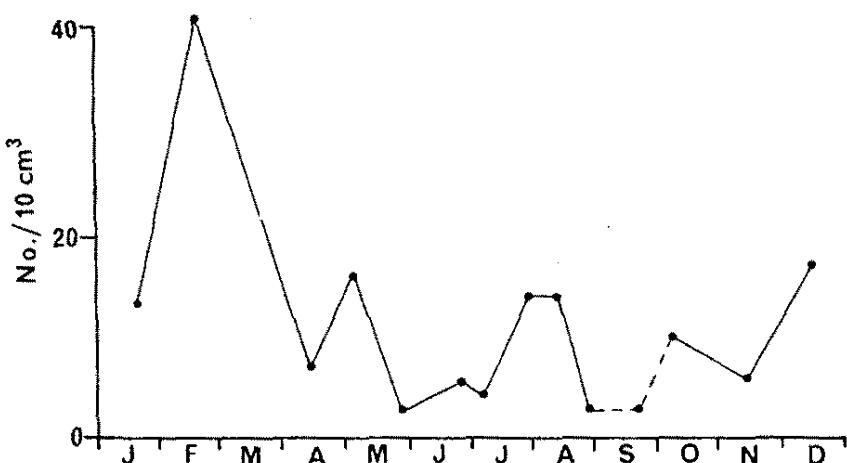


FIG. 28. Seasonal variations in the abundance of *Bassia bassensis* in the vicinity of Bermuda. Redrawn from Moore (1949).

animals, and seasonal changes in hydrographical conditions. He concluded that a false impression of seasonality in a specific population could be generated by local winds or currents transporting differing plankton populations through a single sampling site. Thus localized peaks in biomass (displacement volume) were found at various stations during spring and autumn, but for the whole study area Moore concluded that there were no seasonal changes in biomass. However, in the same region, Menzel and Ryther (1961) found a zooplankton biomass peak in spring, while Deevey (1971) found peaks of numerical abundance in October and April, for the top 500 m of the water column, with a single peak of biomass in April. Deevey noted maximum numbers of siphonophores in April but she did not study the seasonal variations of the individual species.

Seasonal changes in the hydrological conditions in the Florida Current had an even more marked effect on the specific siphonophore population. Moore (1953) found that there was a significant correlation between the abundances of *Diphyes dispar* and *Chelophyses appendiculata* and the presence of Gulf of Mexico water during the spring and summer; and of *Eudoxoides spiralis* and Yucatan Channel water during the autumn and winter. Short-term variations in the hydrography complicated the situation further. Lewis *et al.* (1962), and Lewis and Fish (1969), who made twice-monthly surface tows for two years close to Barbados, also concluded that true seasonal changes in the zooplankton population were masked by much greater changes in the hydrography of the waters entering the Caribbean at various times of the year (Fig. 29). Similarly, changes in water masses associated with the monsoon seasons greatly affected the occurrence of *Diphyes chamissonis* and other siphonophore species in the Singapore Straits (Wlekstedt, 1958) and the Great Barrier Reef (Russell and Colman, 1935).

One of the few studies on seasonality of siphonophores in open-ocean,

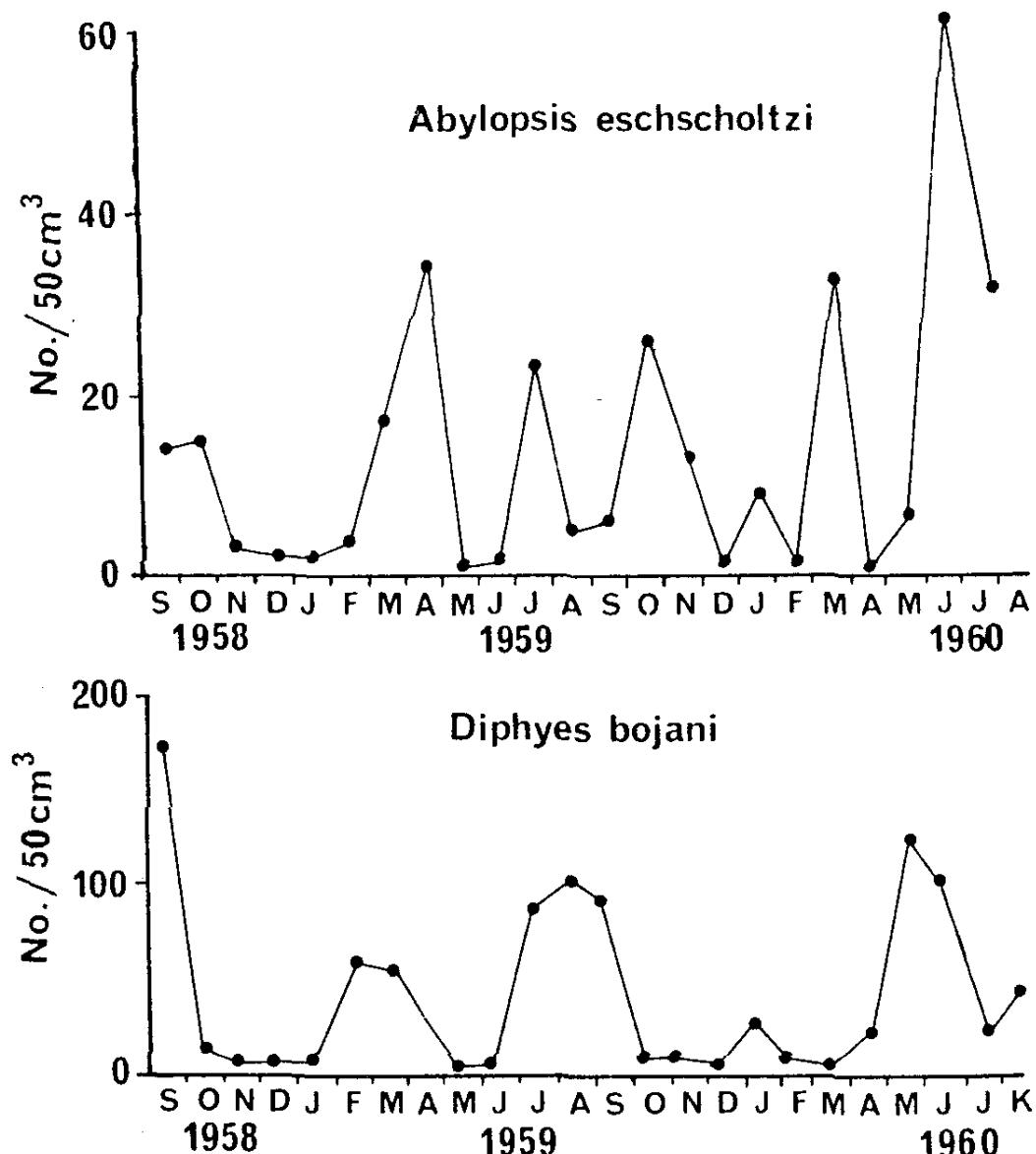


FIG. 29. Seasonal variations in the numbers of eudoxids of *Abylopsis eschscholtzi* and *Diphyes bojani* at the surface in the vicinity of Barbados. Redrawn from Lewis and Fish (1969).

temperate regions, where large seasonal fluctuations in temperature and primary productivity are expected, was made by Williams and Conway (1981). At a station in the NE Atlantic (59° N, 19° W) they fished two types of net at ca 7–14-d intervals. Although the medusa, *Aglantha digitale*, dominated the coelenterate population, three siphonophore species, *Dimophyes arctica*, *Nanomia cara* and *Lensia conoidea*, together showed a marked seasonal change in abundance with maximum numbers during May and June (Fig. 30A) and low numbers for the rest of the year. Seasonal changes in depth distribution were apparent for *D. arctica* and *N. cara* (Fig. 30B, C).

At inshore sites in temperate regions, the seasonal fluctuations in the presence of certain siphonophore species often have been used to indicate water mass changes or current movements. Corbin (1947) and Southward (1962) reviewed the many earlier records for the seasonal distribution of

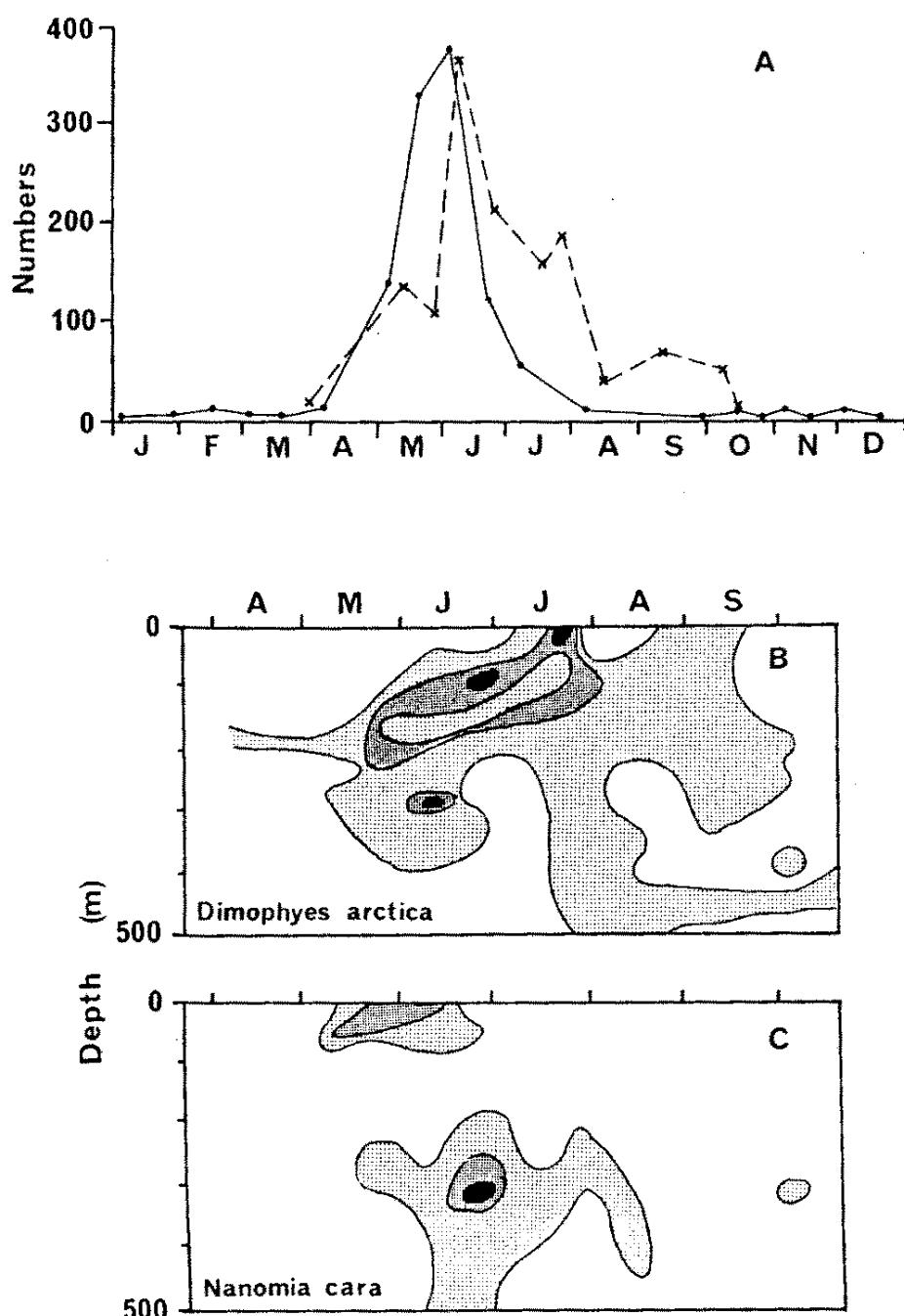


FIG. 30. A Seasonal variations in abundance of total siphonophores at 59° N, 13° W. (●—●) from LHPR Samples (0–500 m). (×—×) from Hensen net hauls (0–100 m). B and C. Vertical distribution and seasonal abundance of *Dimophyes arctica* (B) and *Nanomia cara* (C) at 59° N, 13° W. Contour levels 1, 2 and 4 individuals/10 m³. Redrawn from Williams and Conway (1981).

Muggiaeae spp. in the English Channel and concluded that *M. atlantica* was a south-western, warm water species. However, they cautioned against considering it as an indicator of water movements because of its facility for rapid reproduction. Nonetheless, Southward (1962) concluded that its appearance in the English Channel could be associated with the intrusion of high salinity water from the south-west entrance, although Corbin (1947) noted that it could be brought into the area in association with some lower salinity water from the region of Ushant.

The most detailed studies on the seasonality of siphonophore populations are all for inshore localities, particularly in the Mediterranean Sea and the NW African coast. Unfortunately, even more than in the open ocean, it is not always clear whether the apparent seasonal fluctuations represent the population dynamics of the individual species or hydrographical changes that bring totally different populations to the study area. This is clearly illustrated by the work of Furnestin (1957) along the Atlantic coast of Morocco. She found that over 80% of the siphonophore population sampled was of oceanic origin and that increased numbers both of individual species and of the population as a whole occurred during the spring and summer when warm, saline off-shore waters, moving in a northerly direction, spilled over onto the continental shelf. Correspondingly when these waters retreated in autumn and winter there was a decline in the inshore population. Only one of these oceanic species, *Chelophyses appendiculata*, spilled over into the eulittoral zone (< 60 m depth). In contrast, the neritic species *Muggiaeae atlantica* was found almost exclusively in that zone and reached a maximum abundance in spring, but only in the northern sector.

The effects of seasonal changes in hydrography at inshore stations also become apparent if one compares the results of Cervignon (1958) and Vives (1966) for the Castellon coast of Spain; Razouls and Thiriot (1968), Banyuls-sur-Mer; Patriti (1964), Gulf of Marseille; Leloup (1935), Villefranche-sur-Mer; and Ianora and Scotto di Carlo (1981) for the Gulf of Naples. Although these sites span only a few hundred miles of the northern Mediterranean coastline, there is little concordance between the seasonal changes in the siphonophore populations found at each. Presumably the variations in the coastline aspect result in different hydrographical responses to similar weather patterns. For instance, Patriti (1964) noted that *Lensia conoidea* and *L. meteori* were upwelled into his study area after a Mistral. In general, the advection of superficial oceanic waters, particularly during the summer, brought inshore such species as *Chelophyses appendiculata* and *Eudoxoides spiralis*, while during the winter neritic species, e.g. *Muggiaeae kochi*, *Sphaeronectes irregularis* and *L. subtilis*, predominated. One notable exception was the predominance of *M. atlantica*, during January to June 1966, at Banyuls-sur-Mer (Razouls and Thiriot, 1968), while numbers of *M. kochi* were low. This may have been brought about by an incursion of the Moroccan coast population, which became entrained in the superficial current flowing in through the Straits of Gibraltar, as suggested by Furnestin (1957). However, there may be a permanent population of this species in the western Mediterranean (see p. 153). In addition, Bernard (1955), who studied the seasonal distribution of zooplankton in the Bay of Algiers, found only what he termed "cold-water" species, e.g. *Abylopsis tetragona*, *Chelophyses appendiculata* and *Eudoxoides spiralis*, in the southerly branch of this current.

Other detailed studies on the seasonal changes at inshore localities in the Mediterranean include those of Hure (1955) and Gamulin (e.g. 1979) for the Adriatic Sea. In the shallow northern waters (< 50 m depth) *Muggiae kochi* dominated the population throughout the year. As the water depth increased, to the south, other species, e.g. *Eudoxoides spiralis*, became abundant, but their seasonal distribution was erratic without any consistent abundance peaks. The oceanic species, *Chelophysa appendiculata*, occurred only in the southern sector during the autumn and winter.

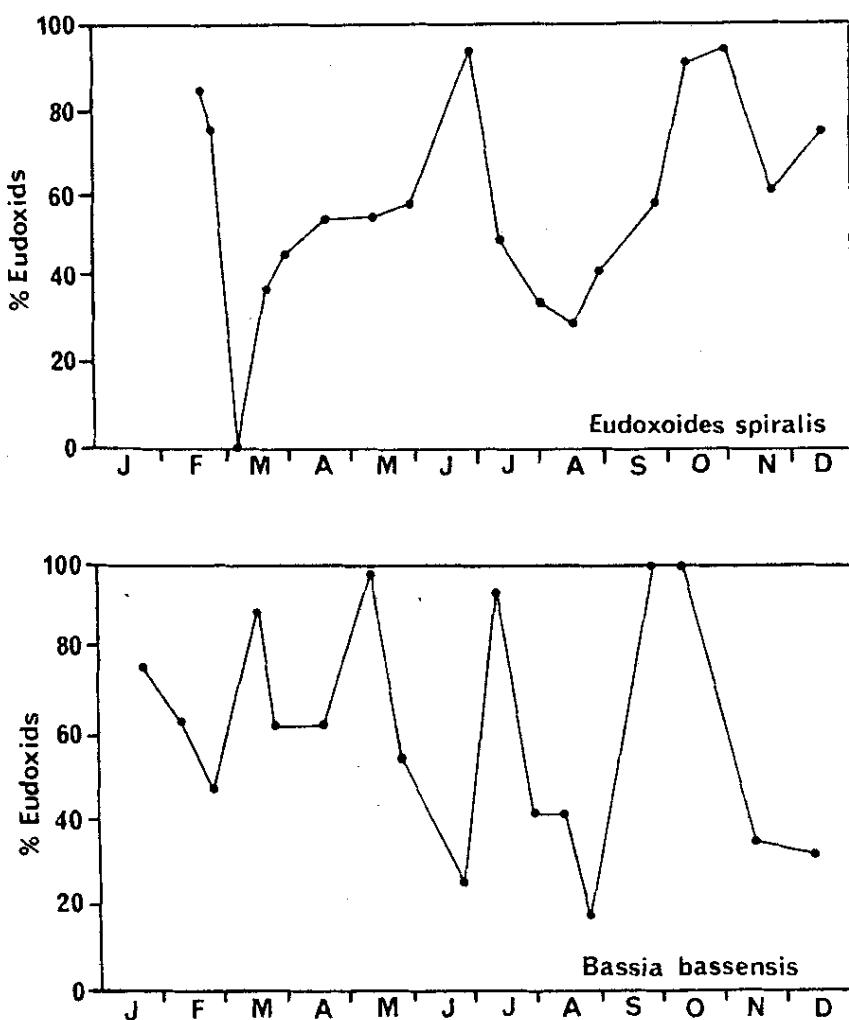


FIG. 31. Seasonal variation in the percentage ratio of the polygastric and eudoxid stages of *Eudoxoides spiralis* and *Bassia bassensis* in the vicinity of Bermuda. Redrawn from Moore (1949).

1. Life cycles

Moore's (1949, 1953) data indicated that there was a cyclical change in the relative abundance of the polygastric and eudoxid (sexual) stages for certain siphonophore species, and that the frequency of these cycles was specifically variable. In the Bermuda region, *Eudoxoides spiralis* (Fig. 31) went through three such cycles each year, while *Bassia bassensis* (Fig. 31) and *E. mitra* had

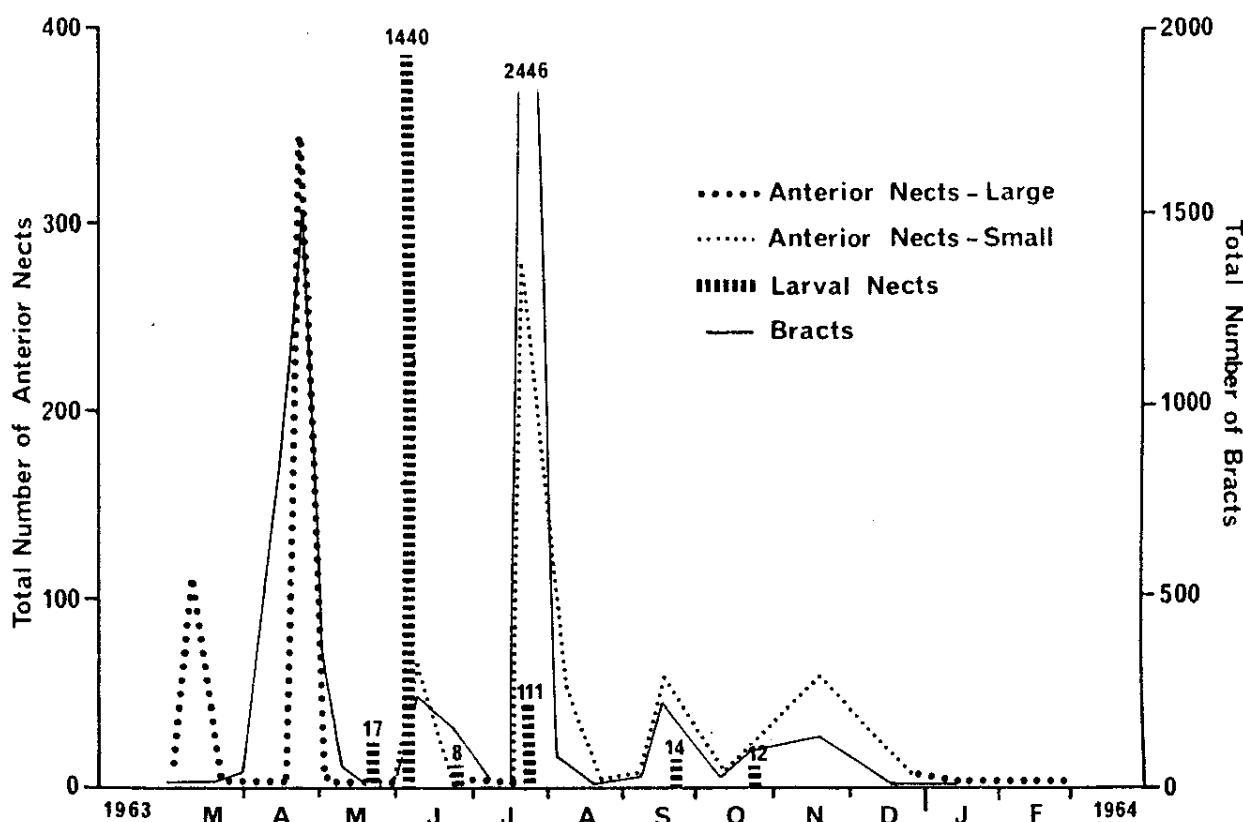


FIG. 32. Seasonal variations in the number of various development stages of *Chelophyes appendiculata* in the Gulf of Marseille. Redrawn from Patriti (1964).

five. Moore suggested that these cycles might be indicative of the life span of each generation but this is difficult to validate as there is little information on this subject. Nonetheless, such information is fundamental to an understanding of the seasonal cycles of siphonophores.

Mills (1982) studied the seasonal change in abundance and vertical distribution of zooplankton in Saanich Inlet, British Columbia, over two consecutive years. This is a relatively closed-system temperate fjord and so not subject to large fluctuations in the hydrological conditions, although showing the usual seasonal variations in temperature and salinity. Mills found that the eudoxid, sexual stage of *Dimophyes arctica*, one of the commonest siphonophore species present, reached maximum numbers during April and early May (130–180 m depth range), while its nectophores were most abundant between May and August (75–130 m depth range). This could indicate that a new generation of nectophores was being developed from the fertilized eggs produced by the sexual stage and, thus, that the species underwent one major reproductive cycle each year. Another common species, *Muggiae atlantica*, whose vertical and temporal distribution largely was separated from that of *D. arctica*, appeared to go through two generations annually. Again, and for both cycles, the eudoxid stage tended to reach peak numbers before the polygastric stage.

Patriti (1964) investigated the reproductive cycles of siphonophores in the

Gulf of Marseille. In the case of *Chelophyses appendiculata*, he recognized three types of nectophore which represented different stages in the development of the polygastric form. Thus the larval nectophore was replaced by a small, definitive anterior nectophore (5–10 mm in height) that subsequently enlarged to *ca* 20 mm in height at the time when the posterior nectophore was developed. He showed that the abundances of these three types of nectophores, and of the eudoxid stage, varied seasonally (Fig. 32), and he conjectured that the population of *C. appendiculata* remained neritic throughout the year and underwent two main reproductive cycles. However, bearing in mind the frequent changes in the hydrographical conditions at such inshore stations (see above), this conclusion is open to doubt. For instance, there must have been some reseeding of the inshore population at the beginning of the year in order to give rise to the peak numbers of the fully developed polygastric stages observed then. Also the rapid disappearance of these stages in early May, after the release of the eudoxids, need not indicate their death but could represent a return of the population to the open ocean, as Patriti himself noted. Patriti's data suggested that the larval nectophore was developed approximately seven weeks after fertilization occurred, and that the anterior nectophore appeared after another similar period. Although detailed studies of the development of this species have not been made recently, Carré (1967) found that in other diphyid species, e.g. *Lensia conoidea*, these developmental processes took about one and two weeks respectively. It can only be concluded that there is still much to learn about the longevity, reproductive cycles and seasonality of specific siphonophore populations.

V. Physiology and Behaviour

A. Behaviour

Because of the difficulty of making behavioural observations in the natural habitat most of what we know on the subject of behaviour and coordination has been gained from laboratory studies made under somewhat artificial conditions. Observations from submersibles (e.g. Barham, 1963, 1966; Rogers *et al.*, 1978; Pugh, 1983; Mackie, 1985) and by SCUBA (e.g. Biggs, 1977a; Purcell, 1981c) are, therefore, especially valuable as they provide a body of information regarding the animals' natural activities against which laboratory generated ideas of behaviour can be checked. Studies in the laboratory work best with small species which are not as seriously constrained by the holding tanks as larger animals. Given regularly replenished seawater at the appropriate temperature, dim light and a supply of food,

some siphonophores will feed, grow and even reproduce in a normal way and their behaviour can then be studied with assurance that it represents normal activity (Bigelow, 1891; Mackie and Boag, 1963; Purcell, 1982).

1. Sensitivity to external stimuli

Since the first report of nerve cells in the stem of *Physophora* by Claus (1878) and of sense cells, also in the stem, by Korotneff (1884) neural and sensory elements have been found throughout the ectoderm of most regions. Special sense organs (ocelli, statocysts etc.) are not present and the palpons, once regarded as specialized tactile organs, are no more sensitive than other regions. Some regions lack nerves completely but are still excitable owing to the presence of impulse-conducting epithelia. One way or another, the whole surface is sensitive.

Touch-sensitivity is widespread. The responses evoked may be local, or they may spread throughout the organism via nervous or epithelial pathways. In addition to responding to direct contact some species appear sensitive to water-borne vibrations (Bone and Trueman, 1982). The receptors involved have not been identified with certainty, but vibrations can be seen to cause quivering movements in the velum. This would be expected to agitate sense hairs in the nerve rings which lie at the base of the velum (Mackie and Carré, 1983).

Light is undoubtedly important in the life of many siphonophores but there is little precise information on the subject. Sudden illumination of dark-adapted specimens in the laboratory can induce locomotion, but turning off the light has no obvious effect (Mackie and Boag, 1963; Mackie and Carré, 1983). In *Nanomia*, stem activity is controlled by two sets of nerves, both of which are photoexcitable. The photosensitive elements are not distributed evenly, for the light must be directed upon the siphosome for locomotion to take place (Mackie, 1964). Experiments with strong light beams and sudden changes in illumination may have little relevance to the behaviour of the animals in nature, and must be interpreted with caution.

The diurnal migrations of siphonophores are probably brought about by active swimming (Barham, 1963; Mackie and Mills, 1983) and it seems probable that changes in light intensity trigger the process. Ocelli are not present which suggests that the nerves themselves may be the photosensitive elements, as in certain hydromedusae (Anderson and Mackie, 1977). Observations from a submersible suggest that *Nanomia cara* is sensitive to changes in light intensity at levels as low as $10^{-8} \mu\text{W}/\text{cm}^2$ (Mackie, 1985). The calycophore *Hippopodius* has been found to aggregate in illuminated parts of a laboratory tank. Changing the position of the light window led to

reaggregation at the new site within about an hour. These movements are best ascribed to orthokinesis (Mackie and Boag, 1963).

In several species light clearly regulates feeding activities. Observed in the laboratory over a 48-h period. *Rhizophysa eysenhardti* was found with tentacles extended during the day and contracted at night (Purcell, 1981a). Such changes are related only to illumination, not to the time of day *per se*. Extension takes place within 1.5 min of illumination. Evidence from stomach content analysis suggests that this species feeds only by day and this also appears to be true in the case of *Rosacea cymbiformis*, but *Agalma okeni* feeds at night. Four other species investigated showed no light-induced behavioural changes (Purcell, 1981a).

There is evidence for chemosensitivity in several siphonophores. Gastrozoids show writhing "searching" movements in the presence of food (Kölliker, 1853), a response which can be evoked either by addition of food juices to the water or by tactile or electrical stimulation of the tentacles (Mackie and Boag, 1963). It is possible that tactile stimuli work indirectly by causing a release of a chemical (e.g. from discharged nematocysts) which then diffuses through the water to the receptor sites. Alternatively the response might be spread by nerves running in the tentacles. In *Nanomia* the response can spread slowly along the stem from one gastrozoid to the next. Ebbecke (1957) observed what may be a similar response in *Diphyes sieboldi* (*Chelophyses appendiculata*) where contractions spread from gastrozoid to gastrozoid with a 0.5 s latency. Whether propagation is chemical (through the seawater) or nervous is unclear, as no one has recorded electrically from the stem while the response is in progress. In *Physalia*, Lenhoff and Schneiderman (1959) were able to evoke the generalized feeding response in isolated gastrozoids by addition of fish juices or of 10^{-5} M reduced glutathione to the water. *Nanomia* also responds to reduced glutathione (Mackie and Boag, 1963). It would be of interest to ascertain whether chemosensitivity plays a more specific role in food capture. Cystonects and probably most siphonophores are quite selective in their feeding (e.g. Purcell, 1981c, 1984a) and might discriminate partly on the basis of chemical cues.

2. General activities

Between swimming episodes siphonophores hang in the water for lengthy periods with stem and tentacles relaxed in a variety of fishing postures (see Section V.D) but even during these relatively quiescent periods various activities are going on. Immature nectophores pulsate spontaneously (Steche, 1907; Mackie, 1960b) like embryonic hearts. In physonects and cystonects, but apparently not in calycophores, the tentacles contract rapidly and lengthen again slowly in a regular rhythm likened by Vogt (1854) to the

casting of a fisherman's line. In *Physalia*, Parker (1932) observed contractions every $30\text{--}75\text{ s}^{-1}$. Mackie (1960b) noted that the frequency depended on the pre-existing state of contraction of the tentacle with periodicities in the range $5\text{--}10\text{ s}^{-1}$ in the case of a small tentacle when contracted, declining to $10\text{--}17\text{ s}^{-1}$ when more extended.

Rhythmic peristaltic contractions occur in the stem, gastrozooids and palpons in association with the mixing and flushing to-and-fro of digested materials (Willem, 1894; Mackie and Boag, 1963). Transport within the canal system probably depends heavily on these movements for, although the endodermal cells lining the central canal are ciliated, many parts of the colony lie at a considerable distance from the gastrozooids. The flushing or tidal cycles of different zooids generally have periodicities in the range of 30–90 s. These activities are not synchronized, although local groups of zooids may fall temporarily into alternating rhythms. In this respect, siphonophores resemble hydroids such as *Cordylophora* where the peristaltic activities are independent, in contrast to *Tubularia* where they are synchronized. Spontaneous contractions of tentacles occur independently of the contractions of the zooids they spring from. Thus, these rhythmic movements cannot be equated with tubularian "concerts". While the writhing, searching movements of gastrozooids are typically a response to the presence of food, waste elimination from the tips of palpons occurs as a modification of the regular flushing cycle.

Gas bubble elimination from the float is sometimes seen in physonects and may occur rhythmically (Jacobs, 1937) but how the process is regulated is not understood. Dramatic rolling movements are performed by *Physalia* in calm water conditions. The float rears up and rolls over, then back again. Wilson (1947) suggests that this activity keeps the float moist. Another proposal is that the rolling represents repeated attempts by the animal to adopt the curved sailing posture, in which the crest is held erect. In the absence of sufficient wind, this posture is unstable, and the float flops back on its side again (Totton, 1960). The righting movements which follow the rolling phase consist of seven or eight discrete contractions (Mackie, 1960a). The float contracts when exposed to air currents from a bellows (Bigelow, 1891) or when splashed with water (Wilson, 1947). One consequence of this contraction is that the crest on top of the float becomes erect as a result of gas entering the dorsal processes of the pneumatostaccus, or inner tube of the float.

3. Protective responses

Most siphonophores have contractile stems which shorten when touched. Contractions are graded in intensity and distance of spread according to the strength of the stimulus. The gastrozooids and palpons may also contract,

and escape locomotion sometimes takes place (see p. 178). Some Calyco-phora (e.g. *Chelophyes*, *Hippopodius*) seem able to change their specific gravity (Jacobs, 1937), with the result that they sink, though this response still needs critical evaluation. Better evidence exists in the Physonectae, some of which (e.g. *Nanomia bijuga*) can definitely release gas from the float when disturbed and so sink in the water column (Jacobs, 1937). Very young *Physalia* are probably capable of the same response (Eschscholz, 1829; Agassiz and Mayer, 1902) but claims that adult *Physalia* can exhibit this behaviour (Haeckel, 1888) are probably groundless. Forms of autotomy serving for defence are considered below (see p. 189).

Hippopodius shows a remarkable set of responses following stimulation, all of which are most plausibly explained in terms of protection (Mackie and Mackie, 1967; Mackie, 1976a; Bassot *et al.*, 1978). The responses are all mediated by impulses propagated in the excitable epithelia of the nectophores. Stimulation of the exumbrella leads to:

- (1) Involution of the margin of the nectosac. This response, comparable to "crumpling" in medusae, is brought about by contraction of the radial muscles running in the velum and subumbrella. The rolling in of the delicate tissues at the margin would prevent laceration in case of contact with planktonic crustaceans.
- (2) Blanching of the outer surface of the nectophores. Passage of impulses in the exumbrellar epithelium is followed in the space of a few seconds by opacification of the outer surface. Transparency is resumed gradually after several minutes if there is no further stimulation. Korotneff (1884) attributed the opacity to Brownian movement of epidermal granules and Chun (1897b), Dubois (1898) and Iwanzoff (1928) also held that the reaction was produced in the epidermis. However, Mackie and Mackie (1967) confirmed the earlier view of Kölliker (1853) that blanching is caused by the sudden appearance of light-scattering granules in the mesogloea underneath the epidermis. The only other siphonophore known to be capable of reversible opacification is *Ceratocymba* (Chun, 1888) though several species show permanently opaque regions, e.g. *Heteropyramis maculata* (Totton, 1965a). The mechanism of blanching is mysterious. The granules can be made to appear and disappear in isolated pieces of mesogloea lacking an epithelial covering by pH changes or by changes in the concentration of Ca^{2+} in the external medium. Under the electron microscope the granules are seen as blobs of amorphous material, probably protein. Blanching would serve a defensive role by making the animal loom up suddenly as a large, frightening, opaque object in a place where nothing was visible previously. By averting contact, the siphonophore would minimize damage to its delicate exumbrellar epithelia.

- (3) Secretion. Impulses invade the endoderm and excite the gland cells of the rete mirabilis, an expanded region of the ventral radial canal of each nectophore. The cells swell up like mulberries and discharge a proteinaceous secretion product which might be an alarm pheromone or a toxic or distasteful substance. Secretion is unusual in appearing to be constitutive (not involving the Golgi apparatus) rather than regulatory (Kelly, 1985).
- (4) Exumbrellar light emission. When, following stimulation, a series of impulses cross the exumbrellar epithelium each impulse after the first three produces a flash of light. Korotneff (1884) pointed out that the effect of luminescence seen at night is similar to that of blanching seen by day. The animal looms up suddenly out of nowhere as a large dismaying, or blinding object. Dubois (1898) located the luminescence to the exumbrellar epidermis and this has been confirmed experimentally (Mackie and Mackie, 1967; Bassot *et al.*, 1978). Prolonged stimulation gives rise to lengthy bursts of impulses and sustained flashing. Not all regions luminesce equally and the active area can shift during a single luminescent episode even though the excitatory impulses spread uniformly.

The response seems to need 'priming' (*amorçage*), possibly owing to a requirement of the photoprotein for a certain amount of calcium, which builds up with each impulse to the critical level for photogenesis (Bassot, 1979). Depletion of free intracellular photoprotein would then lead to failure of light emission after a few flashes. However, it is still not clear why the response is so patchy, nor why the active region spreads progressively across the epithelium "as if by contagion" (Bassot, 1979).

4. Locomotion

Cystonectae. *Rhizophysa* and *Bathyphysa* can writhe about in the water by repeated contraction and relaxation of the stem (Biggs and Harbison, 1976), but neither they nor *Physalia* can swim in the usual sense. Earlier suggestions that *Bathyphysa* can swim by contracting the wing-like ptera of its younger gastrozooids appear to be unfounded (Biggs and Harbison, 1976). Small nectophores are present in the gonodendra of both *Physalia* and *Rhizophysa*. They are thought to create water currents around the gonophores, keeping them well oxygenated especially after the gonodendra detach from the parent colony. *Physalia* is blown about by winds at the surface, a process which it actively assists by adoption of the sailing posture (Totton, 1960).

Physonectae. While most physonects swim by means of nectophores, some species are reported to swim by means of their bracts. *Athorybia rosacea*,

which has no nectophores, can simultaneously contract and lower its bracts in unison (Kölliker, 1853; Keferstein and Ehlers, 1861; Totton, 1965a). However, Biggs (1977a) who observed this siphonophore in the sea makes no mention of such behaviour and it is doubtful that the movements are important in locomotion. "*Nectalia loligo*" (an agalmid larva, see p. 105) was described by Haeckel (1888) as the most rapidly swimming physonect. It swims with its nectophores but can also lower and raise its bracts, which Garstang (1946) suggested function as leeboards.

Benthic siphonophores (Fam. Rhodaliidae), such as *Dromalia*, tether themselves to the bottom by means of their greatly extended tentacles. Observations from a submersible (cited by Pugh, 1983) suggest that these siphonophores can 'walk' along the bottom by detaching and reattaching their tentacles.

Nectophoral locomotion is best known for *Nanomia cara* (Fig. 33). This species can swim in three principal ways (Mackie, 1963, 1964):

- (a) Synchronous forward swimming. This follows stimulation of the siphosome and can be regarded as a rapid escape response. The nectophores all contract together for one or two pulsations. Velocity is estimated at 20–30 cm/s.
- (b) Asynchronous forward swimming. This is shown by animals during their spontaneous periodic swimming bursts. The nectophores contract more or less independently, and the velocity is only 8–10 cm/s. Sometimes the two sides of the column of nectophores fall into an alternating rhythm, producing a zig-zag type of movement.
- (c) Reverse swimming. This is evoked by tactile stimulation of the float or anterior nectophores and presumably serves for escape. Reversal of the locomotory jets (Fig. 33) is achieved by contraction of radial muscles around the velar openings during swimming.

While there is little information on other physonects, *Halistemma rubrum*, *Agalma elegans* and *Forskalia edwardsi* are all capable of bidirectional locomotion. *Physophora hydrostatica*, a short-stemmed physonect, appears incapable of reverse locomotion and some long stemmed forms, such as *Cordagalma*, also can swim in only one direction. Table 5 summarizes information on swimming velocities.

During asynchronous forward swimming, *Agalma okeni* rotates in the counter-clockwise direction. It is not clear exactly how this is achieved but Biggs (1977a) suggests that it is due to alternating contractions in different blocks of nectophores.

Calycophorae. All species show spontaneous swimming. Periodic bursts of activity serve to spread the fishing net in the 'veronica' style in *Muggiaeae*

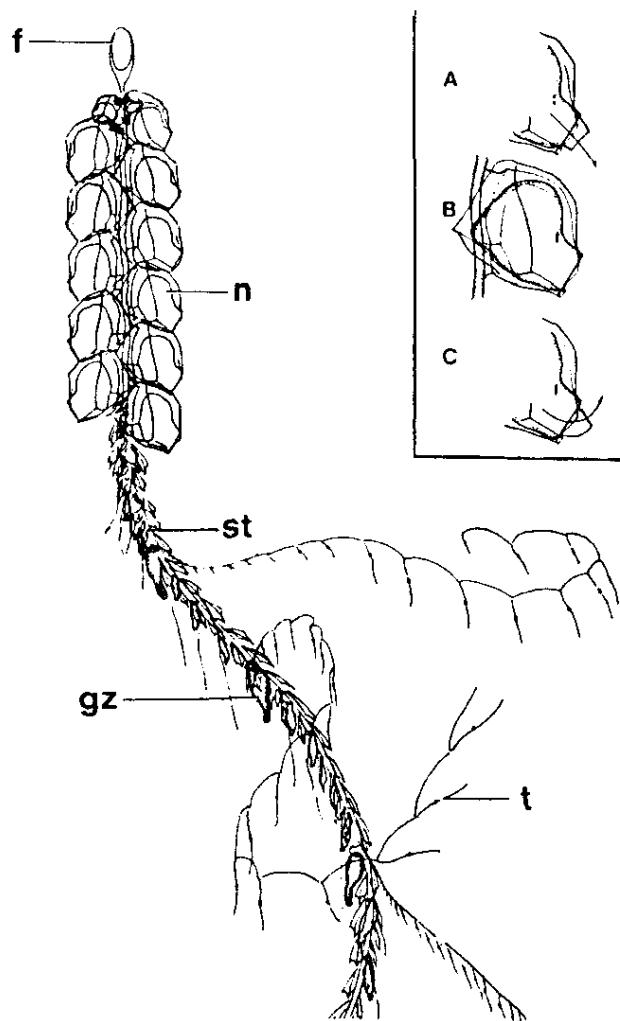


FIG. 33. Upper part of *Nanomia* showing float (f), gastrozooids (gz), nectophores (n), stem (st) and tentacles (t). Inset shows how the velum can direct the water jet downward, as in normal locomotion (A), or upward, as in reverse locomotion (C). After Mackie (1964).

(Mackie and Boag, 1963), *Sulculeolaria* (Biggs, 1977a) and *Chelophyses* (Mackie and Carré, 1983). The diphyids are in general the most versatile swimmers and many are specialized for rapid swimming (Table 5), with streamlined, posteriorly opening nectophores and powerful swimming muscles. Hippopodiids on the other hand are slow swimmers. Although there may be as many as 12 nectophores in *Hippopodius*, only the bottom two are effective in locomotion. The nectosacs of the others open upon the backs of the nectophores below them and their movements do no more than flush water through the interior.

Bone and Trueman (1982) have carried out a detailed comparison of the swimming of *Chelophyses appendiculata* and *Abylopsis tetragona*. The former is a typical streamlined diphyid with a large, pointed, anterior nectophore and a smaller posterior one. It can swim slowly (< 1 cm/s) using the posterior nectophore alone, which may serve to counteract sinking. When stimulated, it performs "escape" swimming in which both nectophores take part, pulsating at frequencies up to 8 Hz. Velocities as high as 30 cm/s are

TABLE 5. SWIMMING SPEEDS OF SIPHONOPHORES

Species	Normal swimming (cm/s)	Escape swimming (cm/s)	Source
<i>Agalma okeni</i>	2-5	10-13	Biggs, 1977a
<i>Nanomia cara</i>	8	-	Berrill, 1930
	8-10	20-30	Mackie, 1964
<i>Physophora hydrostatica</i>	7	-	Biggs, 1977a
<i>Forskalia</i> spp.	1-3	2-5	Biggs, 1977a
<i>Stephanophyes superba</i>	10-15	-	Biggs, 1977a
<i>Rosacea cymbiformis</i>	1-3	3	Biggs, 1977a
<i>Sulculeolaria monoica</i>	2-5	12-16	Biggs, 1977a
<i>Chelophyses appendiculata</i>	7-6	23	Biggs, 1977a
	1.5-20*	<30	Bone and Trueman, 1982
<i>Abylopsis tetragona</i>	8	5-10	Bone and Trueman, 1982
<i>Diphyes dispar</i>	1-3	5-10	Biggs, 1977a

* Lower values refer to swimming in which only the posterior nectophore is active.

recorded. During expulsion of the water jet the velar opening narrows by 50% giving the water jet a high velocity. It relaxes again during filling. Narrowing of the opening is attributable to contraction of the circular muscles lining its inner surface. These muscles are essentially a continuation of the striated swimming muscles which line the bell cavity and they contract at the same time as the latter. Filling takes slightly longer than expulsion and, with the enlarged velar opening, this reduces negative inhalent jet velocity. Chamber pressures in the anterior nectophore during escape swimming are very high, up to 750 Pa.

The abylid siphonophore *Abylopsis* swims with its large posterior nectophore. The contribution of the small, anterior one is negligible. There is no escape response and velocity does not exceed 8 cm/s, frequency 2.5 Hz or chamber pressure 40 Pa. The duration of the jet cycle is two or three times longer than in *Chelophyses*. Jet pressures during expulsion are less than 25% of those measured in *Chelophyses*. Net forward thrust is achieved by increasing the duration of the filling phase rather than by changing the diameter of the velar opening.

Diphyids like *Chelophyses*, including the many species of *Lensia*, are among the most abundant siphonophores and their rapid escape behaviour is probably a factor in their success. However, the powerful escape swimming contraction requires considerable work (9.7×10^{-5} J as against only 5.4×10^{-5} J for normal swimming in *Abylopsis*). Taking all factors into account, Bone and Trueman (1982) show that the unit locomotory cost of swimming in this species is ten times greater than in *Abylopsis*.

The nectophore as a motor unit. The nectophore is a medusa stripped of its gonads, tentacles, mouth and manubrium and reduced to the basic locomotory apparatus. Its swimming muscle is effectively a single motor unit, as the individual fibres function together under common (unitary) motor control. In some siphonophores all the nectophores are the same, with identical swimming muscles, like the serial locomotory muscles of a primitive segmented animal but in diphyids the units in the series are specialized for different tasks. Strictly speaking, the nectophore cannot be said to consist of a single motor unit as there is a second set of muscle fibres, the radial set, which controls the shape of the velum during contraction of the swimming fibres. Thus it is like a simple "limb", with two muscles, except that the two "muscles" are complementary, not antagonistic as they would be in a walking leg.

In swimming, the myoepithelium spreads the signals for its contraction like the vertebrate heart (another unitary muscle), and a subumbrellar nerve plexus is absent, as are nerves in the heart (Chun, 1882; Mackie, 1965). Chain *et al.* (1981) give membrane constants and other data for myoepithelium of *Chelophyses*. The cells are electrically coupled, with a space constant of 280 µm and signals are conducted through the epithelium at 25 cm/s. The impulse appears to be sodium-dependent (unusual in muscle physiology) but the action potentials are complex events which show systematic changes in wave form with repetitive firing. Bone (1981) showed changes in wave form to be correlated with a progressive increase in tension during repetitive firing. Stronger contractions thus appear later in the burst. Bone suggests that this has advantages in allowing the siphonophore to contract its stem before maximum thrust develops. This would prevent damage to the stem.

Diphyid muscles are unique within the cnidaria in possessing a transverse tubular system (Chapman, 1974; Chain *et al.*, 1981; Mackie and Carré, 1983). Bone's (1981) findings suggest that depolarizations of the sarcolemma may spread into the tubules and cause release of calcium ions, as in vertebrates. However, there is no obvious storage site for calcium ions, such as sarcoplasmic reticulum. Cell to cell impulse spread in siphonophore swimming muscles is presumably mediated by gap junctions, first shown to be present in *Hippopodius* (Bassot *et al.*, 1978). The impulses for swimming presumably arise in the marginal nerve rings. They are detectable in extracellular recordings from near the margin (Mackie and Carré, 1983). In long-stemmed physonects and in diphyid calycophorans the marginal nerves are connected directly to the stem, and swimming thus comes under some degree of "central" control.

In *Nanomia* and its relatives, radial muscles are arranged on either side of the velum as the "fibres of Claus" (Claus, 1878; Mackie, 1964). When they contract, they pull the velum out of shape, directing the water jet forward.

causing reverse swimming (Fig. 33). In *Chelophyses*, the radial fibres are arranged symmetrically and do not cause a change in the direction of the water jet. They sometimes contract synchronously with the contraction of the swimming muscle, the result being a 'composite swim' (Mackie and Carré, 1983). At other times the swimming muscle contracts alone. Bursts of swimming have been observed to start with a composite swim and to be followed by simple swims. Presumably, as the effect of radial muscle contraction would be to counteract the tendency of the velar opening to narrow during emission of the water jet, composite swims will produce less thrust than simple swims.

We have already seen that early contractions in a burst produce less muscle tension than later ones, owing to an increase in membrane channel open time. Radial velar contractions would work in the same direction, to weaken the initial swims in a series, and would likewise be explicable in terms of minimizing the risk of damage to the stem. If this is correct, *Chelophyses* has a mechanism like a clutch (in fact, two such mechanisms) which prevent it from tearing its stem off by starting to swim at maximum thrust.

B. Coordination

The subject of coordination has attracted attention because of the peculiar nature of siphonophores as colonies composed of several sorts of zooids specialized for various functions but in most cases clearly recognizable as either polypoid or medusoid individuals. How these individuals, or "persons" (a term no longer in vogue) are coordinated, and the extent to which their action systems are subject to colonial control are interesting questions, central to the whole issue of coloniality. Moreover, they can be addressed by neurophysiological experimentation. Several aspects of this work have been covered in recent reviews (Spencer and Schwab, 1982; Mackie, 1984) so the treatment here will be quite brief.

1. Conduction pathways

The idea that epithelia can conduct impulses without benefit of nerves was originally prompted by the observation that nerves were absent from certain tissues where conduction seemed to be taking place (Chun, 1882, 1897b). Mackie (1960a) proposed that, not only in siphonophores but throughout the hydromedusae, the striated swimming muscle sheet was capable of myoid conduction and that, where nerves were present, they were concerned with radial responses, not with swimming. With some important exceptions,

subsequent research has shown this to be true (Spencer and Schwab, 1982). The observation that nectophores of *Nanomia* remained coordinated in the reverse locomotory response after surgical destruction of the nervous connections with the stem (Mackie, 1964) provided further evidence of non-nervous conduction, this time in the exumbrella. Proof that this tissue could conduct was eventually obtained with *Hippopodius* and other calycophores using electrophysiological techniques (Mackie, 1965). These basic observations have since been verified and extended to other species. Myoid conduction in nectophore swimming muscles has been discussed above (p. 181). Epithelial conduction has been found to occur in the exumbrellas of all nectophores examined and in the covering epithelia of bracts. The subumbrellar endoderm also conducts, and experiments on *Hippopodius* (Bassot *et al.*, 1978) show that this layer is functionally linked with the exumbrellar epithelium at the margin and stem attachment zone by transmesogloal cellular connectives. Similar couplings are present in *Chelophyses* (Mackie and Carré, 1983) and in a number of hydromedusae. The endoderm of the stem is a conducting epithelium in siphonophores, but not the ectoderm. The float of *Physalia* has an excitable endodermal lining, and the invaginated ectoderm of the pneumatostaccus is another nerve-free excitable epithelium. Gastrozooids and palpons probably have excitable endoderms but nerves spread excitation in the ectoderm. Tentacles lack excitable epithelia. Gonophores have not been investigated.

Most excitable epithelia are thin and delicate, which makes investigation difficult, but successful recordings have been obtained from the striated muscle sheet of *Chelophyses* nectophores as noted earlier (p. 181) and from the *rete mirabile* of *Hippopodius* (p. 177). The rete cells are unusually large and can be penetrated with microelectrodes (Mackie, 1976a). The cells are electrically coupled and impulses propagate between them. The impulse is a sodium spike followed by a Ca^{2+} dependent after potential. The rete is a secretory organ and secretion is Ca^{2+} dependent. Treatment with manganese ions, which compete with calcium for membrane channels, blocks both the secretion and the after potential.

Impulse transmission in excitable epithelia is assumed to require gap junctions between the cells, and these are usually present in the expected places. Parts of the exumbrellar epithelium of *Hippopodius* are syncytial (Iwanzoff, 1928; Mackie, 1965). Generally speaking, excitable epithelia show no obvious structural differences from inexcitable epithelia. Excitability is presumably determined by the presence of voltage-sensitive membrane channels capable of mediating ionic fluxes in the directions and with the time courses needed to allow propagative depolarizations to occur, but the presence of such channels is not associated with any distinctive morphological appearance.

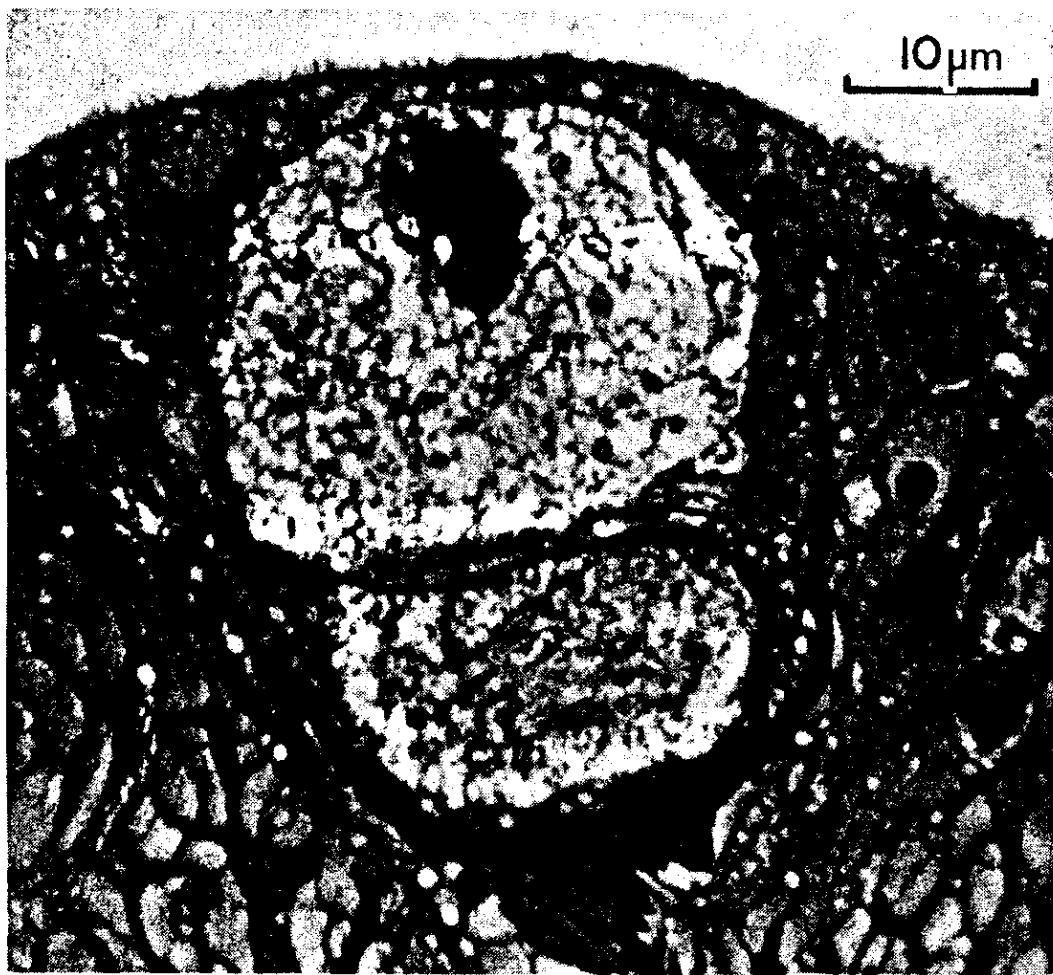


FIG. 34. Cross-section of the stem of *Nanomia* in the region of the two giant axons, after Mackie (1973). The axons lie within the ectodermal myoepithelium in the dorsal midline of the stem. Korotneff (1884) who first observed these cells identified them as nerve elements. Schneider (1892) supported this conclusion and held the axons responsible for the "lightening-quick" contractions of the stem. Schaeppi (1898), however, thought the cells were endodermal processes ("compensation sacs"). Ehle (1913) disagreed with Schaeppi but could come to no firm conclusions as to the function of the giant cells. Mackie (1973) recorded action potentials from them, showing that they were axons.

Since the discovery of nerves in *Physophora* by Claus (1878) nerves have been located throughout most parts of the ectoderm of various species but are absent in the bracts, in the pneumatostaccus and certain parts of the nectophores. The endoderm is less well equipped with nerves. Apart from one questionable report (Schaeppi, 1898) none have been found in the endoderm of the stem, float, nectophores, bracts or tentacles, though they are present in gastrozooids and palpons.

The most noteworthy feature of the siphonophore nervous system is the existence of a double innervation in the stem of certain physonects and calycophores. The two nerve nets may become built up into giant axons running along the mid-dorsal side of the stem (Fig. 34). Recordings from these units show conventional action potentials (Mackie, 1973, 1976b, 1978). In *Forskalia* the larger giant axon has a resting potential of -60 mv and conducts a short duration (10 ms) action potential, overshooting by 35 mv,

at velocities up to 4.0 m/s. Conduction velocities in other regions rarely exceed 0.5 m/s. No information is available on the ionic mechanisms.

2. Local action systems

Two sorts of contraction have been described in *Nanomia*, fast or "twitch" contractions in which the longitudinal muscles are fired by input from two nervous subsystems, and slow contractions which bring about postural changes and are apparently mediated by epithelial conduction in the endoderm. Pathways across the mesogloea allow the endodermal impulses to excite the ectodermal muscle. Excitation from this source produces junctional potentials which can sum with those evoked by nervous input, enhancing twitch responses. Conversely, because of two-way coupling between the layers the endoderm can be excited by nerve-induced depolarizations of the ectoderm. Thus, the slow system is usually activated automatically during twitch responses (Mackie, 1976b, 1984). The presence of a double innervation in the stem is thought to allow graded spread of contractions. Because one system conducts faster than the other, facilitation at the neuromuscular junctions is greatest near to the site of stimulation, and decreases progressively with distance. Conduction velocities are summarized by Mackie (1984).

Evidence for calycophores suggests that their stems work in the same way as those of physonects. Among the cystonects, *Rhizophysa* and *Bathyphysa* have not been investigated neurophysiologically and *Physalia* lacks a stem. Its large float has only a single innervation.

The float consists of outer pneumatocodon ("codon", for short) and inner pneumatosaccus ("soccus"). Both are two-layered, having ecto- and endodermal epithelia but the soccus arises as an invagination during development and so its ectoderm lies on the inside. In *Physalia* the float is large enough to be a convenient object for neurophysiological study (Shelton, 1976; Anderson and Mackie, unpublished results). All four of its layers are myoepithelia and can contract. Nerves are present in the codon ectoderm where they are responsible for spreading excitation, but the other three layers lack nerves and are conducting epithelia. Impulses spread in them at 4.0–6.0 cm/s. There is a neuro-epithelial translation step between the ectoderm of the codon and that of the soccus: depolarizations of the epithelium generated by nerve activity in the codon spread as epithelial impulses in the soccus. The codon and soccus are in continuity at only one point, the gas pore, and it is here that the translation takes place. The two layers of the soccus are connected by cellular processes which run across the mesogloea (Mackie, 1960b). These connections probably account for the fact that the two layers are functionally coupled and spread impulses as if they were a single sheet.

No work has been done on the neurophysiological control of gas secretion or expulsion. The gas gland of *Physalia* is a specialized portion of the wall of the saccus and depolarizations of the saccus cells invade the gas gland. These propagated depolarizations might regulate gas secretion. The float of *Physalia* performs elaborate rolling movements (p. 175), which are presumably organized by the ectodermal nerve net, but no details are available. In physonects such as *Nanomia* the float sits on a short contractile stalk. The float can be pulled down into the shelter of the young nectophores which bud from the stem immediately below the float.

The flushing cycles associated with feeding mentioned above (p. 175) seem to be generated autonomously in the endoderm, which is a conducting epithelium containing some nerves. When a gastrozooid is stimulated electrically, the ectodermal muscles show graded "slow" potentials, which probably represent summed input from the ectodermal nerve net, but the layer can also generate propagating spikes (Mackie, 1978). Chain (1981) showed that these potentials are sodium-based.

Palpons probably operate on the same principle as gastrozooids. Early workers believed that they were special organs of touch, presumably because in species like *Physophora hydrostatica* they exhibit "incessant movement" (Leuckart, 1853) and "serpentine writhings" (Kölliker, 1853). The word palpon itself suggests tactile sensitivity, as do Leuckart's *Taster* and Kölliker's *Fühler*. Kölliker likened palpons to the arms of cephalopods! However there is no evidence that the movements have a sensory function or that palpons are more touch sensitive than any other parts. (They are accessory digestive organs and in some cases can excrete water from a small terminal pore.)

Korotneff (1884) described the tentacles as "miniature copies of the stem" and this statement is supportable in that, in forms like *Nanomia*, both stem and tentacles have a double ectodermal innervation (Fig. 35). However, the endoderm of tentacles is not a conducting epithelium like that of the stem, and there are no giant axons in the tentacles. Tentacles operate largely in independence of the gastrozooid or palpon to which they belong.

As noted above (p. 177) certain species possibly have mobile bracts which can be raised and lowered by the action of muscles in their pedicels. However, in most species the bracts cannot be moved except in the process of being shed by autotomy. The bract ectoderm is an excitable epithelium (Fig. 35), which in *Nanomia* conducts at ca 25 cm/s. Bracts effectively extend the sensory field around the stem.

Gonophores are medusae showing varying degrees of reduction. Tentacles are absent except occasionally as rudiments (e.g. *Lilyopsis*). Gonophores have no mouths and do not feed. They are often incapable of contraction, though in many cases they are observed to pulsate feebly. Such movements

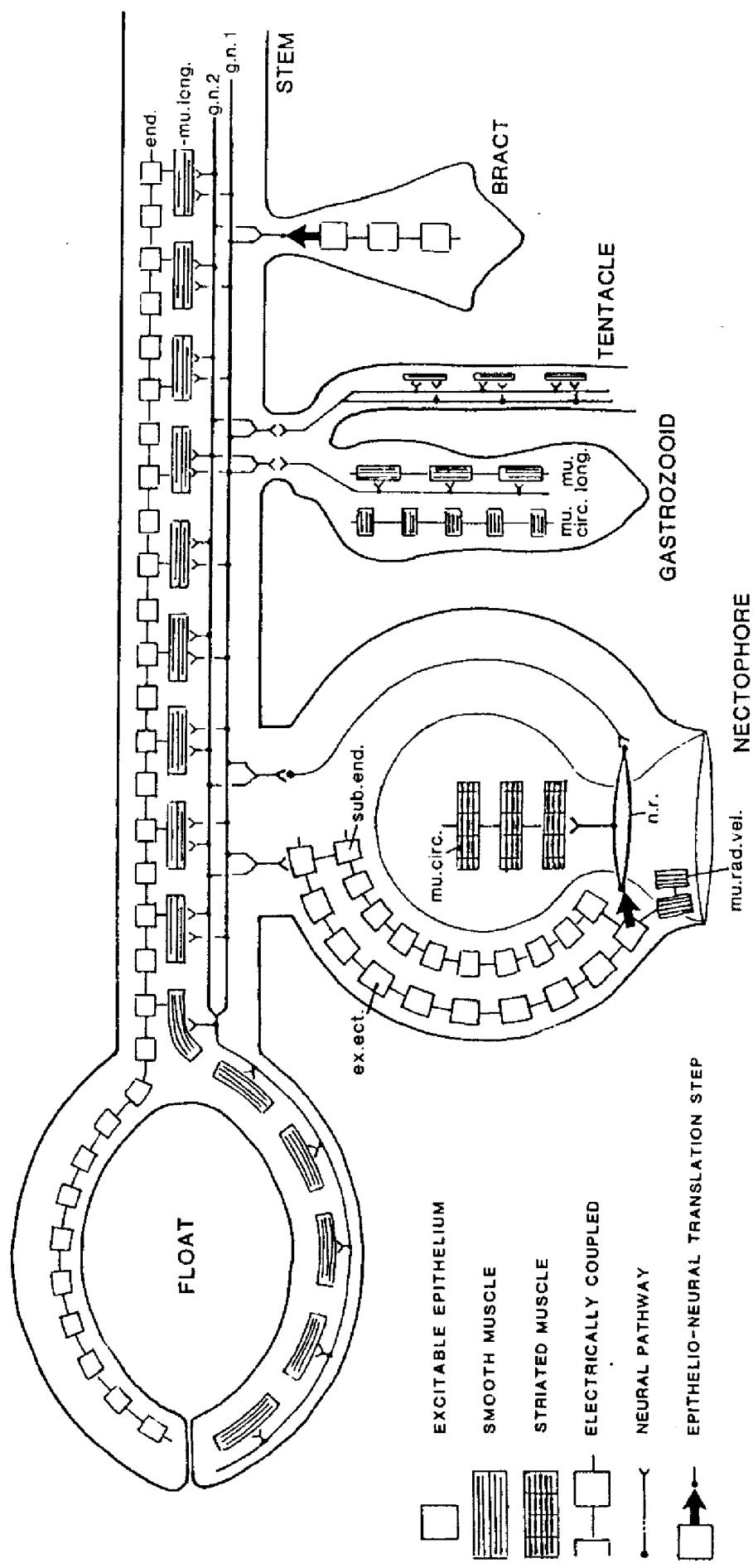


FIG. 35. Simplified wiring diagram of a physonectid siphonophore, based on Mackie (1964, 1976b, 1978), as explained in the text. Only ectodermal nerve pathways are included. end. endoderm, ex. ect. exumbrellar ectoderm, g.n.1, g.n.2, giant nerve axons, mu. circ. circular muscle, mu. long. longitudinal muscle, mu. rad. vel. radial muscle of velum ("fibres of Claus"), n.r. nerve ring, sub. end. subumbrellar endoderm.

may serve for ventilation or dispersal of sexual products. In some cases (e.g. *Hippopodius*, *Sulculeolaria*, *Halistemma*) the gonophores are relatively well developed, detaching and swimming freely in the plankton. In *Hippopodius* histological study shows striated muscle in the subumbrella, along with marginal nerve rings and a subumbrellar nerve net (Mackie, 1965). These gonophores lead a free life for some 24 h before liberating their eggs and dying (Müller, 1871). Physiological studies have not been carried out but it can be assumed that their locomotory rhythms are generated by marginal pacemakers as in other hydromedusae. Some gonophores, for instance in diphyids, have become transformed into asexual, locomotory medusoids equivalent to nectophores, and these are doubtless equipped with similar action systems. They create movement of the water around the stem before the eudoxid is set free, and propel it after it is liberated.

Nectophores are equipped with all the nerves and muscles necessary for swimming. In some cases they also have radial muscles serving to control the direction of the water jet (*Nanomia*). All nectophores examined have excitable epithelia which transmit impulses to and from the stem. Nerve connectives also link the marginal nerves with the stem in some species. Details of these specializations have been given above under Locomotion (p. 177) and Protective Responses (p. 175).

3. Integration of local action systems

A considerable amount of activity in siphonophores is carried on spontaneously at the local level. Gastrozooids and palpons show rhythmic pumping cycles, tentacles shorten and lengthen, the float emits bubbles and gonophores pulsate. The stem itself exhibits a slow, cyclical peristalsis.

Stimulation can also produce local responses. In *Nanomia*, posterior nectophores contract if lightly touched. With stronger stimulation, activity spreads to other nectophores. Similarly, a gastrozooid can capture, manipulate and ingest a small prey object without other parts of the colony being involved, but stronger stimulation leads to stem contraction. Depending on the strength of stimulation, stem contraction itself can be local or general. Escape locomotion occurs only after strong or repeated stimulation of the stem.

The means whereby responses are graded in amplitude and spread have not been completely analysed but certain facts have emerged (reviewed by Mackie, 1984): (1) all parts of the organism, with the possible exception of some gonophores, are in behavioural communication with the stem, and thus with each other (Fig. 35); (2) the links in question involve impulse conduction in epithelia (in the case of bracts), nerves (in gastrozooids and palpons) or both (some nectophores); (3) transmission between zooids and

stem is not a simple one-for-one process, but typically requires the arrival of several impulses in a close time relationship for the transmission block to be overcome. The junctions in question fatigue rapidly, and transmission then fails. Thus, communication between zooids and stem is highly labile; and (4) coordinated responses involving many zooids are typically associated with protection or escape.

Two-way interactions between stem and other parts are summarized in Fig. 35. Noteworthy features of the wiring in both physonects and diphyids are the translation steps (Mackie and Carré, 1983) by which impulses propagating in epithelia can jump into the nervous system. How this occurs has yet to be explained. Because of the existence of epithelio-neural translation steps, stimulation of nerve-free epithelia such as those covering bracts and nectophores can lead to activity in the nerves of the stem. Conversely, nervous activity can translate into epithelial impulses, presumably by conventional synaptic mechanisms.

The possession of independently conducting systems of nerves and epithelia interacting through labile translation steps, the presence of a double innervation in the stem and the development of giant axons combine to give siphonophores behavioural capabilities equalling or surpassing those of other cnidarians. At the same time they allow for a delicate balance to be maintained between the more local and the more general degrees of activity. The siphonophores teach us that coloniality *per se* is no barrier to behavioural coordination. In the evolution of these polymorphic bud colonies the neuromuscular systems needed for local activities have persisted, often with little change from the polypoid or medusoid ancestors, and at the same time mechanisms have arisen for keeping the parts coordinated in responses serving for protection and locomotion.

C. Autotomy

A wide variety of phenomena could be considered under the heading of autotomy. The only previous treatment of the subject (Schaeppi, 1906) covers not only the shedding of nectophores and bracts, which meet the strictest definition of autotomy, but also the shedding of discharged nemato-cysts ("cellular autotomy") and the loss of nematocyst batteries and tentacles which occurs when a prey organism escapes from the siphonophore. To the present writer, it is the 'auto' in autotomy which defines the act. The mere tearing away of parts when prey escape or the detachment of zooids sometimes seen during formalin fixation should not be termed autotomy. In autotomy we are dealing with self-mutilation, not with mutilation caused by outside agencies. The examples to be considered here fall under three

categories: defensive autotomy, autotomy related to dispersion of sexual products and autotomy occurring as a normal part of development or growth.

The best examples of defensive autotomy are the shedding of bracts and nectophores in physonects such as *Nanomia*, *Halistemma*, *Forskalia*, etc. These appendages are attached to the stem by a muscular pedicel which is specialized as an "autotomy joint" no different in principle from such structures in crustacean limbs. The exact mechanism of detachment has not been closely studied, but autotomy occurs whenever the nectophore or bract is strongly and persistently stimulated. If a bract of *Nanomia* is pinched and held with forceps it will detach after a few seconds. No force is needed, it comes away by itself. Detachment always occurs at the point where the pedicel attaches. In both nectophores and bracts, the pedicel contains extensions of the longitudinal stem musculature which fan out and insert on to the attachment zone. It is the contraction of these strands that brings about autotomy. The response is not mediated by nerves but by rapid flurries of impulses in the ectodermal epithelium (Mackie, unpublished). This tissue can be excited at any point by strong electrical or tactile stimulation (p. 186).

It is generally assumed, but hard to prove, that autotomy of this sort represents a sort of voluntary sacrifice, the offering up of an inessential part of the body to a predator as the price of escape. In *Nanomia*, detached nectophores swim vigorously for a short period of time. A visual predator might be expected to pursue such an attractive object. Asymmetries of the nectophore column produced by loss of nectophores are immediately corrected by contraction and torsion of the stem, which together bring about closure of the gap.

It is doubtful if defensive autotomy occurs in the case of gastrozooids, palpons, or their tentacles, or of the float. A possible exception is in *Forskalia*, where molestation sometimes causes spontaneous detachment of palpons (J. Woodley, personal communication). A bright red pigment is simultaneously liberated which spreads through the water in a manner reminiscent of the inking response of squid. Schaeppi (1906) suggests that this substance deters predators.

Reichman (1984) has drawn attention to a principle first enunciated by R. Goss:

"It goes without saying that structures essential to survival cannot regenerate. Conversely, there is nothing to be gained by regenerating appendages that are relatively useless. To qualify for replacement, a structure must lie between these two extremes. It must be important enough to be missed when it is gone, but not so vital that an animal cannot survive its loss long enough to grow a replacement."

The ability of a part to autotomize defensively might be covered by a corollary of Goss's law to the effect that parts qualifying for autonomy must not be so essential that their loss would constitute a serious threat to survival. This is true of nectophores and bracts. Loss of a float, however, would be a more serious disaster in a siphonophore such as *Nanomia*, as the animal would lose its ability to maintain its fishing posture, be unable to hold its position in the water column, and be unable to swim efficiently in an upwards direction during diurnal migrations. Likewise, loss of many gastrozooids would prevent the animal from feeding. Thus, these structures do not autotomize.

Autotomy serving for dispersion of sexual products is seen in the liberation of ripe gonophores in species such as *Hippopodius*, and of eudoxids in various other calycophores. Eudoxids are formed serially as the stem grows. Typically, each consists of a gastrozooid with its tentacle, a bract and a gonophore. Liberation of mature eudoxids from the end of the stem occurs spontaneously by constriction of the stem at specialized weak points (Fig. 36). Following separation, the stem stump is resorbed (Müller, 1871). Whole gonodendra detach in *Rhizophysa* and *Physalia*, a reasonably clear case of autotomy serving for the distribution of sexual products.

In the calycophores *Praya*, *Rosacea* and *Lilyopsis* longer pieces of stem with many groups of appendages may become separated. *Praya dubia* has frequently been observed in the fragmented state floating freely in deep water from the Johnson-Sea-Link submersibles (Pugh, unpublished). While mechanical interference may sometimes cause fragmentation, the siphonophore is apparently so prone to fragment that fragmentation is probably an adaptive process, even if not due to autotomy in the strict sense.

Similarly, among physonects, some species appear especially prone to fragmentation. Schaeppi (1906) observed in the harbour at Messina that fragments of *Apolemia* are often commoner than intact specimens. However, portions of *Apolemia* up to 30 m long have been observed at Villefranche (Carré, personal communication) so fragmentation cannot be regarded as obligatory in this species. While *Cordagalma cordiformis* kept in the laboratory did not fragment spontaneously (Carré, personal communication), the same species observed from a submersible at depths well below 200 m was nearly always in a fragmented state, despite the extremely still water conditions (Mackie, 1985). In the same habitat, *Nanomia cara* was invariably intact.

The third type of autotomy recognized here is the shedding of temporary or worn-out parts. In long-stemmed physonects the nectophores are budded serially with the youngest at the top of the column. It seems likely that there is a zone of stem resorption near the lower end of the nectosome, perhaps coinciding with the siphosomal growth zone, and that nectophores are shed

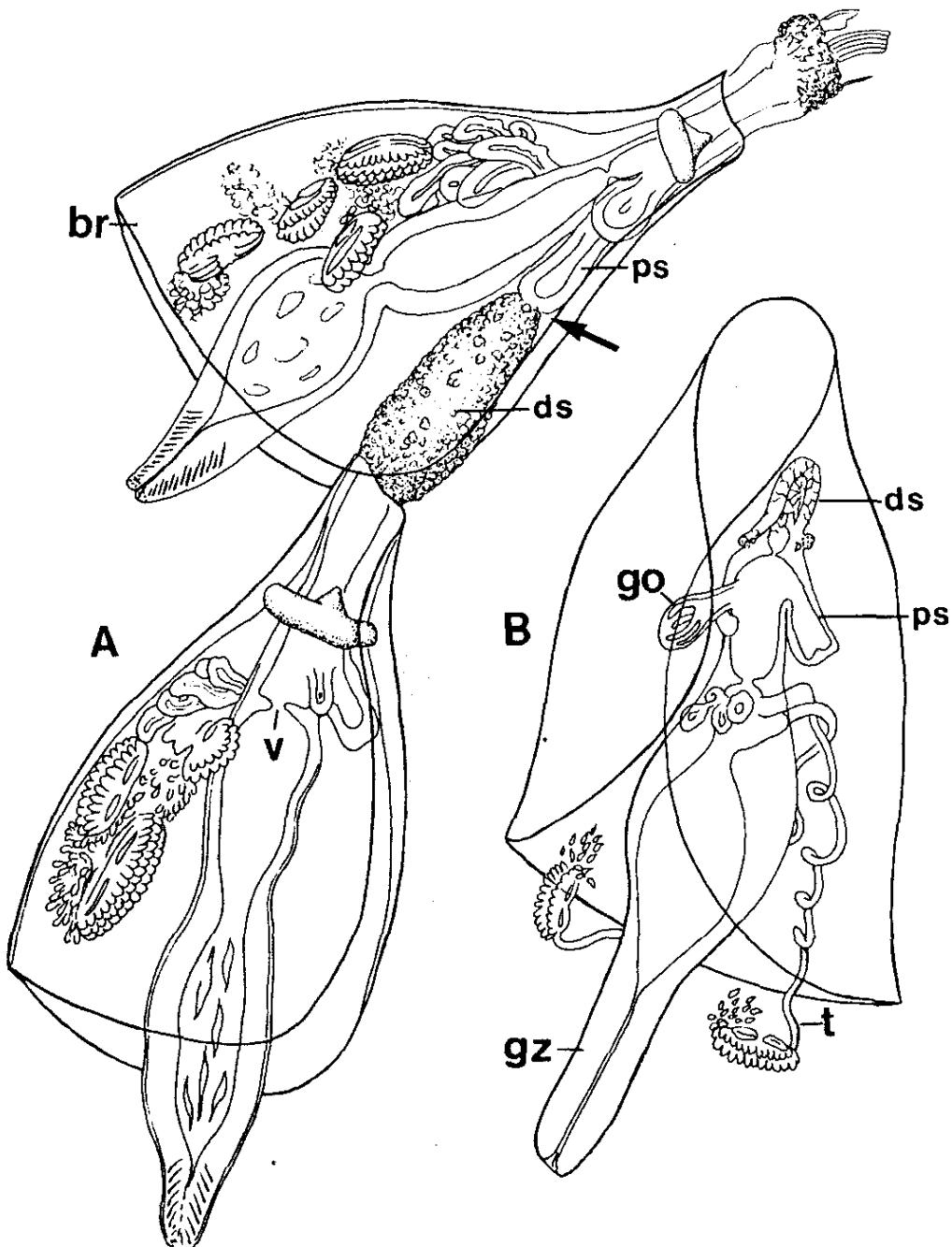


FIG. 36. Eudoxids of *Chelophyes appendiculata* before (A) and after (B) separation from the stem. Separation takes place by means of a constriction (arrow) which pinches the stem in two. The proximal portion of the stem (ps) is eventually resorbed while the distal portion (ds) closes over to become the somatocyst of the eudoxid bract. Its cells inflate and become parenchymatous. Also shown are gonophores (go) in early stages of development, and tentacles (t), contracted in A, unfurled in B. Redrawn from Müller (1871). This drawing also shows a valve (v) at the base of the gastrozooids. Such "pyloric valves" (Huxley, 1859) occur widely in this location in both gastrozooids and palpons. Münter (1912) thought that they were somehow involved in diverting fluid down into the tentacle, but their main function probably is to regulate passage of fluids between the zooid and the stem during digestion (Mackie and Boag, 1963).

spontaneously from this region. Likewise, gastrozooids and terminal stem portions seem to be lost or absorbed at the lower end of the siphosome. No experimental studies are available to document these suggestions however.

In *Hippopodius*, the oldest nectophores at the bottom of the column are sometimes considerably smaller than younger ones higher up in the column

and probably represent relics of an earlier growth stage when the whole animal was naturally smaller or food less abundant. Their shedding restores the column to a symmetrical and efficient shape. Lower (older) nectophores often appear defective in this species. For instance, their *rete mirabile* may be virtually nonexistent. Primary larval nectophores are regularly shed during the development of many calycophores as the definitive nectophores develop. Bracts are produced early in the development of some physonects, subsequently undergoing autotomy as a result of some "inner stimulus" (Schaeppi, 1906). However, they are retained in *Agalma elegans* (Totton, 1956).

D. Flotation

In the sea, animals tend to sink because their protein-based tissues are denser than sea water, *ca* 1.3 compared with 1.026. The attainment of near-neutral buoyancy has advantages in terms of energy saved and postural versatility (Marshall, 1979). Siphonophores achieve buoyancy by two principal means: (a) use of gas filled floats; (b) use of gelatinous tissues which have a low specific gravity owing to partial replacement of sulphate by chloride; and (c) the use of fluids of low specific gravity may apply in the case of *Lynchagalma utricularia*.

1. Cystonectae

Rhizophysa lacks nectophores and bracts and avoids sinking entirely by means of the float. The stem hangs vertically below the float. Jacobs (1937) saw gas bubbles being emitted from the tip, proving that a pore is present as claimed by earlier workers such as Chun (1897a) on the basis of histology. The structure of the gas gland is known from Chun's account (Fig. 37). It consists of giant cells arranged in long, finger-like lobules which extend into the pericystic space. These are visible in living specimens, by virtue of the transparency of the float wall (e.g. Totton, 1965a, Pl. II, Fig. 2). *Rhizophysa* presumably regulates its depth by releasing or secreting gas as in various physonects, but precise information is lacking. In theory, gas volume could be altered without release or resecretion simply by adjustment of the pressure exerted on the gas by the muscles of the float wall. *Rhizophysa* may be capable of such control, as Jacobs (1937) saw specimens rhythmically rising and sinking in the water column without any sign of gas release.

The Portuguese man-of-war is seemingly incapable of expelling sufficient gas to sink below the surface except possibly in its earliest postlarval stages. The need for gas secretion would therefore be limited to replacing diffusional losses and keeping up with expansion of the float as the animal grows.

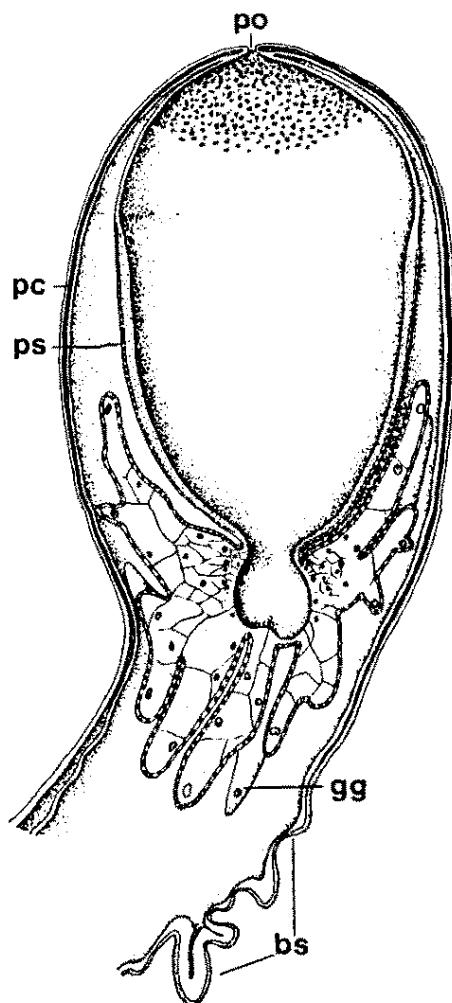


FIG. 37. Float of *Rhizophysa filiformis* showing budding zone for stem appendages (bs), gas gland cells (gg), pneumatocodon (pc), pore from which gas is released (po) and pneumatosaccus (ps). Redrawn from Chun (1897c).

Living at the surface at atmospheric pressure simplifies the physics of gas secretion, and the gas gland is not only small in relation to the size of the float, but histologically very simple (Mackie, 1960b; Copeland, 1968). The main component of the gas secreted is carbon monoxide, derived from L-serine in a pathway using tetrahydrofolates as cofactors (Wittenberg, 1958, 1960; Wittenberg *et al.*, 1962). Larimer and Ashby (1962) found a maximum secretory rate of 120 µl/h using gas glands maintained *in vitro*. Secretion may be more rapid in young animals (Hahn and Copeland, 1966).

2. Physonectae

Thanks chiefly to the work of Jacobs (1937), a good deal is known about the physiology of gas secretion in physonects, especially in *Nanomia* ("Stephanomia") *bijuga*. Float structure in this species is known in detail from the work of Carré (1969b). Moser (1924) treated the lack of an apical pore as a diagnostic character of the physonectae but in both *Nanomia cara* and *N.*



FIG. 38. Varying degrees of dependence on gelatinous parts for flotation. *Rhizophysa filiformis* (A) is completely dependent on the float for support and lacks gelatinous parts. *Nanomia bijuga* (B) has gelatinous nectophores and bracts but is still largely dependent on the float. In *Agalma elegans* (C), the float supports only a short anterior portion of the stem, the rest being buoyed up by gelatinous parts. This species, unlike the other two, cannot regulate the volume of gas in its float or otherwise alter its specific gravity. After Jacobs (1937).

bijuga gas bubbles are regularly emitted from the tip of the float, and a pore is demonstrable in paraffin sections. Moser also held that the float functioned more as a sense organ than as a hydrostatic organ. This may be true in species such as *Forskalia* where there is an abundance of gelatinous bracts and nectophores and where removal of the float has only a minor effect on buoyancy, but in *Nanomia*, where there is less gelatinous tissue, the float is an essential hydrostatic organ. Removal of the float or release of its gas by decompression causes the animal to sink to the bottom. On this basis, Jacobs distinguishes two types of long-stemmed physonects (Fig. 38).

Spontaneous gas release in *Nanomia* is associated with sudden, periodic stem contractions, following which a wave of peristalsis runs up the float

TABLE 6. SULPHATE CONCENTRATIONS AND CALCULATED LIFTS OF SIPHONOPHORES
(BIDIGARE AND BIGGS, 1980)

Sample	n	mg SO ₄ ²⁻ /ml ($\bar{X} \pm S_x$)	Calculated lift (mg/ml) ($\bar{X} \pm S_x$)	% SO ₄ ²⁻ excluded ($\bar{X} \pm S_x$)
Phylum Cnidaria				
Order Siphonophora				
Suborder Physonectae				
<i>Agalma okeni</i>	2	1.8 ± 0.1	1.0 ± 0.1	44 ± 3
<i>Forskalia edwardsi</i>	1	1.8 ± 0.1	1.0 ± 0.1	44 ± 3
Suborder Calycophorae				
<i>Diphyes dispar</i>	5	0.8 ± 0.2	1.6 ± 0.1	75 ± 6
<i>Hippopodius hippocampus</i>	4	1.1 ± 0.1	1.4 ± 0.1	66 ± 3
<i>Rosacea cymbiformis</i>	3	1.2 ± 0.2	1.4 ± 0.1	63 ± 5
<i>Stephanophyes superba</i>	4	1.8 ± 0.2	1.0 ± 0.2	45 ± 8
<i>Vogtia glabra</i>	3	1.9 ± 0.2	0.9 ± 0.2	41 ± 8
<i>Vogtia spinosa</i>	4	1.8 ± 0.1	1.0 ± 0.1	43 ± 3

wall in the circular muscle layer of the pneumatocodon, forcing a bubble out of the tip. It is not clear whether the pneumatostaccus is also actively involved. In floats partially emptied by decompression, Jacobs observed secretion of new gas in the form of small bubbles arising in the vicinity of the gas gland. As the float refills, the animal gains buoyancy and starts to rise toward the surface. Observed in a glass cylinder, specimens showed a 35 min cycle of gas release, sinking, resecretion and rising. Compression (300 mmHg) caused a decrease in float size and resecretion restored the original dimensions within 10 min under maintained decompression. Under natural conditions a pressure increase of 60 mmHg is enough to cause a specimen to become negatively buoyant.

Mechanical stimulation such as shaking or stirring may cause gas release and sinking. This could be significant in the context of escape. Jacobs reports some results which suggest that the animal can 'fine tune' its buoyancy by adjusting muscular tone in the float wall but in general it seems likely that gas release and resecretion are the chief mechanisms involved in buoyancy control. The question of how the float "knows" when to release or to secrete gas, and in what amounts, has yet to be elucidated. As in *Physalia*, the gas secreted is carbon monoxide (Pickwell *et al.*, 1964).

Forskalia and *Agalma* have no float pores and cannot release gas. After removal of the float the nectosome droops slightly but the animal retains its buoyancy thanks to the abundance of gelatinous appendages. A *Forskalia* taken out of the water looks like a gelatinous fir cone. The gastrozoooids are

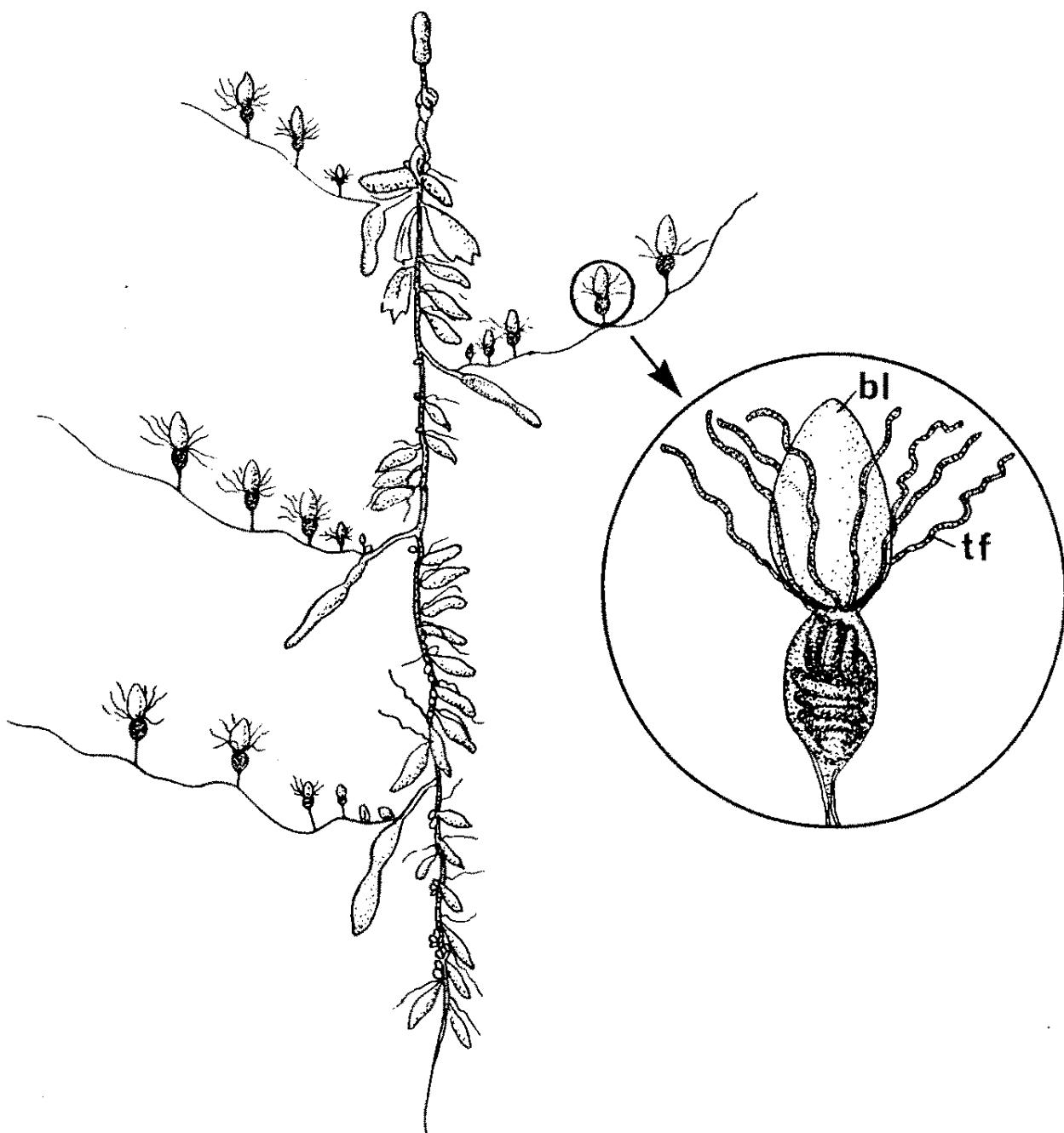


FIG. 39. *Lychnagalma utricularia* redrawn from Claus (1879) (no scale given). The tentacles are buoyed up by flotation bladders (bl) in the tentilla, one of which is shown enlarged. Each tentillum has eight terminal filaments (tf).

carried on long stalks which bring them outside the wall of bracts. *Forskalia* nectophores float to the surface when detached, which is rarely the case in *Nanomia*. Bracts invariably float. All other parts are heavier than water and sink. Lift of gelatinous parts is obtained by sulphate exclusion (Bidigare and Biggs, 1980 and Table 6).

Lychnagalma ("Agalmopsis") utricularia is exceptional in having flotation bladders on the gastrozooid tentacles (Claus, 1879). Instead of hanging downward as in most siphonophores, the tentacles are held out horizontally around the sides (Fig. 39). The bladders appear to be expanded versions of the terminal ampullae associated with the nematocyst batteries in other

agalmids, such as *A. okeni* and *A. elegans*, to which no flotation role has been ascribed. The presence of eight terminal filaments per battery in *Lynchagalma* (in contrast to the usual two) is probably related to the horizontal posture of the tentacles, which must involve less risk of tangling. Thus, the presence of flotation ampullae would tend to increase the effective fishing surface. The physiological basis of buoyancy in the ampullae has not yet been studied. Pugh has recently obtained new material of *L. utricularia*; sections of the bladders show them to be thin-walled, presumably fluid-filled structures rather than being gelatinous. In other animals, fluids of low specific gravity are created by ion pumping, as in cranchiid squid (Denton *et al.*, 1969). It would be worth examining the less well developed ampullae of other agalmids to see if they too play some role in flotation.

Physophora hydrostatica was first observed to release gas from a pore at the base of the float by Keferstein and Ehlers (1861). These authors, and Chun (1897c), reported rapid resecretion of gas in this species. There is no doubt that a pore exists, but it is not clear that it communicates directly with the gas cavity as Leloup (1941) states. According to Chun (1897c) it leads into the pericystic cavity. If so, it could not function routinely in gas release although it might do so under exceptional circumstances, for instance if an animal became positively buoyant through traumatic loss of appendages and started on an uncontrollable ascent toward the surface, when gas might rupture through the gas gland into the pericystic cavity and so escape via the pore. Pugh (1983) further discusses this question.

Rhodaliid physonects have very large, gas-filled floats. The gas secreting tissue forms a conspicuous structure, the aurophore, projecting to one side below the float. We owe to Pugh (1983) the realization that rhodaliids are epibenthic animals not, as most authors have supposed, pelagic (p. 154). Recent observations from submersibles cited in Pugh (1983) confirm that rhodaliids are bottom dwellers. *Dromalia* is positively buoyant and floats like a hot air balloon above the substratum tethered by its tentacles. *Thermopalia* (the Galapagos "dandelion" Fig. 6D) has been seen swimming freely in a neutrally buoyant state. It seems that slight adjustments around the point of neutral buoyancy would be needed to allow the animal to function normally in this habitat. Haeckel's (1888) drawings show a pneumatic duct leading directly from that gas space to the exterior through the aurophore. This is probably an error. The gas cavity is probably completely enclosed (Pugh, 1983). However, emergency venting by rupture could occur as proposed for *Physophora*.

The rhodaliid float is a very large structure but, assuming that the tissues have an organic content representing about 10% of the wet mass (as in other benthic animals such as sea anemones), Pugh calculates that the lift provided by the float would be sufficient to balance the weight of the heavy parts. The

enormous size of the gas gland is doubtless a reflection of the physical problem of secreting gas at high partial pressures. Rhodaliids are found down to 3000 m. The same problem faces deep sea fishes and here the length of the *rete mirabile* (the gas secreting structure) has been shown to increase with the depth at which the fish lives (Macdonald, 1975).

3. Calycophorae

Jacobs (1937) established beyond question the importance of gelatinous tissues in flotation of siphonophores, especially of the Calycophorae where there are no gas filled floats. Gelatinous animals owe their buoyancy to the replacement of SO_4^{2-} by Cl^- , a lighter ion, as first shown by Robertson (1949). Bidigare and Biggs (1980) provide data on lift and sulphate exclusion for various species. Siphonophores exclude from 41–75% of their sulphate (Table 6). Oil drops are sometimes present in the somatocysts and elsewhere but probably play no significant role in flotation (Jacobs, 1937).

Jacobs (1937) showed that the posture of the floating siphonophore depends on the distribution of light and heavy parts. In some cases (e.g. *Sulculeolaria*, *Rosacea*, *Praya*) the bracts are buoyant enough to support the stem in a horizontal position but normally it trails beneath the buoyant nectophores. *Hippopodius* has a variable centre of gravity. When the stem is fully contracted the whole animal turns somersault. In this position, any swimming that takes place will drive the animal downward. *Hippopodius* and *Chelophyses* both appear capable of varying their specific gravity over a period of 30 min to 1 h but how they do so is unknown. Such changes might be important in vertical migration. Some medusae have been reported to be capable of changing their buoyancy in a similar way (Bethe, 1910) but a recent study showed no evidence of sulphate changes over the 24-h cycle as would be expected if ionic regulation were taking place (Mills and Vogt, 1984).

E. Colour, Luminescence, Camouflage, Mimicry

Many siphonophores are strikingly coloured, but little is known about the chemistry of the pigments concerned. The adaptive purposes served by the coloration are a matter for speculation. In some cases the colour may be due simply to ingested food, like the black pigment in the endoderm of *Erenna richardi*, which is thought to feed on deep water fishes (Totton, 1965a). In a recent dive in the Johnson-Sea-Link submersible Pugh (unpubl.) caught a large *Apolemia* in the act of devouring a coronate medusa, *Periphylla*. Analysis of the pigment from the gastrozooids of the siphonophore by Dr Herring

(Institute of Oceanographic Sciences, Wormley, UK) showed it to be a porphyrin, like the pigment of *Periphylla*.

The surface-living *Physalia*, like other members of the pleuston community, is blue. The float is deep blue or blue-green, tinged with pink at the crest and magenta at the pore end. The tentacles and other parts lying below the surface are also blue. The blue pigment was investigated chemically by Fox and Pantin (1944), who concluded that it was a carotenoprotein like the pigment of *Velella* and *Porpita*, and by Ball and Cooper (1974) who identified it as a chromatoprotein. A new study by Herring (1971) shows it to be a biliprotein complex, the prosthetic group of which is bilatriene. Other bile pigments are probably chiefly responsible for the other colours, although an ommochrome is present in the tentacles. All these pigments are probably derived from the food.

Planktonic siphonophores often have splashes of vermillion on the float, gastrozooids, tentacle batteries and stem. *Pyrostethos* gets its name ("fiery garland") from its brilliant vermillion coloration. Vivid scarlet or pink patches distinguish the gastrozooids of *Halistemma rubrum* and *Physophora*. The more delicate hues of *Athorybia rosacea* are well shown in sketches by Sabine Bauer (in Totton, 1954). One of the most effective representations of siphonophore pigmentation remains Chun's (1891) lithograph of *Stephanophyes superba*. Some deep-living species are completely colourless (e.g. *Cordagalma cordiformis* and *Lensia baryi* in deep coastal inlets of British Columbia) but others are strongly coloured in dark tones of red, brown and purple (such as *Marrus antarcticus* (Totton, 1954)). At least some rhodaliids are pigmented, e.g. *Stephalia corona* with its overall orange hue, and *Dromalia alexandri*, with its striking vermillion gastrozooids (Pugh, 1983).

The patchy type of patterning seen in *Agalma*, *Stephanophyes*, *Nanomia*, *Halistemma*, *Forskalia* etc. has been interpreted as a form of disruptive coloration (Mackie, 1962). By highlighting scattered, disconnected points, the pigmentation tends to break up the outline of the colony as a whole. Parts not pigmented are transparent. The overall effect is similar to that produced by a cloud of small, dispersed zooplanktonic organisms such as copepods. Thus the siphonophore tends to disappear in water containing these organisms.

The resemblance of pigmented parts to isolated zooplankters has evolved furthest in *Athorybia rosacea* and *Agalma okeni* where it is possible to speak of true mimicry (Purcell, 1980). In *Athorybia*, some of the nematocyst batteries are elongated structures with a pair of spots resembling eyes at the base, mimicking a fish larva (see Fig. 46B). Occasional rapid contractions of the tentilla make the batteries move like a larval fish. Red nematocyst batteries are present in *A. okeni*, each with a pair of long terminal filaments resembling the antennae of a copepod. Here too movements of the mimic



FIG. 40. Male gonophores of *Nanomia cara* showing red chromatophores in progressive stages of expansion following exposure to light after being kept in the dark. (A) contracted, (B) partially expanded, (C) fully expanded. Smallest spots (arrow in A) are thought to be single cells. Larger patches would be multicellular or syncytial "chromatosomes".

appear to simulate activity of the model. These structures probably serve as lures to attract prey.

Nanomia (and probably related physonects) can expand and contract some of its pigment patches (Mackie, 1962). The pigment, possibly an ommochrome, is contained in single chromatophores or in multinuclear, possibly syncytial, chromatosomes. Those located in the nectophores, gonophores (Fig. 40) and gastrozooids have been shown to expand in light and to contract in the dark. The transformation from fully dispersed to fully concentrated states takes about 45 min. The response appears to be evoked locally by the direct action of light on the chromatophore, which can thus be regarded as an independent effector. *Nanomia* migrates away from the surface during the day, but even in broad daylight specimens may be found at depths where there is sufficient light to support the activity of visual predators (Mackie, 1985). Under these conditions the dispersed and readily visible pigment could serve its postulated role in form disruption, but why

the pigment should become concentrated in the dark, when the animal is invisible anyway, is a mystery.

The blanching of *Hippopodius* has been considered earlier in Section 8 (p. 176). This unique response does not involve a pigment and is not a colour change in the usual sense. It serves not to disrupt the form of the animal but to make it more visible, possibly a defensive strategy. Bioluminescence was first described in *Hippopodius* by Korotneff (1884). Dubois (1898) reported light emission in "Praya", "Diphyes" and "Abyla". David (cited by Totton, 1954) added *Vogtia glabra* to the list. Nicol (1958) measured emission spectra and intensity in *V. glabra*, *V. spinosa* and *Rosacea plicata*. The only physonects known to luminesce are *Nanomia cara* (Mackie, 1962) and *Agalma okeni* (Pugh, unpublished). It is likely that many more species will prove capable of light emission.

In *Hippopodius* and *Vogtia* the light is produced in waves which spread diffusely over the surface of the nectophores. The stem and attached zooids are not luminescent. The light emitted in these species and in *Rosacea* is bluish. The spectral emission maximum for *V. glabra* was reported to be 470 nm by Nicol (1958), 455 nm by Herring (1983). Nicol obtained a value for radiant flux emission in *Vogtia spinosa* of $3.2 \times 10^{-3} \mu\text{W}/\text{cm}^2$ at a distance of 1 cm. He calculated that the animal could be seen 30 m away in clear water by an organism having visual sensitivity similar to that of man. Luminescence is evoked by mechanical disturbance in these cases. In *Hippopodius* the light is produced within the ectoderm and the response is propagated by electrical impulses in that tissue (Mackie and Mackie, 1967; Bassot *et al.*, 1978; Bassot, 1979).

In *Nanomia*, patches of luminescent cells are present in the ectoderm of the nectophores (Mackie, 1962, 1964) where they form two oblong patches situated symmetrically on either side of the exumbrella near the margin (as shown in Fig. 4 of Mackie, 1964). The bracts also have two, symmetrical photophores on the upper side near the tip (Freeman,* personal communication). The photophores develop early during the differentiation of the nectophores and bracts. Luminescence is first observed in the siphonula larva at about 48 h of development. Freeman finds that the smallest bracts and nectophore buds luminesce when stimulated with KCl after removal from the colony. As the nectophores and bracts age, they lose cells from the photophores, and may eventually lose the ability to luminesce. This "aging" process calls to mind the progressive shrinkage and eventual loss of the *rete mirabile* in older nectophores of *Hippopodius*. Freeman reports further that the bioluminescent response in *Nanomia* is mediated by a calcium specific photoprotein. Homogenated material extracted in a medium containing EGTA luminesces on addition of calcium, but not of KCl. A calcium specific photoprotein is responsible for luminescence, but the photophores differ

* See Addendum (p. 262).

from those of hydromedusae such as *Aequorea* in lacking green fluorescent material.

As to the functional role of these responses, the bright overall glow of *Hippopodius* and *Vogtia* probably serves to confuse, dismay or blind interlopers at night, much as the blanching response would by day. The conditions under which flashing occurs in *Nanomia* are poorly understood. Flashing has been seen in nectophores swimming away following autotomy. Under these circumstances, the exumbrellar epithelium, in which the photophores lie, experiences intense bursts of epithelial impulses, and it is therefore likely that the photophores are fired by propagated epithelial signals as in *Hippopodius*. Both bracts and nectophores are deciduous organs and autotomize following strong stimulation. Possibly, therefore, light emission of detached bracts and nectophores serves to distract the attention of predators from the intact colony, a role similar to that suggested for the scales of polynoid worms. The photophores in *Nanomia* are arranged in doublets like the ventral photophores of euphausiids, and the detached parts might therefore mimic crustacean microplankton.

IV. Nutrition and Ecology

A. Associations

1. Fish

The juveniles of several species of fishes have been found associated with neustonic *Physalia physalis* (Table 7). These associations are generally non-specific and temporary and the same species are more commonly associated with scyphomedusae than with *P. physalis* (Mansueti, 1963). Only the Man-of-War fish, *Nameus gronovii*, is found with *P. physalis* as adults. This association is cited as "the classic case of symbiosis between fish and jellyfish" (Mansueti, 1963), yet it cannot be considered an obligate association because *N. gronovii* also has been found with scyphomedusae and a chondrophoran (Table 7).

Nameus gronovii appears to swim among the tentacles of *P. physalis* unharmed. This species is not immune to the toxins of *P. physalis*, although it can withstand ten-times the dosage that kills other fishes (Lane, 1960), and has at least one antibody against the toxin (Mayo, 1968). Jenkins (1983) observed that *N. gronovii* did not display acclimating behaviour, and was stung upon contact with the tentacles. He concluded that *N. gronovii* is neither immune, nor acclimatized, but simply avoids contact with the tentacles.

The associations of small fishes with *Physalia physalis* are complex—both

TABLE 7. FISH ASSOCIATED WITH *Physalia physalis*

	Relationship	Location	Alternate hosts	References
Fam. Stromateidae <i>Peprilus alepidotus</i> (harvestfish)	facultative, temporary, juveniles	N Amer Atlantic and Gulf Coasts	<i>Chrysaora quinquecirrha</i> , <i>Cyanea capillata</i> , <i>Chiropsalmus quadrumanus</i> , unidentified	in Mansueti, 1963; Phillips et al., 1969
<i>Peronotus triacanthus</i> (butterfish)	facultative, temporary, juveniles	N Amer Atlantic and Gulf Coasts	<i>Chrysaora quinquecirrha</i> , <i>Cyanea capillata</i> , <i>Stomolophus meleagris</i> , unidentified	in Mansueti, 1963; Phillips et al., 1969
<i>Mupus maculatus</i> (spotted ruff 5.5 cm)	facultative, temporary, juveniles	Atlantic, Madeira	—	in Mansueti, 1963; Maul, 1964
<i>Mupus ovalis</i> (10 cm)	facultative, temporary, juveniles	Madeira	—	Maul, 1964
<i>Nomus gronovii</i> (Man-of-War fish)	permanent, juveniles and adults	Atlantic, Gulf of Mexico, Pacific	<i>Stomolophus meleagris</i> , <i>Porpita porpita</i> , unidentified	in Mansueti, 1963; Phillips et al., 1969
Fam. Carangidae <i>Caranx bartholomaei</i> (yellow jack 24-45 mm)	facultative, temporary, juveniles	Florida	—	in Mansueti, 1963
<i>Naucrates ductor</i> (pilot fish 5-15 mm)	facultative, temporary, juveniles	Atlantic, and China Seas	<i>Velilla</i> sp., unidentified	in Mansueti, 1963
Fam. Centriscidae <i>Macrorhamphosus scolopax</i> (longspine snipefish)	facultative, temporary, juveniles	Atlantic, Florida	—	in Mansueti, 1963

fish and siphonophore may benefit, and both may be at risk. The fishes seek refuge among the virulent tentacles of *Physalia physalis* and other jellyfish when they are frightened (Mansueti, 1963; Maul, 1964), probably gaining protection from potential predators. They may feed on the siphonophore, as seen for *Nomeus gronovii* in the laboratory (Jenkins, 1983) and they may feed on prey captured by *P. physalis* (as suggested for commensals of scyphomedusae (Mansueti, 1963; Phillips *et al.*, 1969). The primary foods of *P. physalis* are fish and fish larvae (Purcell, 1984b), and *N. gronovii* sometimes are caught and eaten by *P. physalis* (Jenkins, 1983; Purcell, personal observation). *Forskalia tholoides* has been reported to have juvenile fishes, with red and brown pigmentation similar to that of the siphonophore's stem groups, sheltered among the tentacles (Biggs, 1976a).

2. Invertebrates

Epipelagic, warm-water hyperiid amphipods, belonging to 12 or 13 families, are obligate symbionts of gelatinous zooplankters (Biggs and Harbison, 1976; Madin and Harbison, 1977; Harbison *et al.*, 1977; Laval, 1980). Five of these families (Paraphronimidae, Lyceopsidae, Pronoidae, Platyselidae, and Parascelidae), are associated exclusively with siphonophores (Fig. 41). Only two of the other families, Brachyscelidae and Lycaeidae, have no reported associations with siphonophores (Harbison *et al.*, 1977).

Amphipods are not found often on cystonect species. None are known from *Physalia physalis*, nor were any amphipods seen on hundreds of colonies of *R. eysenhardti* from the Gulf of California (Purcell, unpubl.). There is only a single record of an amphipod (*Thyropus* sp.) collected on *Rhizophysa filiformis* (Biggs, 1976a). Both *Thyropus edwardsii* and *Schizoscelus ornatus* have been reported from *Bathyphysa sibogae* (Biggs and Harbison, 1976).

Small, rapidly-swimming siphonophores seem to have low infestations of amphipods. No amphipods were seen on any of dozens of specimens of the temperate, neritic calycophorans *Muggiae atlantica* and *Sphaeronectes gracilis* (Purcell, unpublished.). *Lycaeopsis themistoides* occupies the cavity of the anterior nectophore of two diphyid species. *Paralycea* spp. apparently are associated principally with *Sulculeolaria* spp. *Rosacea cymbiformis* is a host for *Sympronoe parva* (Harbison *et al.*, 1977), and have very large infestations (one amphipod per seven cormidia (Purcell, unpubl.)).

Physonect siphonophores with many nectophores often have large infestations of juveniles (especially of *Thyropus* spp.) and encysted juveniles (*Eupronoe*). Some of the associations reported by Harbison *et al.* (1977) are based on single specimens, and they could not always establish the specificity of the associations, or determine the frequency of infestation.

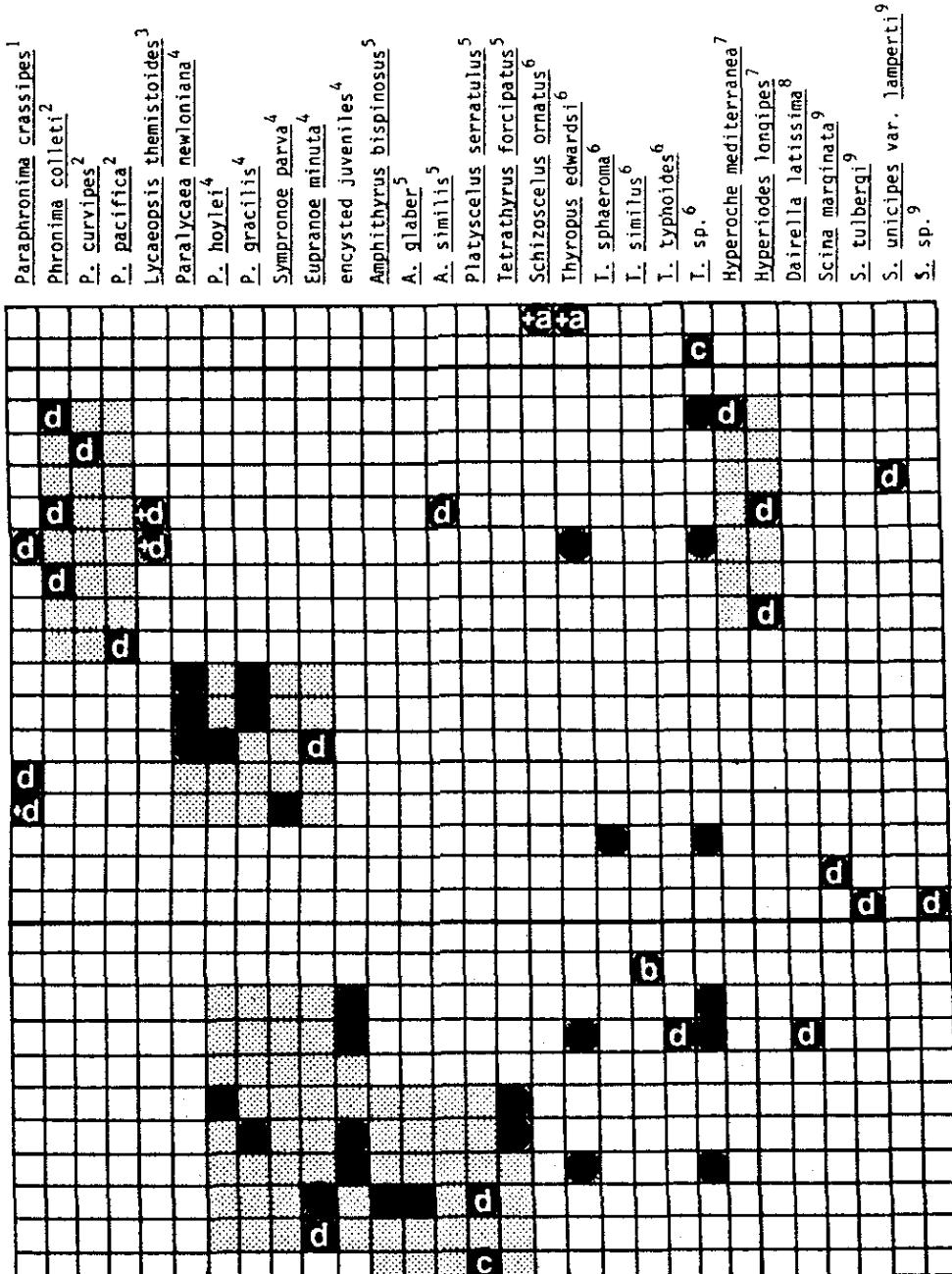
- Cystonectae**
- Bathyphysa sibogae
 - Rhizophysa filiformis

Calyphorae

 - Abyla trigona
 - Ablyopsis tetragona
 - Ceratocymba sigittata
 - Chelophyes appendiculata
 - Diphyes dispar
 - Diphyes
 - Lensia conoidea
 - L. fowleri
 - Sulculeolaria chuni
 - S. monoica
 - S. quadrivalvis
 - Geleolaria (=Sulculeolaria)
 - Rosacea cymbiformis
 - Stephanophyes superba
 - Hippopodius hippopus
 - Sphaeronectes gracilis

Physonectae

 - Athorybia lucida
 - A. rosacea
 - Forskalia spp.
 - Cordagalma cordiformis
 - Nanomia bijuga
 - Agalma clausi
 - A. okeni
 - A. elegans
 - Apolemia uvaria
 - Physophora hydrostatica



- 1 Fam. Paraphronimidae
- 2 Phronimidae
- 3 Lyceopsidae
- 4 Proniidae
- 5 Platyselidae
- 6 Parascelidae
- 7 Hyperiidae
- 8 Dairellidae
- 9 Scinidae

- a Biggs and Harbison, 1976
 - b Biggs, 1978
 - c Biggs, 1976a
 - d Laval, 1980
- all others — Harbison et al., 1977

FIG. 41. Hyperiid amphipods associated with siphonophores. ● = documented associations; shading = possible specific family associations (Purcell, unpublished).

Most of the amphipod species occurred on the surfaces of their siphonophore hosts or in natural cavities (in the bracts of *Rosacea cymbiformis*, or nectophores of the physonects), and appeared to cause little damage to the hosts (Harbison et al., 1977). However, they also state that "many hyperiids will eat the host's food or the host's tissue, depending on availability". Juvenile *Lycaeopsis themistoides* dig a burrow that connects the anterior nectosac to the hydroecium in diphyids. The amphipod then has protection

plus access to the stolon, where it can steal food or eat the gastrozooids. Juveniles also eat the epidermis of the nectosac.

The adult amphipods and the young that are deposited in the host tissues gain protection and probably food from the host. The hosts seem not to be seriously harmed by the associations, and sometimes may benefit. The amphipod symbiont of *Rosacea cymbiformis* occasionally was found partly digested in the gastrozooids (11 of 914 prey items (Purcell, unpublished)).

The phyllosoma larvae of lobsters have been observed by SCUBA divers riding on the siphonophores *Agalma okeni* and *Diphyes dispar* (Biggs, 1976a) as well as on other gelatinous zooplankton.

Immature specimens of the octopod *Tremoctopus violaceus* carry fragments of the tentacles of *Physalis physalis* along the rows of suckers of their four dorsal arms (Jones, 1963). Jones suggests that this octopod might be immune to the nematocyst venom, or the modified suckers insensitive to it. The tentacle pieces must be acquired carefully, unless the octopod is immune to the stings. This is especially clear because small cephalopods were the second most important prey of *P. physalis* (Purcell, 1984b). The tentacle fragments proved to be an effective defence against handling by scientists, but Jones suggests that in addition to defence, the tentacles would be very effective in subduing prey for the octopod. Jones believes that this association may be related to the habits of pelagic octopods in the families Tremoctopodidae and Argonautidae, which are not strong swimmers, and rest by attaching to pelagic cnidarians.

3. Parasites

Only a few parasites have been described from siphonophores. The peridiarian dinoflagellate, *Diplomorpha paradoxa*, was found in the subumbrellar ectoderm of the nectophores and bracts of *Forskalia* sp., *Chelophys* sp. and *Abylopsis* sp. (Rose and Cachon, 1951). Cachon (1953) transferred these parasites from *Forskalia* sp. to the gastrozooids of *A. tetragona*, where they became turgid with liquid absorbed through fingerlike projections. The parasites were expelled after 10–30 min and went through spore formation. Similar protozoans were seen on the exoskeletons of copepods, therefore it may be that *Diplomorpha* parasites are a stage in the life cycle of *Actinodinium* parasites of crustaceans.

Cachon *et al.* (1972) presented evidence that what were thought to be two stages in a complex life cycle of the protozoan *Trypanophysis grobbeni* may be two distinct parasites. The flagellate form of *T. grobbeni* was found in the gastrovascular cavities of physophorid and other physonect siphonophores, in the polygastric and eudoxid stages of *Chelophys*, *Diphyes*, *Muggiae*, and *Lensia*, and in the endodermal canals of the bracts of *Halistemma*. This

flagellate was conclusively identified in the Bodonidae. The second gregarine form, found in the mesogloea of *Chelophyses* and other siphonophores, greatly resembled a sporozoan germ.

Totton (1954) described the infestation of a specimen of *Hippopodius hippocampus* with 50 cercaria larvae of a trematode (*Lepocraedium album*), that made tubular tunnels in the mesogloea and lost their tails.

B. Predators

1. Vertebrates

Loggerhead turtles, *Caretta caretta*, often have been observed feeding on *Physalia physalis* (see Wangersky and Lane, 1960), but the importance of this siphonophore in the turtle's diet is unknown. They discuss how the turtles might be able to consume such a toxic meal. Their results suggested that although *C. caretta* lacks blood antibodies to the toxin of *P. physalis*, the turtles might possess localized tissue antibodies. Possibly, the skin of the head simply is impenetrable to nematocysts, and the acid of the digestive system could deactivate the nematocysts.

The sparse information about predation on siphonophores by other vertebrates has come mainly from studies on the diets of the predators (Table 8). Den Hartog (1980) identified nematocysts in the stomach contents of a leatherback turtle to be the distinctive birhopaloides of the siphonophore *Apolemia uvaria*, as well as others from at least one unidentified species of siphonophore, and a scyphomedusa. The importance in the diet is unknown. *Bassia bassensis* was a common prey of smallwing flyingfish (Table 8).

2. Invertebrates

Gelatinous zooplankters may be important predators of siphonophores. The siphonophore *Rosacea cymbiformis* consumed *Rhizophysa eysenhardtii* on two occasions *in situ* (Purcell, unpublished). The hydromedusa *Aequorea victoria* is known to feed on other gelatinous zooplankton (Arai and Jacobs, 1980). Polygastric and eudoxid stages of *Muggiaeae atlantica* averaged 7% of the prey items in the stomach contents of this medusa during March–June, 1983, although they generally constituted only 0.01–0.5% of the available zooplankton. *Dimophyes arctica* and *Nanomia bijuga* were much less abundant than *M. atlantica* and were eaten occasionally by *A. victoria* (Table 8). Other gelatinous predators of siphonophores include ctenophores, several hydromedusae, and scyphomedusae (*Chrysaora hysoscella* and *Pelagia*

noctiluca also had consumed unidentified siphonophores (Larson, 1976) (Table 8).

Pelagic molluscs also feed on siphonophores. The pneumatophores of *Nanomia bijuga* were found in the stomach contents of the heteropod *Carinaria cristata* (Seapy, 1980). Even if only the pneumatophore is eaten, it cannot be regenerated, and the siphonophore probably is destroyed. In the neuston, the snail *Ianthina prolongata* and the nudibranch *Glaucus atlanticus* consume *Physalia physalis* and chondrophorans (Bieri, 1966). Thompson and Bennett (1969) found that *G. atlanticus* and *Glaucilla marginata* stored the larger of the two size classes of *P. physalis* nematocysts undischarged in their dorsal cerata. This provides the nudibranchs with a potent defence against predators, and proved to be very painful to humans. The pelagic nudibranch *Cephalopage trematoides* feeds exclusively on *Nanomia bijuga* (Senz-Braconnot and Carré, 1966). Young nudibranchs were found attached to the stem of the siphonophores, and large ones were free-swimming and were seen mating in the Gulf of California. Forty-six percent of 50 siphonophore colonies collected during six days in August, 1978 had nudibranchs attached; 17 with 1 nudibranch, 3 with 2, 1 with 3, and 2 with 6 (Purcell, unpublished). The siphonophore colonies had a mean of seven gastrozooids, and occurred at a mean density of one colony/15 m³ at 5–10 m depth. Free-swimming nudibranchs averaged one/10 m³. The nudibranchs probably graze on the siphonophore colonies and do not consume them entirely, but at these densities, the nudibranchs may significantly affect the siphonophore populations.

The importance of siphonophores as food of vertebrates and zooplankton is poorly understood, due to the lack of dietary information on the predators and the difficulty of recognizing and identifying siphonophores in the gut contents of the predators.

C. Nematocysts

1. Development

Studies on living siphonophores by Carré (1972, 1973, 1974a,b,c), Carré and Carré (1973), and Skaer (1973) have been important in elucidating the processes of formation, migration and maturation of nematocysts. Siphonophores were valuable for these studies because they are transparent, some of their nematocysts are very large, and the tentacle nematocysts develop in a cuff 1 mm wide and 6–8 cells thick around the aboral end of the gastrozooid. In this region, clones of associated nematocysts arise from the same primordial cell, and are all of the same type and in the same stage of

TABLE 8. PREDATORS OF SIPHONOPHORES

Predator Species	Prey Species	Importance in diet	Location	Reference
Cnidaria				
Siphonophore	<i>Rhizophysa eysenhardti</i>	2 obs in situ	Gulf of California, Mexico	Purcell, unpubl
<i>Rosacea cymbiformis</i>			Strait of Georgia, Canada	Purcell, in prep
Hydromedusae			Strait of Georgia, Canada	Purcell, in prep
<i>Aequorea victoria</i>	<i>Muggiae australica</i>	5.8% of prey	Strait of Georgia, Canada	Purcell, in prep
	eudoxids, polygastric	<0.1% of prey	Strait of Georgia, Canada	Purcell, in prep
	<i>Dimophyes arctica</i>	0.2% of prey	Strait of Georgia, Canada	Purcell, in prep
	eudoxids, polygastric	NQ	Western N Atlantic	Biggs, 1976b
	<i>Nanomia cara</i>	NQ	Western N Atlantic	Madin, in Biggs, 1976b
	<i>Abylopsis eschscholtzii</i>			
leptomedusa	<i>Physophora hydrostatica</i>			
<i>Orchistoma</i> sp.				
Scyphomedusa				
<i>Phacellophora camtschatica</i>	<i>Muggiae australica</i>	12.6% of prey	Queen Charlotte Islands, Canada	Purcell, in prep
	eudoxids, polygastric			
Ctenophora				
	<i>Cestum veneris</i>	0.5% of prey	N Atlantic	Madin, pers comm
	<i>Eurhamphea vexillifera</i>	2.7% of prey	N Atlantic	Madin, pers comm
	<i>Ocyropsis maculata</i>	NQ	Western N Atlantic	Biggs, 1976b
	<i>Chelophyses appendiculata</i>	NQ	Western N Atlantic	Biggs, 1976b
	calycophoran	3.7% of prey	N Atlantic	Madin, pers comm
	<i>C. appendiculata</i>	NQ	Western N Atlantic	Biggs, 1976b
Mollusca				
Heteropods	<i>Nanomia bijuga</i>	3% of prey	Southern California, USA	Seapy, 1980
	physosnec bracts	5 obs in situ	Florida Current	Hamner et al., 1975
Nudibranchs				
	<i>Carinaria cristata</i>			
	<i>Pterotrachea coronata</i>			
	<i>Cephalopage trematoides</i>			
	<i>Glaucus atlanticus</i>			
	<i>Physalia physalis</i>	100% of diet	Villefranche, France	Sentz-Braconnet and Carré, 1966
		preferred to	Gulf of California, Mexico	Purcell, unpubl
		<i>Velella</i> and <i>Porpita</i>	Seto Marine Lab, Japan	Bieri, 1966

<i>Glaucilla marginata</i>	<i>Physalia physalis</i>	NQ		Southeastern Australia	Thompson and Bennett, 1969
Snail					
<i>Ianthina longigata</i>	<i>Physalia physalis</i>	not preferred		Seto Marine Lab, Japan	Bieri, 1966
Polychaete	<i>Eudoxoides spiralis</i>	NQ		Western N Atlantic	Biggs, 1976b
Crustacea					
Barnacle	<i>Physalia physalis</i>	NQ		Seto Marine Lab, Japan	Bieri, 1966
Vertebrates					
Turtles				various	
<i>Caretta caretta</i>	<i>Physalia physalis</i>	NQ		Malta, Mediterranean	
<i>Dermochelys coriacea</i>	<i>Apolemia uvaria</i>	NQ			
	unidentified species				
Fish					
<i>Oxyporhamphus micropterus</i>	<i>Bassia bassensis</i>	13% by weight		Solomon Islands	Lipskaya, 1980
<i>Trachurus symmetricus</i>	unidentified				Konchnina, 1980
black marlin	<i>Physalia physalis</i>	in 0.2% of fish			Hubbs and Wisner, 1953
oceanic filefish	<i>Agalma elegans</i>	observations			
		shipboard obs			Biggs, 1976b

NQ = not quantified

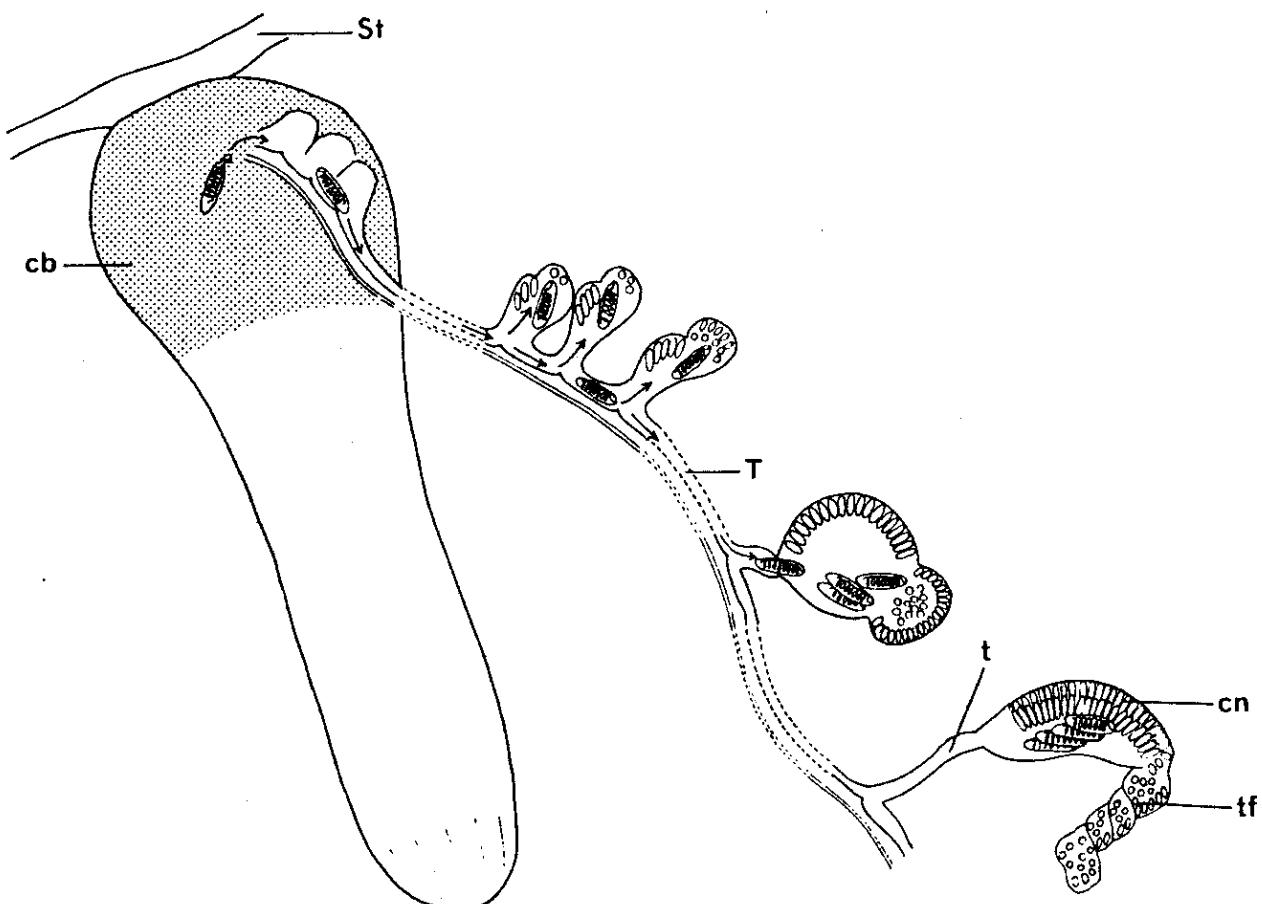


FIG. 42. Migration of developing nematocysts from the cnidogenic band in the gastrozoids to the nematocyst batteries. St. stem, cb. cnidogenic band, T. tentacle, t. tentillum, tf. terminal filament, cn. cnidoband. After Carré (1974a) (no scale given).

development (Carré, 1974a). The number of nematoblasts (cells) in a clone depends on the nematocyst type and differs among species. In *Apolemia uvaria*, birhopaloïdes and isorhizas occur in clones of 16 cells, and mastigophores and stenoteles in clones of eight cells, but in *Rhizophysa filiformis*, isorhizas and stenoteles occur in clones of four cells. The size of the clone is not controlled solely by a predetermined number of mitoses in the primordial cell, but appears to depend on activation (induction) by a number of interstitial cells.

Carré (1972) and Skaer (1973) examined the development of nematocysts in the siphonophores *Muggiae kochi* and *Rosacea cymbiformis*, respectively. The development of nematocysts begins with formation of the capsule. A tube external to the capsule grows out from it by accretion of secretory droplets from the associated Golgi apparatus in the enclosing nematocyte. The tip of the external tube then inverts, beginning at the tip, and progressively travels down the inside of the tube and into the capsule. Earlier researchers of nematocyst development in other cnidarians believed that the tubule formed inside the capsule and that the external tubules observed were due to partial discharge caused by fixation. Invagination requires about 2 h in *Hippopodius hippopus* (Carré, 1974a), and about 4 h in *Rosacea cymbifor-*

mis (Skaer, 1973). During this process of invagination, the tubule walls become triply pleated at right angles to the axis of the tubule and the barbs begin to form in three helices along the inverted surface of the tubule.

Migration of the nematoblasts from the cnidogenic band in the gastrozooid to their final positions begins before the invagination of the nematocyst tubule is complete (Fig. 42) (Carré, 1974b). The nematoblasts migrate, probably by amoeboid movements, at the base of the ectodermal layer. The speed of migration is 0.1 to 0.5 mm h⁻¹ and was measured precisely by observing stenoteles migrating to the tip of the palpons of *Physophora hydrostatica* at 0.4 mm h⁻¹.

The maturation process is discussed by Carré (1974c). In some types of nematocysts, the first stage of maturation (spine formation) begins in the cnidogenic band in the gastrozooids, but in other types, maturation begins when the nematoblasts arrive in the developing tentilla. Maturation includes spine formation on the nematocyst thread, shape changes of the capsule, chemical changes, and formation of the cnidocil (trigger, a modified flagellum). Changes in the nematocyst are accompanied by changes in the nematoblasts, which first were primarily secretory, next migratory, and lastly modified for the controlled discharge of the nematocyst.

Carré (1974c) believes that the production of nematocysts is regulated by interstitial cells, and that the destiny of each is determined in the cnidogenic band in the gastrozooid. She summarizes the duration of the different stages of nematocyst formation:

secretion of the capsule and thread—2 to 3 days
invagination of the thread—1 to 2 h
migration—a few hours
maturation—1 day.

The entire process requires 4–5 days, in accordance with information on nematocyst formation in *Hydra*.

2. Types

The nematocysts of calycophoran and physonect siphonophores are concentrated in nematocyst batteries (Fig. 43), one battery on each of several side branches (tentilla) of the tentacles. Nematocyst batteries consist of a cnidoband with many rows of homotrichous anisorrhizas, several larger microbasic mastigophores or stenoteles along the cnidoband, an elastic ligament, usually one or two terminal filaments with small nematocysts, and an involucrum that encloses part of the battery in some species. The battery nematocysts fire as a unit when the terminal filaments are pulled and stretch the elastic ligament.

Nine or ten of the 25 recognized nematocyst types (Mariscal, 1974) are

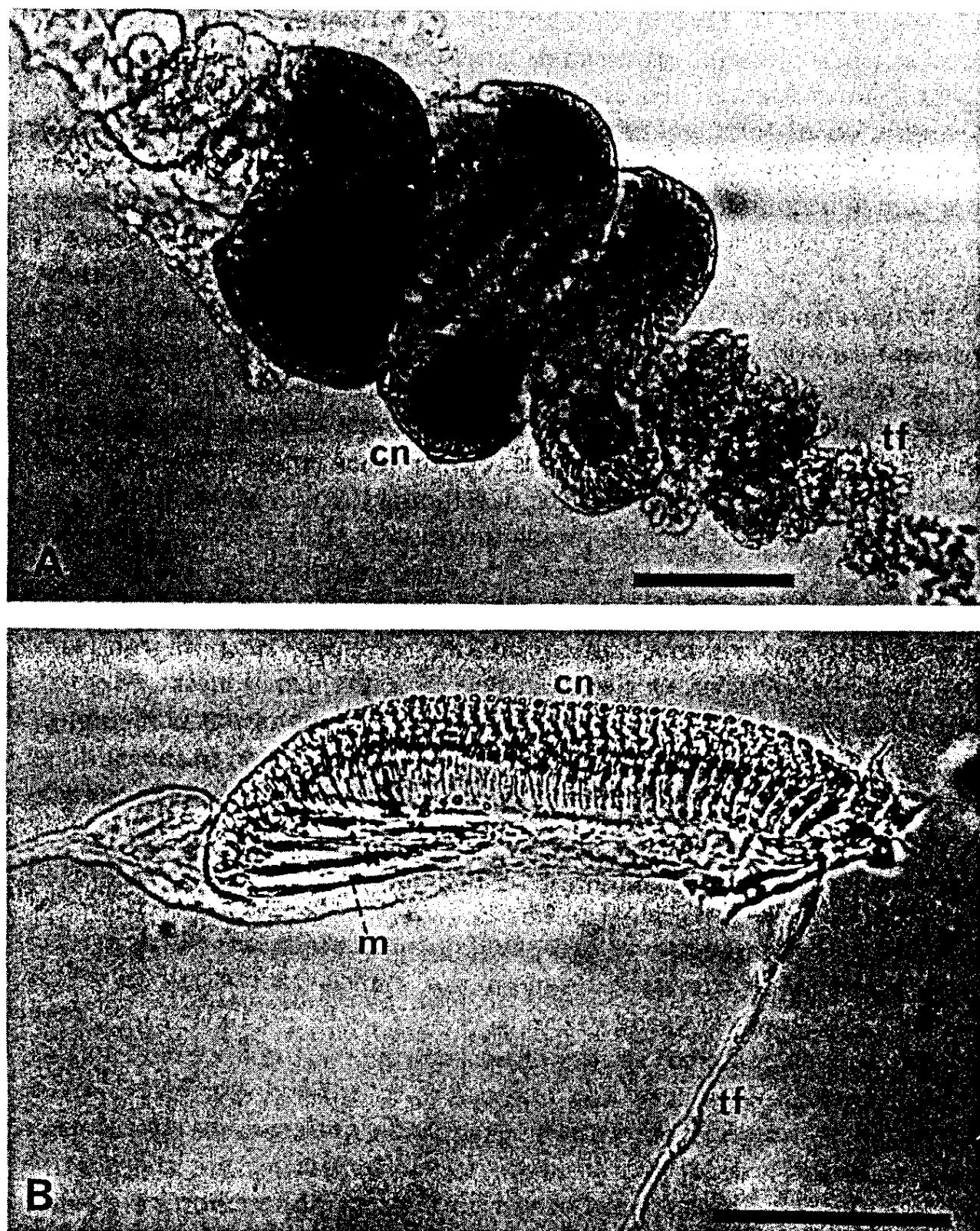


FIG. 43. Nematocyst batteries of siphonophores. A *Physonect Nanomia bijuga*. B *Calyco-*
phore Diphyes dispar. cn. cnidoband, tf. terminal filament, m. mastigophore. Scales = 100 µm
(from Purcell, 1984a).

found in the tentacles of siphonophores (Table 9). Purcell (1984a) compiled information on siphonophore nematocysts in the batteries from earlier studies (notable among those are Iwanzoff, 1896; Schneider, 1899, 1900; Weill, 1934; Werner, 1965), and identified nematocysts from numerous

TABLE 9. NEMATOCYST TYPES FOUND IN SIPHONOPHORES

	Cystonectae	Physonectae	Calycophorae
Rhopalonemes			
anacrophores*	—	TF	TF
acrophores*	—	TF	—
Spironemes			
desmonemes	—	TF	TF
Haplonemes			
atrichous isorhizas	T	B (?)	—
holotrichous isorhizas	T	—	TF, NB
homotrichous anisorrhizas*	—	NB	NB
Heteronemes			
microbasic mastigophores	—	NB	NB
microbasic euryteles	—	N	NB (?)
stenoteles	GA, GO	NB, P	—
birhopaloides*	—	T	—

* Exclusively in siphonophores; ?, uncertain identification; B, bract; GA, gastrozooid; GO, gonozooid; N, nectophore; NB, nematocyst battery; P, palpon; T, tentacle; TF, terminal filament; —, absent.

epipelagic species. Calycophorans had from 50–2000 homotrichous anisorrhizas (12×2 – $45 \times 9 \mu\text{m}$) aligned in rows in their straight cnidobands, several holotrichous isorhizas (7×5 – $23 \times 13 \mu\text{m}$) at the unattached end of the battery, from 4 to 50 microbasic mastigophores (36×7 – $111 \times 13 \mu\text{m}$) at the attached end of the battery, and anacrophores, desmonemes and/or holotrichous isorhizas in the single terminal filament (Fig. 44). As pictured in Biggs *et al.* (1978) for *Rosacea flaccida*, the terminal filaments have a pair of rhopalonemes between each desmoneme. Each calycophoran species generally had five distinct nematocyst types in the batteries. Physonect species had 150 to 20 500 holotrichous isorhizas (22.5×5.5 – $72.5 \times 12.5 \mu\text{m}$) in rows in the coiled cnidobands, either 4–80 stenoteles (22.5×12.5 – $32.5 \times 7.5 \mu\text{m}$) or, in the genus *Agalma*, 11–120 microbasic mastigophores (112.5×20 – $180 \times 28 \mu\text{m}$) along the cnidoband, and 1 or 2 nematocyst types (acrophores, anacrophores, or desmonemes) in the terminal filaments (Fig. 44). Each physonect species had 3 or 4 distinct nematocyst types in the batteries.

Cystonect siphonophores have only isorhizas in the tentacles (Fig. 44). Holotrichous tubules occur in *Physalia physalis* and *Rhizophysa filiformis*, and atrichous tubules in *R. eysenhardti*. These nematocysts are not organized into batteries, but occur in clusters in *Bathyphysa sibogae* (Biggs and Harbison, 1976) and in *R. filiformis* (Totton, 1965a; Purcell, 1984a), and in bands in *P. physalis*.

There is some confusion in the literature regarding the precise identity of some siphonophore nematocysts. Anacrophores, acrophores and desmo-

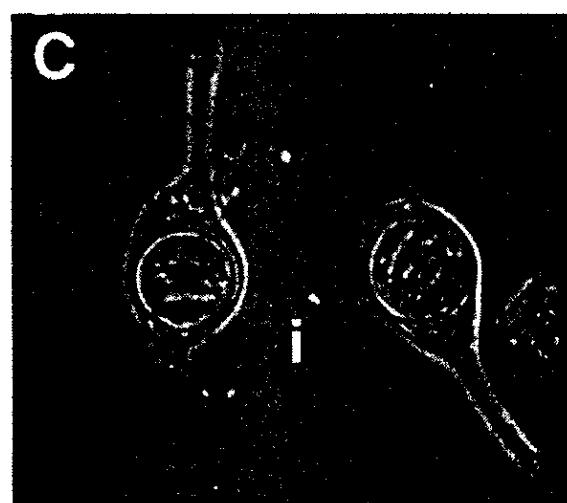
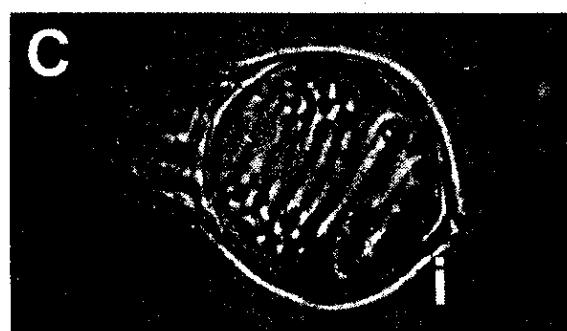
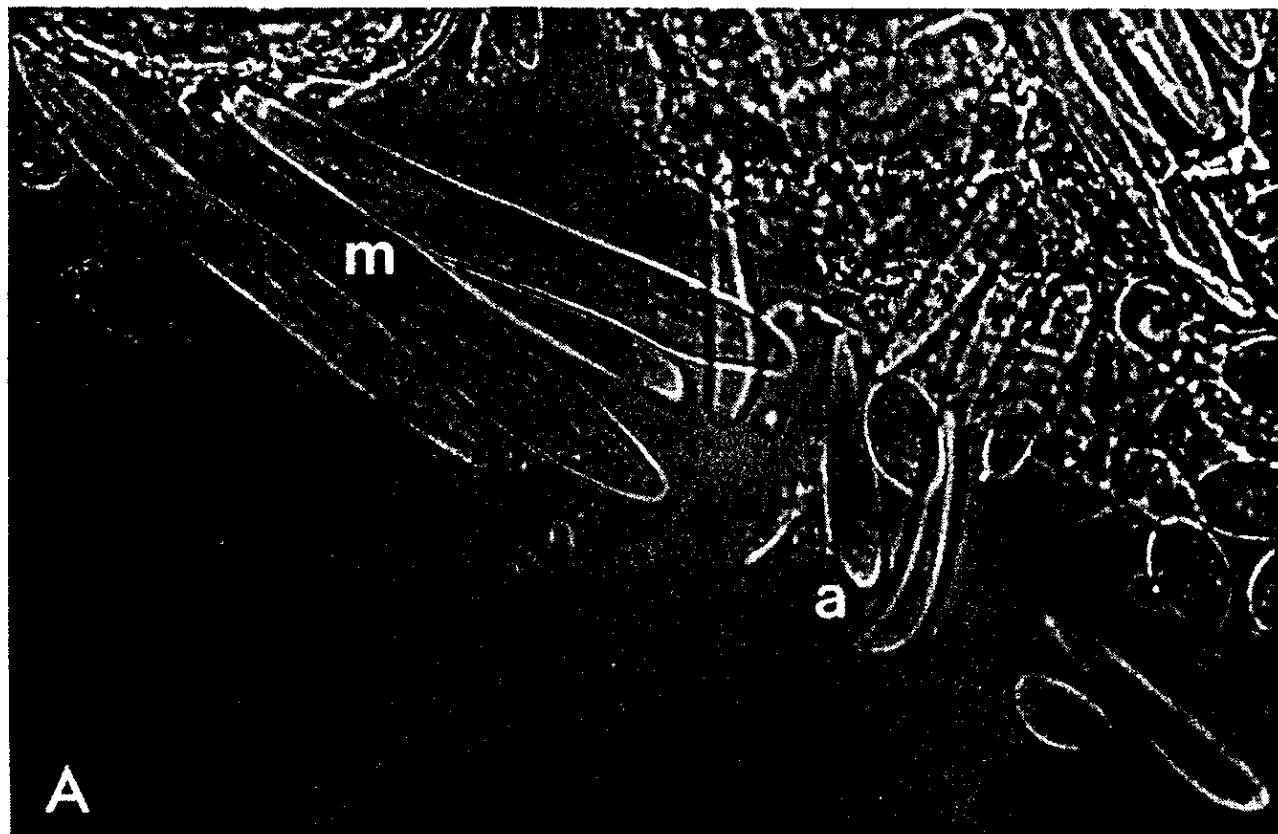


FIG. 44. Nematocysts of siphonophores. A *Calycophore Rosacea cymbiformis*. B *Physonect Nanomia bijuga*. C *Cystonect Physalia physalis*. Scale = 10 μm . m. microbasic mastigophore; a. homotrichous anisorhizas; i. holotrichous isorhizas; s. stenotele (from Purcell, 1984a).

nemes, which are small nematocysts (3.0×1.5 – $23.0 \times 3.0 \mu\text{m}$) found in the terminal filaments, may have been confused with one another or identified in an undischarged state in some cases. Several authors, working without benefit of scanning electron microscopy, identified some nematocysts as atrichous when, in fact, minute spines are present on the tubules (e.g. the isorhizas in *Physalia physalis* (Weill, 1934; Werner, 1965). This may be the case in *Muggiae atlantica* (in Russell, 1938), because only homotrichous (not atrichous) anisorhizas have been seen in other siphonophores. Werner (1965) considers macrobasic euryteles to be present in the cnidome of siphonophores, unlike other authors. Microbasic euryteles are intermediate in appearance to stenoteles and microbasic mastigophores, and may be confused with either type, as may have been the case for *Agalma elegans* (Russell, 1939; Werner, 1965).

The nematocysts examined to date are almost exclusively from the tentacles of the siphonophores, with the following exceptions. Isorhizas were identified from the bracts of *Apolemia uvaria*, and stenoteles from the palpons of *A. uvaria* and *Physophora hydrostatica*, and the gastrozooids of *Rhizophysa filiformis* (Carré, 1974a,b). Russell (1939) identified microbasic euryteles (stenoteles?) from the velar opening of the nectophores of *Agalma elegans*, and Weill (1934) identified stenoteles from the gonophores of *Physalia physalis*. There cannot be full confidence in the completeness of the list of nematocyst types in Table 9 until the other parts of the siphonophore colonies are examined in a systematic manner and a greater proportion of the species have been examined.

3. Use in feeding

These differences in nematocyst types are related to differences in feeding among the three suborders (see p. 228). Most calycophorans feed primarily on small copepods; most physonects consume larger zooplankton, including copepods and other crustaceans; and cystonects consume soft-bodied prey, mostly larval fishes. Purcell (1984a) gave natural prey to siphonophores in the laboratory, then retrieved the prey after capture, but before ingestion, and examined them by scanning electron microscopy in order to determine the effects of nematocysts on various prey. Prey capture seemed to result from entanglement (Fig. 45). The nematocyst tubules of calycophorans and physonects adhered to the surfaces of both hard-bodied and soft-bodied prey. No penetration of the prey by the nematocyst tubules was evident, except possibly by some stenoteles at the joints in crustacean exoskeletons where the cuticle is thin. The mechanism of penetration of crustacean exoskeleton by stenoteles was described by Tardent and Holstein (1982). In contrast, the nematocyst tubules of *Physalia physalis* penetrated fish larvae,

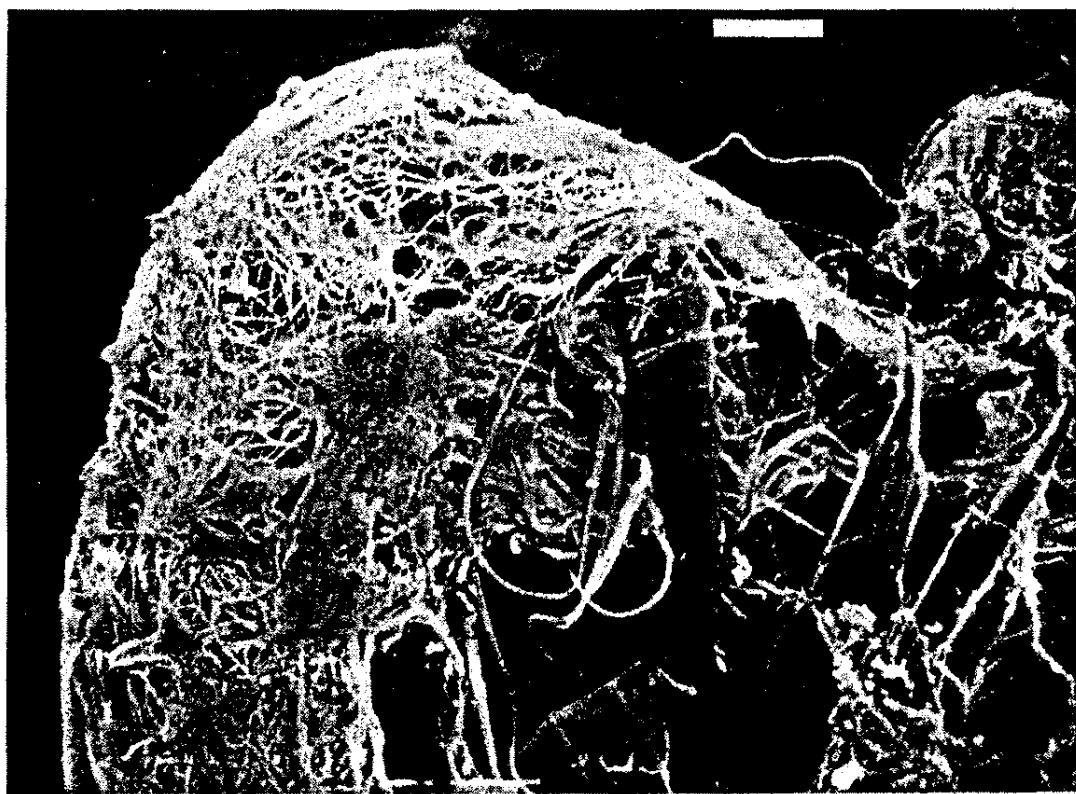


FIG. 45. Copepod entangled in the nematocyst tubules of *Forskalia edwardsi*. Scale = 100 µm (from Purcell, 1984a).

but were not seen to penetrate or adhere to a shrimp. The tubules of cystonect nematocysts had minute spines or none, and may penetrate soft tissue but not adhere well. The tubules of most calycocephoran and physonect nematocysts have comparatively large spines that clearly adhere to prey, but may be unsuitable for penetration. Thus, differential prey capture among the three suborders is related to the types of nematocysts. There also may be differences among suborders in the appropriate chemical and/or mechanical stimulus required for nematocyst discharge, but this remains to be determined.

The nematocyst batteries of some physonects resemble small zooplankton, and may be used to attract large prey to these weakly-swimming siphonophores (Fig. 46) (Purcell, 1980). The batteries of *Agalma okeni* resemble copepods, and some of those of *Athorybia rosacea* resemble fish larvae. The periodic contractions of the tentilla bearing these batteries may attract zooplankton or other predators by visual or vibrational stimuli. Fishes were attracted by the sergestid shrimp-like nematocyst batteries of an unidentified mesopelagic siphonophore in the Santa Barbara Basin (B. H. Robinson, personal communication).

4. Discharge

Cormier and Hessinger (1980b) examined the ultrastructure of the cnidocil apparatus of *Physalia physalis*. The cnidocil apparatus consists of a modified

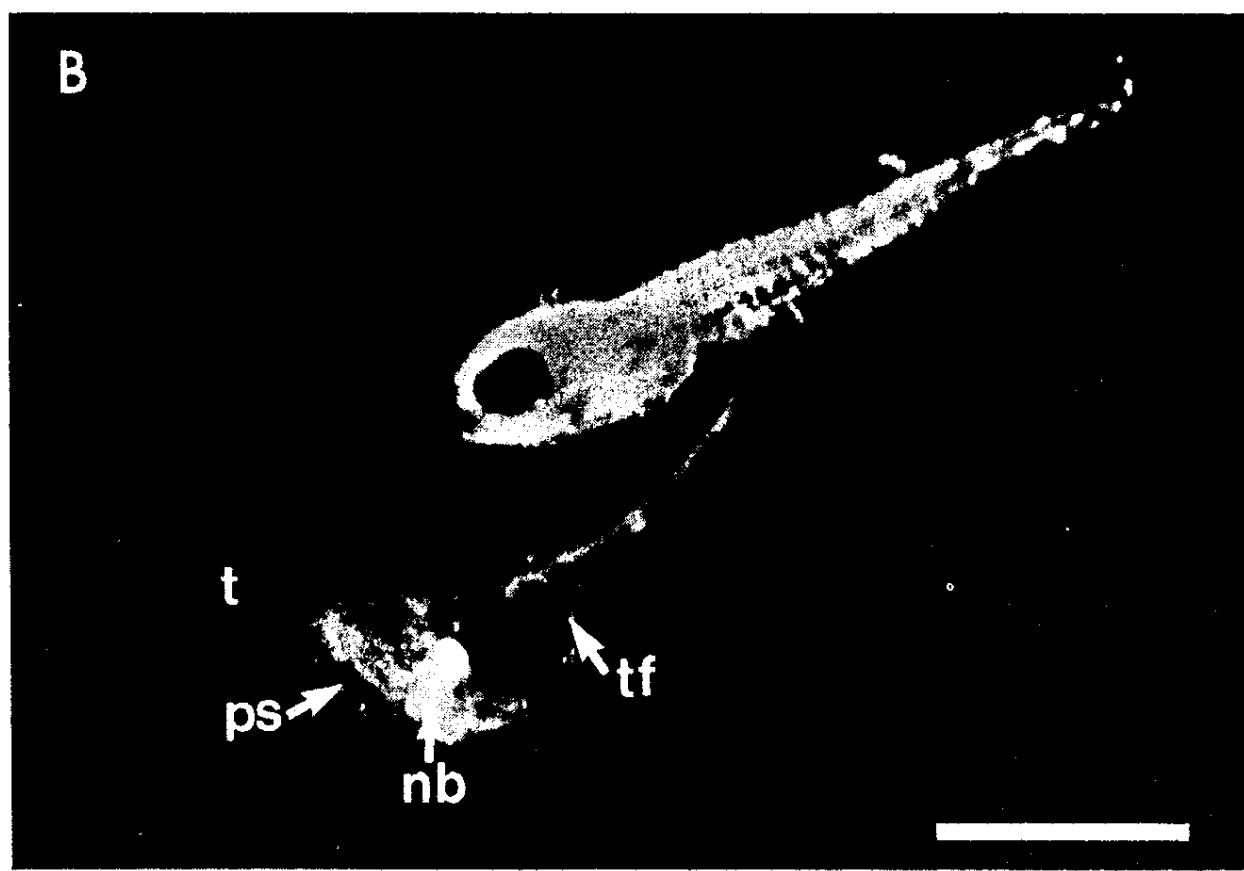
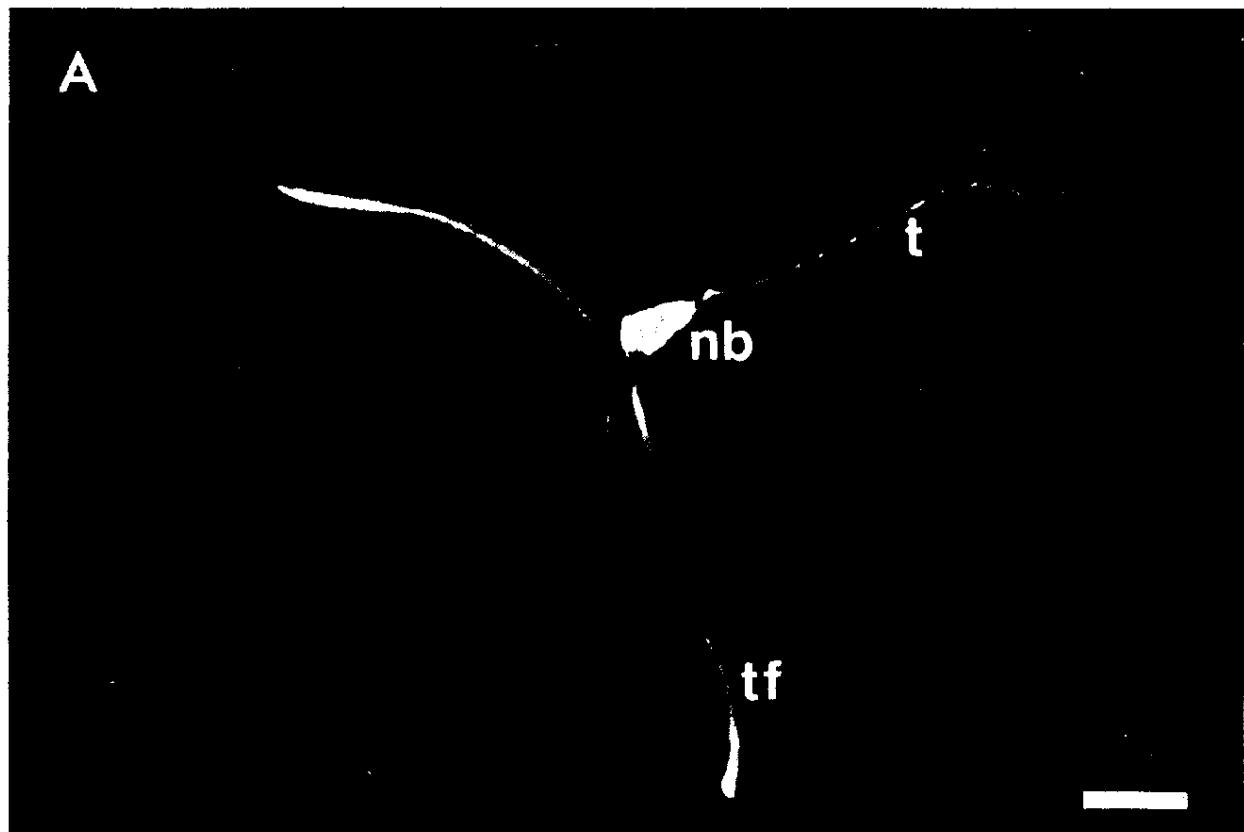


FIG. 46. *A* *Agalma okeni* nematocyst battery resembling a copepod. The terminal filaments (tf) appear similar to the antennae of a copepod. *B* Comparison of a fish larva (top) with a nematocyst battery from *Athorybia rosacea*. Two pigmented spots (ps) at the enlarged "head" resemble eyes, two terminal filaments (tf) curl back in the position of pectoral fins. t. tentillum; nb. nematocyst battery. Scale bars = 1.0 mm (from Purcell, 1980).

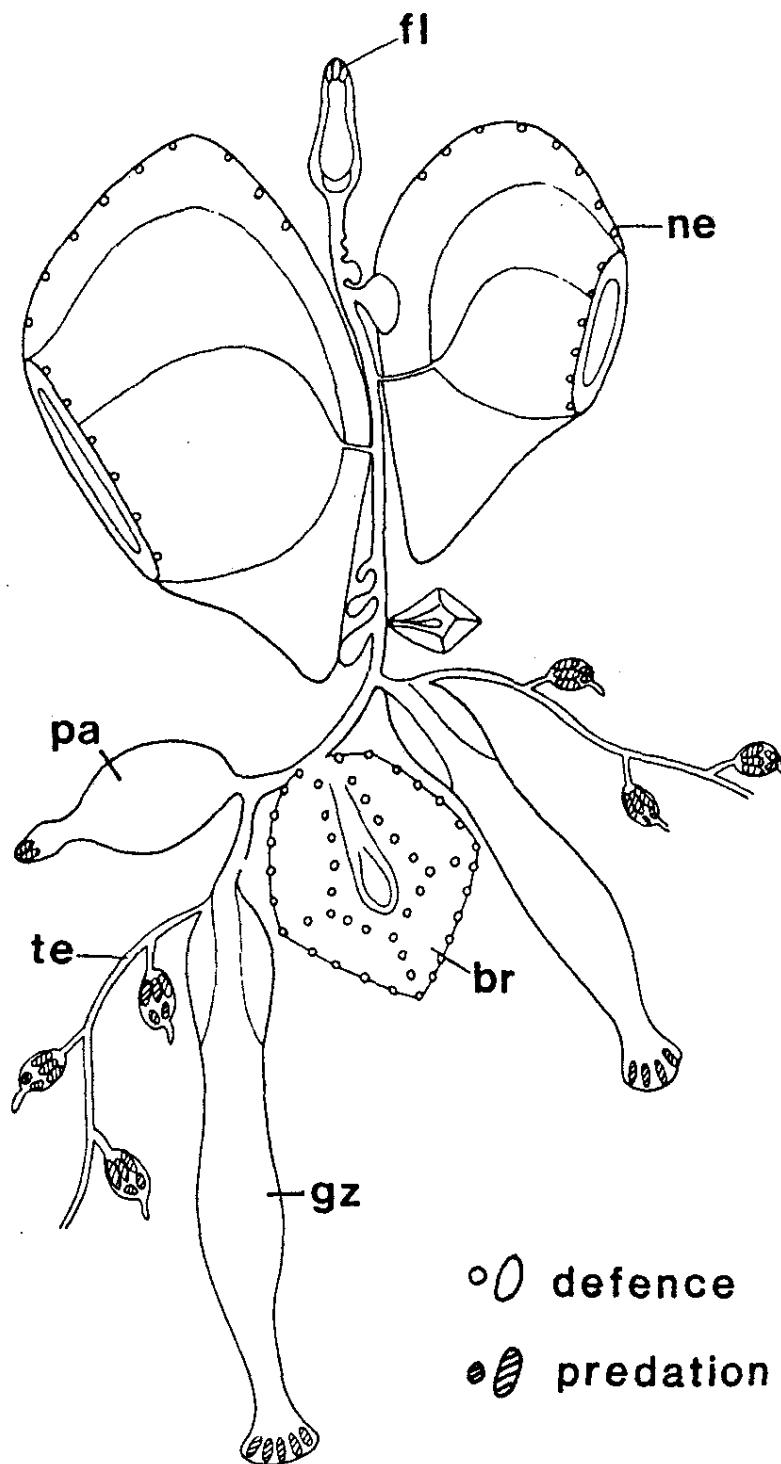


FIG. 47. Distribution of nematocysts used for predation and defence in a young colony of *Cordagalma cordiformis*, 1 cm. long. After Carré and Carré (1980). br. bract. fl. float, gz. gastrozooid, ne. nectophore, pa. palpon, te. tentacle.

cilium 2.5 nm in length that shows the classical 9+2 microtubule arrangement of most cilia and flagella only in the basal plate region. Distally, 27 microtubule doublets surround a central core of numerous singlet microtubules. The central cilium is ringed by 15–21 shorter stereocilia, all of equal height. A striated rootlet extends from the basal body, and joins the fibrillar basket along the outside of the nematocyst capsule, which anchors the nematocyst to the acellular mesogloea of the tentacle (Cormier and Hessinger,

1980a). A striated rootlet from each stereocilium forms the fibrillar collar which is in close proximity to the cnidocil and the operculum and may function to cause discharge. They suggest that the stereocilia and fibrillar system may be responsible for mechanoreception, and that the microtubule arrangement of the cnidocil resembles known chemoreceptors. They propose that the nematocyte alone receives and transduces sensory stimuli and causes nematocyst discharge.

Carré and Carré (1980) addressed the question of whether nematocysts are independent effectors, or whether they require nervous control for discharge. Both categories of nematocysts were found in the siphonophores *Apolemia uvaria* and *Cordagalma cordiformis* (Fig. 47). Nematocysts presumably used for defence were found in the pneumatophore, nectophores, and bracts. These lacked nerve connections, but could be affected by epithelial conduction (see p. 182). Nematocysts presumably used for feeding, found in the nematocyst batteries, palpons and mouth of the gastrozooids, had nerve synapses to the cnidocytes. All cnidocytes had cnidocils, indicating that an external receptor is required. Carré and Carré suggested that the nematocysts under nervous control have a variable threshold for discharge, subject to the physiological state of the siphonophore, but that those without nerve connections have a fixed threshold, and fire automatically upon appropriate stimulation.

5. Toxinology

The toxic characteristics of the nematocysts have been of great interest in *Physalia physalis* because of their health hazard to humans, but have not been studied in other siphonophore species. *Physalia physalis* is considered to be the second most toxic and deadly stinging marine organism, only less dangerous than the sea wasp, *Chironex fleckeri* (Cubomedusae). The symptoms in humans of stinging by *P. physalis* include intense pain, inflammation and haemorrhage of the skin, weakness, nausea, muscle and vascular spasms, difficulty and pain in respiration, pulmonary congestion, vertigo, renal failure, and shock (Russell, 1984).

In order to study the characteristics and effects of the nematocyst venom, Lane and Dodge (1958) and subsequent workers have isolated undischarged nematocysts, discharged them, and attempted to purify the released toxins. This method presumably prevents contamination by tissues that are known to have toxic properties distinct from those of the nematocyst toxins. The resulting crude toxic extract or "venom" causes paralysis and death when injected into fiddler crabs, frogs, fish, mice, and dogs. It stops the beat of the myogenic heart of vertebrates, possibly by affecting membrane ionic conductance, and stops the beat of the neurogenic heart of crustaceans, apparently

by blocking the myoneural junction (Mariscal, 1974). It also stops muscle contraction, possibly by reducing Ca^{2+} transport in the sarcoplasmic reticulum. It causes increased sodium transport in membranes and damages membranes of cellular organelles (Burnett and Calton, 1977).

The crude venom can be separated by gel electrophoresis or chromatography into 8–9 fractions (Burnett and Calton, 1977). These are primarily proteinaceous, but include free fatty acids and cholesterol. Six enzymatic actions are seen, namely ATPase, non-specific aminopeptidases, RNAase, DNAase, AMPase, and fibrinolysin. The major component of the venom is physalitoxin, a three-subunit protein of 240 000 MW, which comprises 28% of the total venom protein (Tamkun and Hessinger, 1981). This is the first haemolytic toxin purified from isolated nematocysts, and seems to be responsible for the venom's haemolytic and lethal properties. The doses of whole venom and purified physalitoxin that resulted in 50% mortality (LD_{50}) in groups of mice were 145 μg protein/kg mouse and 200 μg /kg mouse, respectively. The intermediate doses that caused between 0% and 100% mortality were narrow, ranging from 0.9–1.4 times- LD_{50} for the venom and 0.7 to 1.2 times- LD_{50} for physalitoxin. They conclude that physalitoxin is 5–6 orders of magnitude more potent than cobra cardiotoxin or melittin, and 3 orders of magnitude more potent than haemolytic toxin from the sea anemone *Stoichactis helianthus*.

Lin and Hessinger (1979) suggest that the haemolytic mechanism of *Physalia* venom involves initial binding of the haemolytic factor to sites on the red blood cell membrane, and subsequent lesion of the membrane. They show that glycophorin, one of the integral membrane glycoproteins of red blood cells, may be the binding site for the haemolytic factor.

The symptomatic pain apparently is caused by destructive enzymes or kinin-like substances, but histamine, serotonin, and prostaglandins *E* and *F* are not present in the venom (Burnett and Calton, 1977). The symptoms can be explained by toxin-induced histamine release from the victim's mast cells (Cormier, 1981; Flowers and Hessinger, 1981). Eighty per cent of the cells' histamine was released. Lactate dehydrogenase, a cytoplasmic marker, was also released, indicating that the toxin causes histamine release by cytolytic means, causing lesions in the plasma membrane (Flowers and Hessinger, 1981). The venom also causes vasodilation in vascular smooth muscle. Only a small part of this effect is histaminergic, but rather it is mediated by stimulating synthesis of the victim's endogenous prostaglandins (Loredon *et al.*, 1985). In summary, the toxin of *Physalia physalis* nematocysts is complex. Its actions are principally due to proteins that disrupt cell membrane structure and function.

Production of an antiserum against the venom of *Physalia physalis* has not been possible due to severe toxicity causing death upon repeated immuniza-

tion. Gaur *et al.*, (1982) isolated hybridomas that secreted monoclonal antibodies against mouse lethal factors from the venom. Their immunofluorescence experiments indicated that part of the lethal action is localized to the walls or tubules of the nematocysts. These experiments may lead to effective immunization and to identifying the location of the venom within the nematocysts.

D. Feeding

1. Structure

Siphonophores capture zooplankton prey using tentacles armed with nematocysts. Each gastrozooid of the siphonophores bears one tentacle, which has side branches (tentilla), each with a nematocyst battery (see p. 213) except in three species. The cystonect *Bathyphysa conifera* is reported to have unbranched tentacles, unlike its congener *B. sibogae* (Totton, 1965a). In *Physalia physalis* there are two types of unbranched tentacles. One type is blue-pigmented, helically-coiled and may extend at least 10 m in length (Mackie, 1960b). The other type is more numerous, white, and only extends a metre or so. Both types have bands of isorhiza nematocysts perpendicular to the length of the tentacle. The tentacles of the physonect *Apolemia uvaria* are unique among the siphonophores in several respects (Totton, 1965a): (1) *A. uvaria* bears a bunch of tentacles at the base of each nectophore; (2) each cormidium bears one or more gastrozooids, each with an unbranched tentacle, and 50 or more palpons, each with a similar unbranched tentacle (palpacle); (3) the tentacles and palpacles lack nematocyst batteries; and (4) the nematocysts, birhopaloides ($2 \times 12 \mu\text{m}$ capsule), have a tubule with two swellings, and are unique among all cnidarians so far examined.

2. Fishing behaviour

Siphonophores other than *Physalia physalis* feed while drifting motionless in the water with their tentacles extended. This is in contrast to many hydro-medusae and scyphomedusae, which feed as their tentacles are moved continually through the water by active swimming and/or sinking behaviours (Mills, 1981a). Thus, siphonophores depend upon prey to swim into contact with their tentacles.

Most calycophoran and physonect siphonophores swim in short bursts in order to spread their tentacles in a three-dimensional array, and the different species show various swimming abilities (Mackie and Boag, 1963; Biggs, 1977a; Purcell, 1980). In siphonophores within extremely long siphosomes,



FIG. 48. Calycozoite *Sulculeolaria quadrivalvis* in feeding posture with tentacles spread. The tentacles appear as a string of dots which are the nematocyst batteries. n. nectophores, g. gastrozoooids. Scale = 2 cm (photo by J. M. King, from Purcell, 1984a).

such as *Apolemia uvaria* (reported at lengths of 20 m (Trégouboff and Rose, 1957)), *Rosacea* spp., and *Praya reticulata*, the stem assumes a generally horizontal orientation and the tentacles hang in a vertical curtain. Swimming probably is not important in extending the tentacles, and these species

have few nectophores, small in relation to the overall size of the colony. Moreover, pieces of stem disconnected from the nectophores can occur frequently *in situ* (Purcell, 1981c, personal observations; Mackie, 1985). The lifetime of these partial colonies, during which they feed and reproduce, is not known. Siphonophores with comparatively short, non-contractile stems (*Agalma okeni*, *Forskalia* spp.) swim weakly and may rotate to spread the tentacles. Siphonophores with moderately long, slender, flexible stems having limited contractility (*Stephanophyes superba*, *Agalma elegans*, *Nanomia* spp., *Cordagalma cordiformis*) show fairly rapid swimming in order to spread the tentacles. Species with long stems that are highly contractile and can be partly or entirely withdrawn into a hydroecium (diphyids, *Sphaeronectes* spp., abylids) are often very streamlined and show rapid swimming in an arc or spiral to set their tentacles (Fig. 48). Cystonects, which lack nectophores, cannot swim. Rhizophysids contract their stem sharply, which may aid in spreading the tentacles. *Physalia physalis* is blown by the wind.

Tentacle-spreading results from relaxation of the tentacles, and is aided by the swimming movements of the siphonophores (Biggs, 1977a; Mackie and Boag, 1963). The latter described in detail the behaviour of *Muggiae atlantica*, which swims in an arc to spread its tentacles (the "veronica" display). Purcell and LaBarbera (unpublished) found that in *M. atlantica*, the three-dimensional tentacle array results solely from drag acting on the relaxing stem and tentacles as the nectophore swims in an arc. The nematocyst batteries would act to increase drag at the ends of the tentilla and thereby aid in spreading.

The frequency of swimming bouts to reset the tentacles differs among species (from < 12 times/h in physonects to 100 times/h in *Chelophys appendiculata* (Biggs, 1977a)), and probably also depends on temperature and food concentration. Once their tentacles are spread, the siphonophores do not swim for periods of several minutes. They are virtually motionless while in the fishing posture. Changes in the configuration of the tentacle net arise as structures of different density slowly sink or rise relative to other parts (e.g. nematocyst batteries sink relative to the tentacles). In some physonects, periodic contractions of the tentilla occur in a manner that resembles the casting of fishing lines (Vogt, 1854; Mackie and Boag, 1963; Purcell, 1980). The resulting movements of the nematocyst batteries may cause them to serve as lures that attract zooplankters (Fig. 46) (Purcell, 1980).

3. Ingestion, digestion, and egestion

When a prey organism contacts a siphonophore tentacle and is immobilized by the nematocysts, only the tentacle or tentacles attached to the prey contracts to bring the prey to the mouths of the gastrozooids (Purcell,

personal observation). The capture and ingestion of a prey item causes only a localized disturbance, and the rest of the colony continues fishing. The nearby gastrozooids begin to writhe, possibly in response to reduced glutathione (GSH) released from the captured prey, which has been shown to stimulate writhing, mouth opening and spreading (as in *Hydra*) in gastrozooids of *Physalia physalis* (Lenhoff and Schneiderman, 1959) and *Nanomia cara* (Mackie and Boag, 1963). Duvault (1965) suggested that this feeding response in *Abylopsis tetragona* and *Chelophyes appendiculata* is caused by a chemical released from the nematocysts. The prey is engulfed completely by a gastrozooid, or sometimes by two or three if the prey is large. Many gastrozooids spread over a large fish if captured by *P. physalis*. The time between capture and complete ingestion of copepods is on the order of one to two minutes. Sometimes two or three prey are found in a single gastrozooid (Purcell, 1981b,c).

Digestion of the prey involves both extracellular and intracellular processes, as described by Mackie and Boag (1963) for *Nanomia cara*. Breakdown of the food is apparent in 5–10 min and is accompanied by rhythmic pumping movements of the gastrozooid. The basigaster of the gastrozooid apparently is the primary site for phagocytosis of the small particles produced as the result of extracellular digestion. In physonects, these particles are flushed between the stem canal and the nearby palpons by alternate pumping actions in the gastrozooids and palpons. Particles are taken up by the endodermal cells of the gastrozooids and palpons, where intracellular digestion occurs. After 4 h these cells were observed to become distended, detach from the endoderm, and then disintegrate in the coelenteric fluid within about 30 sec. Presumably, these released products of intracellular digestion are absorbed by endodermal cells throughout the colony. The high percentages of free amino acids found in siphonophores by Ceccaldi and Daumas (1967) (39.4–44.8% in Agalmidae, 25.4–30.8% in *Forskalia* spp., 11.1% in *Rosacea cymbiformis*, and 25% in *Hippopodius hippocampus*) may be due to these digestive processes. Histological evidence suggested that cells in the buccal and mid regions of the gastrozooids in the calycophore *Abylopsis tetragona* were secretory and those in the basigaster were absorptive (Mettey and Hamon, 1949). Rose (1931) suggests that the somatocyst of calycophorans is an accessory digestive structure. The palpons of *Physalia physalis* also participate in digestion and absorption (Purcell, personal observation).

Undigested parts of prey are egested from the mouth of the gastrozooid. Only the exoskeletons of crustaceans and the hard parts of other prey are egested. These undigested parts, such as the eye lenses of fish larvae, mouth bristles of chaetognaths, shells of pelagic molluscs, and beaks of cephalopods, are valuable in identifying soft-bodied prey. To egest the undigested

prey remains, the mouth of the gastrozooid opens and the lips turn back, turning the gastrozooid partly inside out. The valve of the basigaster is closed when the basal region of the gastrozooid contracts, expelling the waste as a small pellet. The lengths of time required to clear the gastrozooids of prey remains ("digestion rates") are examined later (see p. 234). Particulate waste accumulates in the terminal bulb of the palpons, and is expelled through a pore at the tip of the palpon (Mackie and Boag, 1963).

4. Day-night differences

In some of the siphonophore species that have been studied, feeding was restricted to either day or night time. Purcell (1981a,b) showed that the cystonect *Rhizophysa eysenhardti* feeds only during the day, based on gut analysis and behavioural observations. The physonect *Agalma okeni* feeds only at night in surface waters (Biggs, 1976b; Purcell, 1981a) however, this species also is reported from depths where feeding might be continuous at low-light levels. Tentacle extension and retraction in these species was linked to light or dark and not to time of day (Purcell, 1981a). *Rosacea cymbiformis* showed a marked response to abrupt changes in light conditions, suggesting that it feeds during light periods. It is not known whether gradual changes in light cause the same response.

Other siphonophore species are known to be sensitive to light (see p. 173), and many species migrate vertically on a diel basis (see p. 156). Vertical migration of the siphonophores and of many prey taxa undoubtedly result in important daily cycles in the types and quantities of prey captured. Few data exist to substantiate this due to the difficulty of collecting intact siphonophores at night in the open ocean, and because the migrating siphonophores are below SCUBA depth range in the daytime. Gut analysis of species collected in the same locations during the day and at night showed that a greater percentage of gastrozooids had food at night than during the day—*Chelophyses appendiculata* (7.0 vs 4.0%), *Diphyes dispar* (11.1 vs 4.6%), and *Muggiaeae atlantica* (6.9 vs 2.0%). Ostracods are important vertical migrants in the Sargasso Sea and comprised 37.5, 66.7 and 100% of the prey found in *C. appendiculata*, *D. dispar*, and *Hippopodius hippopus*, respectively, at night, but not in the daytime (Purcell, 1981a).

5. Diets

The natural prey of 26 species of epipelagic siphonophore species have been determined by examination of zooplankton remains in the gastrozooids (Biggs, 1977a; Purcell 1980, 1981a,b,c, 1982, 1984a, unpublished data; Purcell and Kremer, 1983). General trends exist among the three siphono-

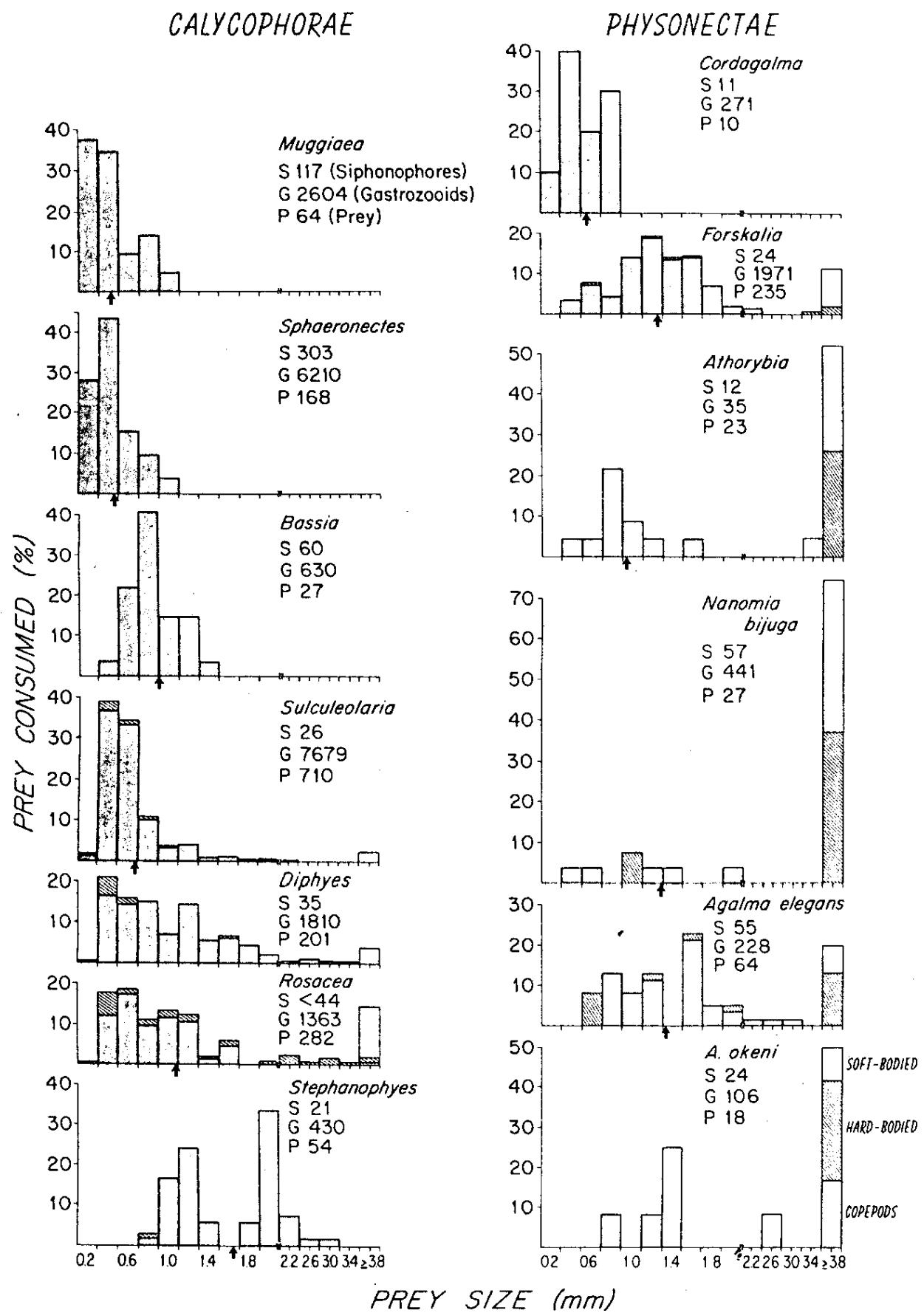


FIG. 49. Diets of calycophoran and physonect siphonophores. S = number of siphonophores examined, G = total number of gastrozooids examined, P = number of prey found. Arrows indicate lengths of the gastrozooids (Purcell, unpublished).

phore suborders (Fig. 49): calycophorans eat primarily small copepods; physonects eat somewhat larger copepods and larger hard-bodied and soft-bodied prey; and cystonects consume exclusively soft-bodied prey, primarily fish larvae. In addition to copepods, other common calycophoran and physonect prey items include the following: barnacle nauplii and cyprid larvae, crab zoea and megalopa larvae, anomuran and stomatopod larvae, euphausiid and caridean larvae, cladocerans, amphipods, ostracods, polychaete larvae, chaetognaths, mollusc veliger larvae, thecosome pteropods, atlantid heteropods, and fish larvae. *Apolemia uvaria* is unusual in that it consumes a large number of gelatinous zooplankters, including salps, ctenophores, and hydromedusae.

Fish larvae are the principal prey of cystonect siphonophores, and no other prey were found in extensive gut analysis of *Rhizophysa eysenhardti* (Purcell, 1981b). The few specimens examined of *Bathyphysa sibogae* and *R. filiformis* contained fish larvae (Purcell, 1981a), and also a polychaete in *R. filiformis* (Biggs, 1976a). Reports of *Physalia physalis* eating fish 4–10 cm long, including herring, flying fish, and silversides, date back to 1864, however, 90% of the fish they eat are larvae only 2–20 mm in length (Purcell, 1984b). Fish and fish larvae were found in 94–100% of the specimens (74–94% of the diet), cephalopods in 38–47%, and chaetognaths and leptcephalus larvae of eels occurred in specimens collected at night. Thus, cystonect siphonophores are the most selective invertebrate predators of larval fishes known (Purcell, 1984b, 1985).

6. Selectivity

The dietary differences seen among various siphonophore species collected from the same environments are especially intriguing because, in order to encounter prey, the siphonophores depend on locomotion of the prey. The sizes and types of prey captured by the different siphonophore species are related to their morphology and behaviour (Purcell, 1980, 1984a). The sizes of prey captured differ among the various species of calycophorans and physonects (Fig. 49). In general, species that swim rapidly to spread their tentacles tend to capture small prey, and species that swim weakly capture much larger prey. This difference in swimming behaviour may affect the probability of encounters with different prey types. Strongly swimming siphonophores change locations frequently, thus increasing their chances of encountering high-density patches of slow-swimming copepod prey. Weakly swimming siphonophores may rely more on ambush and the swimming of their large, active prey to bring them into the tentacles. Siphonophores that capture small prey have small gastrozooids, and fewer, smaller nematocysts

in their nematocyst batteries, but have more gastrozooids, tentacles and batteries (Table 10) (Purcell, 1984a). This probably reflects less effort required to catch each small prey item, and greater chance of encountering the more numerous small prey types. Conversely, siphonophores that capture large prey have large gastrozooids and more, larger nematocysts in each battery, and fewer gastrozooids, tentacles and batteries. This reflects greater effort needed to catch each large prey item, and less chance of encountering the less abundant large prey.

Purcell (1981c) examined prey selection in the siphonophore *Rosacea cymbiformis*, which ate a wide variety of prey in the Gulf of California. This species consumed fewer small copepods, chaetognaths, pteropods, and veligers than availability of these prey would suggest, and consumed more large copepods, heteropods, crab zoea larvae and mysids than expected. This indicates that *R. cymbiformis* consumes more large active prey than predicted based on their availability.

Purcell (1981c) likens the tentacles of siphonophores to the fibres of a biological filter that have much greater spacing than the diameters of the prey. Thus, the chance of direct interception of a prey on a tentacle depends only on the prey diameter. The frequency of prey encounter with a tentacle depends on the number passing the tentacle, which is a function of the prey swimming speed and abundance. At equal abundances, larger, faster prey would encounter a tentacle more frequently than smaller, slower prey. Swimming speeds and diameters of copepods increased with increasing length. Selection was greatest for the largest copepods of the sizes consumed, and decreased with decreasing copepod size for *R. cymbiformis* (Purcell, 1981c), *Muggiae atlantica* (Purcell, 1982), and *Sphaeronectes gracilis* (Purcell and Kremer, 1983). It may be true for siphonophores generally that larger, more active prey are more likely to encounter their tentacles.

The ability of siphonophores to capture the various prey that contact their tentacles differs among species. Evidence from differences in gut contents, and behavioural observations indicates that small prey apparently do not trigger nematocyst discharge in some species, e.g. *Agalma okeni* (Biggs, 1977a), and that large prey can escape from other species, e.g. *Sulculeolaria quadrivalvis* (Purcell, personal observations). The various species of calycophoran and physonect siphonophores have different numbers and sizes of nematocysts in their nematocyst batteries, and different numbers of tentacles and batteries, all of which would affect their ability to catch prey (Table 10). Calycophoran and physonect siphonophores have nematocysts that primarily appear to entangle hard-bodied prey, and cystonect nematocysts apparently penetrate soft-bodied prey. These differences in nematocyst structure are critically important in feeding, and prey selection in siphonophores (see p. 217).

TABLE 10. CALYCOPHORAN (C) AND PHYSONECT (P) SIPHONOPHORES LISTED IN ORDER OF INCREASING PREY SIZE (COPEPODS ONLY) (PURCELL, 1984a)

Species	Sub-order	Mean prey size (mm)	Large nematocyst volume (μl)	Nematocysts per battery (no.)	Batteries per tentacle (no.)	Tentacles (no.)	Number of batteries
<i>Muggiae atlantica</i>	C	0.36	0.68	306	20	20–30	400–600
<i>Sphaeronectes gracilis</i>	C	0.36	0.92	54	25–30	20–60	500–1800
<i>Chelophyes appendiculata</i>	C	0.42	1.24	456	25–30	10–20	250–600
<i>Cordagalma cordiformis</i>	P	0.45	1.84	157	60–70	20–30	1200–2100
<i>Sulcoleolaria quadrivalvis</i>	C	0.57	1.40	208	80–90	85–520	6800–46,800
<i>Bassia bassensis</i>	C	0.79	7.74	408	5–10	5–15	25–150
<i>Athorybia rosacea</i>	P	0.84	17.22	850	120	1–10	120–1200
<i>Hippopodius hippopus</i>	C	0.86	5.32	210	30–100	10–20	300–2000
<i>Rosacea cymbiformis</i>	C	0.98	2.25	430	80–90	10–100	800–9000
<i>Diphyes dispar</i>	C	0.99	6.46	262	40–50	90–180	3600–9000
<i>Abyla trigona</i>	C	1.10	18.02	413	10–20	10–20	100–400
<i>Forskalia edwardsi</i>	P	1.17	9.94	3030	10–20	10–320	100–6400
<i>Nanomia bijuga</i>	P	1.18	4.29	4535	15–20	15–20	225–400
<i>Agalma elegans</i>	P	1.33	27.21–73.85	17,030	12–50	5–30	60–150
<i>Stephanophyes superba</i>	C	1.52	9.82	2050	30–40	10–30	300–1200
<i>Agalma okeni</i>	P	1.97	40.69	20,620	15–35	2–9	30–315

E. Nutrition

Measured rates of physiological processes can be used to estimate the ecological importance of siphonophores. Oxygen consumption can be used to calculate minimum food intake. Ammonium is a preferred nitrogen source for phytoplankton, and its excretion by zooplankton is important for nutrient cycling in the ocean. Digestion and assimilation rates are critical factors used to calculate ingestion rates *in situ* and energy budgets.

1. Respiration and excretion rates.

Biggs (1977b) and Purcell and Kremer (1983) measured metabolic rates of epipelagic siphonophores collected intact in glass jars (Table 11). Metabolic rates measured from siphonophores collected in nets, and possibly damaged were lower by comparison (Nival *et al.*, 1972; Ikeda, 1974; Musayeva and Shushkina, 1978). Biggs emphasizes that differences in collection, handling, and experimental protocol can affect the measured metabolic rates.

Several trends in metabolic rates are seen among the species studied to date. Smaller siphonophores generally have higher weight-specific metabolic rates than larger ones. Slow-swimming, inactive species (e.g. cystonects, *Agalma okeni*, *Athorybia* spp., *Rosacea cymbiformis*, *Hippopodius hippopus*, and abyliids) have lower metabolic rates than fast-swimming, active species (e.g. *Agalma elegans*, *Nanomia bijuga*, *Stephanophyes superba*, and *Sulculeolaria* spp.).

Metabolism is affected by temperature and nutritional state. Biggs (1977b) found that respiration decreased 2–5 times at temperatures 5 °C lower than environmental temperatures (23–28 °C). Purcell and Kremer (1983) found that metabolism was 1.7 times greater at prey densities 4 times higher (2.7 times greater ingestion). Metabolic rates of siphonophores were comparable to those of other carnivorous gelatinous zooplankters, but were lower than those of salps, which are very active herbivores (Biggs, 1977b). He standardized the metabolic measurements to protein weight. Comparison of his results with other studies using dry weight or carbon weight requires approximate conversions, because a protein to carbon conversion was determined only for *Agalma okeni* ($\log C = 0.894 (\log P) - 0.137$) (Biggs, 1976a). Rates of oxygen consumption, primarily from Biggs' studies, are used to calculate ingestion rates later in this section.

Siphonophores occurring in high densities may be important to nutrient cycling. Biggs (1977b) states that one gelatinous zooplankter could release the same amount of ammonium as all the other zooplankton present in 1 m³ of water. Ikeda *et al.* (1982) measured comparable rates of ammonium

TABLE II. RESPIRATION AND EXCRETION RATES OF SIPHONOPHORES

	Respiration ($\mu\text{l O}_2/\text{mg protein/h}$)	Excretion ($\mu\text{g NH}_4/\text{mg protein/h}$)	Reference	
	<u>0.1-1.0 mg[†]</u>	<u>1.1-10.0 mg[†]</u>	<u>0.1-1.0 mg[†]</u>	<u>1.1-10.0 mg[†]</u>
Physonectae				
<i>Agalma okeni</i>	12 ± 3.9 (7)	12 ± 5.5 (46)	1.3 ± 0.8 (3)	1.0 ± 0.6 (15)
<i>A. elegans</i>	39 ± 12.7 (4)	16 ± 2.5 (3)	—	Biggs, 1977b
<i>Cordaglalma cordiformis</i>	27 ± 4.0 (6)	—	2.5 ± 0.7 (4)	Biggs, 1977b
<i>Nanomia bijuga</i>	31 ± 5.1 (8)	14 ± 3.3 (11)	1.5 ± 0.7 (5)	Biggs, 1977b
<i>Forskalia</i> spp.	20 ± 5.1 (8)	17 ± 4.7 (10)	1.1 ± 0.5 (6)	Biggs, 1977b
<i>Athorybia</i> spp.	40 ± 13.7 (3)	11 ± 2.3 (4)	0.9 ± 3.3 (2)	Biggs, 1977b
Calycophorae				
<i>Stephanophyes superba</i>	22 ± 3.2 (4)	14 ± 6.3 (13)	1.8 ± 0.4 (2)	Biggs, 1977b
<i>Rosacea cymbiformis</i>	8 ± 3.6 (2)	8 ± 2.5 (11)	0.8 ± 0.4 (4)	Biggs, 1977b
<i>Chelophys appendiculata</i>	—	8 ± 3.3 (5)	—	Biggs, 1977b
<i>Diphyes dispar</i>	—	8.1-13.1*	—	Nival <i>et al.</i> , 1972
<i>Sphaeronectes gracilis</i>	17 ± 7.4 (7)	12 ± 3.8 (4)	0.6 ± 0.1 (2)	Biggs, 1977b
<i>Sutcoleotaria quadrivalvis</i>	2.5 (20)	—	0.26 (20)*	Purcell and Kremer, 1983
<i>S. monoica</i>	45 ± 17.1 (3)	36 ± 13.9 (6)	2.1 ± 0.3 (2)	Biggs, 1977b
<i>S. chuni</i>	32 ± 15.2 (7)	21 ± 2.3 (2)	1.5 ± 0.9 (6)	Biggs, 1977b
<i>S. biloba</i>	75 ± 25.2 (4)	—	2.7 ± 1.0 (4)	Biggs, 1977b
<i>Abyla</i> sp.	—	13 ± 0.5 (2)	—	Biggs, 1977b
<i>Hippopodius hippopus</i>	—	5 ± 0.5 (3)	—	Biggs, 1977b
<i>Abylopis tetragona</i>	17.3 (1)	3.5 (1)	—	Nival <i>et al.</i> , 1972
<i>Bystrophysa sibogae</i>	—	4.4-12.2*	—	
Cystonectae				
<i>Rhizophysa filiformis</i>	—	—	6.9 (1)	Biggs, 1977b
	—	—	5 ± 2.5 (2)	Biggs, 1977b

* Calculated by J.E.P. Numbers of measurements are in parentheses. Nival *et al.* (1972), 15° C. Biggs (1977b), 23-29° C. Purcell and Kremer (1983), 13-14° C.

[†] Colony size in mg protein.

excretion for *Diphyes* sp., and also measured phosphate excretion at 13–29 ng P/animal/h.

2. Digestion and assimilation rates

Purcell (1983) measured the elapsed times between ingestion and egestion of prey for four siphonophore species at ambient temperatures, and found that digestion rates for the same copepod prey differed substantially among the four species, from a mean minimum of 1.6 h to a maximum of 9.6 h (Table 12). Digestion rates seemed to be related to metabolic rates in the four species, and like metabolism, are probably affected by temperature. In all cases, small prey were digested more rapidly than large prey (Table 12).

Digestion of prey by siphonophores is very complete. Purcell (1983) found that assimilation of copepod prey was 87–94% for carbon, and 90–94% for nitrogen, and assimilation of fish larva prey was even greater at 98% (Table 12). These values are higher than assimilation efficiencies reported for other planktonic carnivores (Purcell, 1983). The measurements of digestion rates and assimilation efficiencies make it possible to estimate feeding rates and energy budgets of siphonophores.

3. Ingestion rates

The aim of much recent research on siphonophores has been to determine how important they are as consumers in the pelagic environment. Three methods have been used to estimate ingestion rates of siphonophores. In order to make comparisons among the various studies, the following conversions for copepods were used: caloric content = 6096.2 cal per gram dry weight (Beers, 1966) and carbon content = 40% of dry weight (Purcell, 1983; Purcell and Kremer, 1983).

Metabolic rate method (Table 13). Biggs (1976a,b) used the oxygen consumption rates of *Agalma okeni* to estimate the minimum ingestion needed to meet the energetic demands of metabolism and growth. Oxygen consumption (12 µl O₂/h), multiplied by an oxycaloric equivalent (4.9 cal/ml), gives 1.4 cal consumed/day by a specimen with 1 mg protein. J.E.P. has used metabolic rates measured by Biggs (1977b) (Table 11) for *Forskalia* spp., *Sulculeolaria quadrivalvis*, *Diphyes dispar*, *Stephanophyes superba*, and *Rosacea cymbiformis* (in Purcell, 1981c), and by Purcell and Kremer (1983) for *Sphaeronectes gracilis* to calculate ingestion in the same way (Table 13). Methods of collection and maintenance in the laboratory can affect the condition of the specimens. Metabolic rates can be used to estimate only

TABLE 12. DIGESTION AND ASSIMILATION RATES OF SIPHONOPHORES

Prey	Temperature (°C)	Digestion time (h)	Assimilation (%) carbon, nitrogen	Reference
<i>Physalia physalis</i>	fish larvae 15 mm	21 ± 1	—	Purcell, 1984a
<i>Rhizophysa eysemardti</i>	fish larvae 4–7 mm	23 ± 1	97.8	Purcell, 1981b
	8–12 mm			
	13–15 mm			
<i>Agalma okeni</i>	A	NA	3.6 ± 1.5 (15) 4.0 ± 1.0 (26) 5.1 ± 1.7 (3)	Biggs, 1977b
	shrimp, megalopa			
<i>Forskalia</i> spp.	C, 1.7–2.7 mm	21–22	4.1 ± 1.0 (50)	Purcell, 1983
	A	NA	2–3 (2), 3–6 (2)	Biggs, 1977b
<i>Diphyes dispar</i>	C, 1.7–2.7 mm	21–22	5.8 ± 1.4 (22)	Purcell, 1983
	A	NA	3–4 (3)	Biggs, 1977b
<i>Sphaeronectes gracilis</i>	C	13–14	—	Purcell and Kremer, 1983
	<0.4 mm	2–4		
	0.4–0.9 mm	4–6		
<i>Muggiaea atlantica</i>	C	8–10	—	Purcell, 1982
	0.1–0.35 mm	2–4		
	0.35–0.9 mm	4–6		
<i>Rosacea cymbiformis</i>	C, 1.7–2.7 mm	21–22	9.6 ± 2.9 (20)	Purcell, 1983
	A	NA	10–24 (1), 8–18 (1)	Biggs, 1977b
<i>Stephanophyes superba</i>	C, 1.7–2.7 mm	21–22	1.6 ± 0.5 (60)	Purcell, 1983
	A	NA	4–6 (2), 6–8 (1)	Biggs, 1977b

C = copepods; A = *Artemia nauplii*; NA = not available; numbers of measurements are in parentheses.

TABLE 13. INGESTION RATES OF SIPHONOPHORES CALCULATED BY THE METABOLIC RATE METHOD

	Feeding rate (per siphonophore/day)	Reference
<i>Rhizophysa eysenhardti</i>	354.1 µg C*	Purcell, 1981b
6-7 cormidia	5.4 cal	
<i>Agalma okeni</i>	3-4 <i>Candacia</i> copepods	Biggs, 1976a,b
1 mg protein	91.8 µg C*	
	1.4 cal	
<i>Forskalia</i> spp.		
5 mg protein	590.2 µg C*	Smith, 1982
	9 cal	
10 mg protein	1128.5 µg C*	Biggs, 1977b
	17.6 cal*	
<i>Diphyes dispar</i>	300.9 µg C*	Biggs, 1977b
10 mg protein	4.7 cal*	
<i>Sphaeronectes gracilis</i>	5.3 µg C	Purcell and Kremer, 1983
6.7 ± 1.2 mg d.w. (2.8% C)	0.08 cal	
38.5 ± 9.6 gastrozooids		
<i>Muggiae atlantica</i>	2.9 µg C	Purcell, 1982
1.7 ± 0.6 mg d.w. (7.5% C)	0.04 cal	
av. 22 gastrozooids		
<i>Sulculeolaria quadrivalvis</i>	1600 µg C*	Biggs, 1977b
10 mg protein	25.0 cal*	
<i>Rosacea cymbiformis</i>	252 µg C*	Purcell, 1981c
av. 40 cormidia/colony	3.8 cal	
4 mg protein (= 72 mg C)		
<i>Stephanophyes superba</i>	1053 µg C*	Biggs, 1977b
10 mg protein	16.4 cal*	

* Calculated by J.E.P.

minimum ingestion, and do not necessarily reflect predation rates *in situ*.

Clearance rate method (Table 14). The number of prey consumed by siphonophores has been estimated by quantifying the prey density before and after the siphonophores have fed for a period of time in laboratory containers. Purcell (1982) and Smith (1982) presented *Muggiae atlantica* and *Forskalia edwardsi*, respectively, with copepod species and densities typical of the environment, and found that feeding increased linearly with prey density. The results of this type of experiment can be affected greatly by the types and sizes of prey offered (Purcell, 1982; Purcell and Kremer, 1983). The latter found that laboratory conditions reduced feeding rates, and Smith (1982) used large volume containers (177 l) in order to minimize that effect.

Gut content method (Table 15). Purcell (1981a,b, 1982, 1984b, unpublished) and Purcell and Kremer (1983) estimated ingestion rates from the number of prey in the gastrozooids divided by the time required for egestion of the prey (Table 12). It is important to consider diel feeding patterns (see p.

TABLE 14. INGESTION RATES OF SIPHONOPHORES CALCULATED BY THE CLEARANCE RATE METHOD

	Prey type and abundance	Feeding Rate (per siphonophore/d)	Reference
<i>Agalma okeni</i>	<i>Acartia</i>	2.6–2.9 l	Biggs, 1976a
	6000–8000/m ³	10.3–10.9 prey*	
	11,000/m ³	4.3–5.8 l	
		14.2–16.7 prey*	
<i>A. elegans</i>	<i>Pleuromama</i>	3.4 l	Biggs, 1976a
	5000/m ³	13.3 prey*	
	13,000/m ³	3.6–8.4 l	
		13.8–31.6 prey*	
<i>Forskalia</i> spp.	<i>Acartia</i>	4.6–8.2 l	Biggs, 1976a
	5000–6000/m ³	17.1–30.5 prey*	
	11,000–12,000/m ³	16.8–13.2 l	
	copepods 1–4 mm	50–63.8 prey*	
	51/m ³ †	no feeding	
	113/m ³ †	96 l, 10.8 prey*	
	226/m ³	3.2 cal*, 217 µg C*	
		96 l, 21.7 prey*	
	452/m ³	6.5 cal*, 434 µg C*	
		96 l, 43.4 prey*	
<i>Sphaeronectes gracilis</i>	<i>Acartia</i>	13 cal*, 868 µg C*	Smith, 1982
	250/m ³ calculated†	0.5 prey, 0.02 cal*, 1.1 µg C*	
	5,000/m ³	13.8 prey, 0.4 cal*, 29.4 µg C*	
	20,000/m ³	36.9 prey, 1.2 cal*, 78.6 µg C*	
<i>Muggiae atlantica</i>	nauplii and copepods <10,000/m ³		Purcell, 1982
	95.8%, 5.2%†	7 prey, 0.04 cal*, 3.3 µg C*	
	86.6%, 12.4%	17.8 prey	
	56.5%, 43.5%	22.8 prey	

* Calculated by J.E.P.

† Representative of densities *in situ* (Table 15).

l = Litres cleared.

227), but this is not always possible, and constant feeding often must be assumed. Specimens collected in nets yielded lower estimates of feeding than did specimens collected intact by divers (Purcell and Kremer, 1983). Digestion rates must be determined carefully at environmental temperatures using appropriate prey.

Comparison of the three methods shows that ingestion rates determined

TABLE 15. INGESTION RATES OF SIPHONOPHORES CALCULATED BY THE GUT CONTENT METHOD

Location	Prey type and abundance	Feeding rate (per siphonophore/d)	% prey population consumed daily	Reference
<i>Physalia physalis</i>	fish larvae 0.2/m ³	av 120 prey (94.1%)†	60	Purcell, 1984b
<i>Rhizopysa eysenhardtii</i> av 8 gastrozooids	fish larvae av 28/m ³	av 8.8 prey (100%)† 7300 µg C*	28	Purcell, 1981b
<i>Forskalia</i> spp. av 109 gastrozooids	copepods NA	107 cal 80 prey* (85.7%)† mean 1596.3 µg C* 25 cal*	—	Purcell, unpubl
<i>Diphyes dispar</i> av 128 gastrozooids	copepods av 852/m ³	547.2 prey* (89.7%)† mean 1580.7 µg C* 24.7 cal*	—	Purcell, unpubl
<i>Sphaeronectes gracilis</i> (as in Table 13)	copepods av 250/m ³	8.1–15.5 prey (100%)† 3.9–6.2 µg C 0.06–0.09 cal	2–4	Purcell and Kremer, 1983
<i>Muggiaea atlantica</i> (as in Table 13)	copepods av 9121/m ³	5.5–10.5 prey (100%)† 2.6–4.2 µg C 0.03–0.05 cal*	0.1–0.2	Purcell, 1982
<i>Sulculeolaria quadrivalvis</i> av 397 gastrozooids	copepods av 852/m ³	347* (93.4%)† mean 1449 µg C* 22.6 cal*	—	Purcell, unpubl
Gulf Stream av 180 gastrozooids	av 467/m ³	269 prey* mean 342.4 µg C*	—	Purcell, unpubl
<i>Rosacea cymbiformis</i> (as in Table 13)	copepods av 1495–1695/m ³	5.4 cal*	8*	Purcell, 1981c
<i>Stephanophyes superba</i> av 79 gastrozooids	copepods av 852/m ³	89.4 prey (75.4%)† 616–2068 µg C* 9.4–31.5 cal 397.5 prey* (100%)† 17,165 µg C* 268.3 cal*	—	Purcell, unpubl

* Calculated by J.E.P.

† Percentage of prey items in diet.

NA = Not available.

by gut contents, in many cases, were far greater than minimum ingestion calculated from metabolic demands, i.e. *Rhizophysa eysenhardtii* (19.8 times), *Forskalia* spp. (1.4–2.8 times), *Rosacea cymbiformis* (2.5–8.3 times), *Diphyes dispar* (5.2 times), and *Stephanophyes superba* (16.4 times) (Tables 13 and 15). This suggests that the siphonophores had much excess energy to devote to growth and reproduction (see below). Approximately equal ingestion rates were determined by metabolism and gut contents for the small species *Sphaeronectes gracilis* and *Muggiae atlantica*. At environmentally realistic prey densities, clearance rate experiments yielded lower rates than estimated from the other methods, possibly due to impaired feeding (as suggested for *S. gracilis* feeding at 250 copepods/m³), and high rates when high proportions of large active prey were used (as for *M. atlantica* feeding when the ratio of copepods to nauplii was increased, and for *S. gracilis*) (Table 14). Ingestion rates determined from gut contents probably are most accurate, because metabolic rates underestimate feeding *in situ*, and clearance rate experiments are highly subject to laboratory conditions.

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$$P = [(I \times A) - R] / I$$

where P = production, I = ingestion, A = assimilation, and R = respiration. Production rates calculated for siphonophores in the laboratory (Biggs, 1976a; Purcell and Kremer, 1983) and *in situ* (Purcell, unpublished) show that much of the energy ingested is allocated to growth (Table 16). Production rates calculated *in situ* are highly dependent on local prey availability.

Short-term growth rates have been measured directly for *Agalma okeni* and *Muggiae atlantica* (Biggs, 1976a; Purcell, 1982, respectively). Biggs (1976a) maintained small colonies of *A. okeni* in the laboratory at 24–26 °C for up to four days, and calculated growth in protein from the number of nectophores budded. Growth coefficients, from the equation $W_t = W_0 e^{kt}$ ranged from 0.04–0.26 [calculated by J.E.P. from Biggs (1976a)]. Purcell (1982) measured growth of *M. atlantica* at 8–10 °C at different food levels in terms of eudoxid production by polygastric colonies, and carbon increases in eudoxids. Production of eudoxids was constant over 6 d at each food level and significantly greater at high food levels. Starved colonies stopped budding eudoxids. Eudoxid growth was exponential and significantly greater at high food levels. At 10 prey/l, $k = 0.2$ and at 20 prey/l, $k = 0.35$.

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1 mg protein	48	32	20	
<i>Diphyes dispar</i> *	75	19	6	Purcell, unpubl
<i>Sphaeronectes gracilis</i>				Purcell and Kremer, 1983
3 prey/l	72	18	10	
20 prey/l	79	11	10	
0.25 prey/l*	<5	>84	10	
<i>Muggiae atlantica</i> *	<21	>69	10	Purcell, unpubl
<i>Rosacea cymbiformis</i> *	47-76	12-41	12	Purcell, unpubl
<i>Forskalia</i> spp.*	53	37	11	Purcell, unpubl
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* Calculated by J.E.P. based on *in situ* digestion (Table 15).

Gonophore maturation required a minimum of 6 d at the highest food levels and at least 11 d at food levels comparable to those *in situ*. Growth rates and population dynamics clearly are related to food availability.

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1. Abundance

Accurate determination of their abundances is critical in estimating the importance of siphonophores in pelagic communities. Unfortunately, their often large size and fragile colonial structure make quantitative collection by nets impossible, except for the smaller calycophorans. Few abundance data exist even for these siphonophores. Several studies on distribution patterns and seasonality have presented abundance data on siphonophores in the numbers per net haul, or in approximate or relative terms that usually cannot be translated into the number per cubic metre. Rather than attempt to transform such data, only the quantitative data from ecological studies on siphonophores is presented (Table 17). Many of these latter studies used alternative methods of estimating abundances developed with the application of SCUBA diving to the study of gelatinous zooplankton. Purcell (1981b,c) swam with a 1 m diameter hoop and flowmeter, counting siphonophores that passed through the hoop. Biggs *et al.* (1981), and Biggs *et al.* (1984) used three 5 m × 5 m grids, from 0–15 m depth, which were towed slowly beneath a zodiac raft. One diver enumerated gelatinous zooplankters that passed through each of the grids. The volume of water searched was estimated by measuring the speed of water moving past the grid. This method is useful only for large specimens. Recently, submersibles have been used to study deep-living gelatinous plankton (e.g. Youngbluth, 1984). Mackie and Mills (1983) visually estimated the distance between specimens, and calculated that the numbers/m³ = 1.41/(distance in m³). Their visual density estimates agreed well with simultaneous net collections (Table 17), but they concluded that this method can be applied only when organisms are abundant.

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	Siphonophores	Medusae	Ctenophores	Method	Reference
Gulf of Mexico (No/10 000 m ³)					
spring (4) a	physonects 2.0 ± 3.4	calycophorans 0	1.7 ± 2.2	10.2 ± 9.9	grid
summer (8)	0	0	0	0	Biggs <i>et al.</i> , 1984
fall (11) b	8.8 ± 7.1	<0.8 ± 1.0	<8.7 ± 20.7	36.6 ± 51.0	
winter (8) c	4.1 ± 2.3	2.6 ± 2.1	3.4 ± 3.5	31.2 ± 53.8	
<i>Physalia physalis</i>	av 1/200 m ²	—	—	timed obs	Purcell, 1984b
North Atlantic (No/10 000 m ³)		calycophorans			
temperate (4)	15.2 ± 24.5	27% d	14.2 ± 13.4	38.5 ± 31.9	grid
transitional (6)	6.2 ± 10.4	62% d	11.5 ± 9.7	24.7 ± 36.1	Biggs <i>et al.</i> , 1981
subtropical (7)	8.0 ± 4.5	90% d	2.6 ± 3.0	2.1 ± 3.2	
Bahamas (No/10 000 m ³)	total 8.3 ± 13.1	total 9.0 ± 7.8	52.3 ± 59.9	grid	Biggs <i>et al.</i> , 1981
Gulf of California <i>Rhizophysa eisenhardtii</i>	cove 0.9 ± 0.5/m ³	—	—	hoop	Purcell, 1981b
<i>Rosacea cymbiformis</i>	channel 40 ± 4/1000 m ³	—	—	hoop	Purcell, 1981c
Southern California (No/m ³)	eudoxids 8.3 ± 4.6	6.3 ± 5.4	4.6 ± 1.7	2.5 ± 1.5	net
<i>Sphaeronectes gracilis</i>	6.7 ± 3.7	17.3 ± 11.5	4.6 ± 1.7	2.5 ± 1.5	net
<i>Muggiae atlantica</i>	0.02 ± 0.02	—	0.06	0.05 ± 0.02	submersible
<i>Apolemia</i> sp. (450 m)	—	—	—	—	submersible
<i>Nanomia bijuga</i>	0.3	—	—	—	Barham, 1963

Strait of Georgia
(No./m³)

	<i>Muggiaea atlantica</i>	polygastric	eudoxids			
October		1.4 ± 0.8	8.0 ± 3.8	0.7 ± 0.5	0.1 ± 0.2	net
November		2.7 ± 1.8	7.2 ± 4.1	1.4	0.08	net
March		2.0 ± 2.6	common	2.9–10.5	0.8–5.5	submersible
June		0.03	0.27	1.3	0	net
	<i>Dimophyes artica</i>			11.6	2.9	net
November		0.2 ± 0.1	0.2 ± 0.1	1.4	0.08	net
		<0.2	few	2.9–10.5	0.8–5.5	submersible
	<i>Nanomia cara</i>					
November		0.04		1.4	0.08	net
Gulf of Maine				—	—	
	<i>Nanomia cara</i> (50–200 m)	<0.1–8/m ³		—	—	submersible
						Rogers <i>et al.</i> , 1978

a *Agalma*, *Physophora*; b *Forskalia*, *Agalma*, *Athorybia*, *Cordagaima*, *Rosacea*, *Stephanophyes*; c *Forskalia*, *Agalma*, *Nanomia*, *Cordagaima*; d *Diphyes*, *Chelophyes*, *Rosacea*; Numbers in parentheses are the number of SCUBA dives.

excretion for *Diphyes* sp., and also measured phosphate excretion at 13–29 ng P/animal/h.

2. Digestion and assimilation rates

Purcell (1983) measured the elapsed times between ingestion and egestion of prey for four siphonophore species at ambient temperatures, and found that digestion rates for the same copepod prey differed substantially among the four species, from a mean minimum of 1.6 h to a maximum of 9.6 h (Table 12). Digestion rates seemed to be related to metabolic rates in the four species, and like metabolism, are probably affected by temperature. In all cases, small prey were digested more rapidly than large prey (Table 12).

Digestion of prey by siphonophores is very complete. Purcell (1983) found that assimilation of copepod prey was 87–94% for carbon, and 90–94% for nitrogen, and assimilation of fish larva prey was even greater at 98% (Table 12). These values are higher than assimilation efficiencies reported for other planktonic carnivores (Purcell, 1983). The measurements of digestion rates and assimilation efficiencies make it possible to estimate feeding rates and energy budgets of siphonophores.

3. Ingestion rates

The aim of much recent research on siphonophores has been to determine how important they are as consumers in the pelagic environment. Three methods have been used to estimate ingestion rates of siphonophores. In order to make comparisons among the various studies, the following conversions for copepods were used: caloric content = 6096.2 cal per gram dry weight (Beers, 1966) and carbon content = 40% of dry weight (Purcell, 1983; Purcell and Kremer, 1983).

Metabolic rate method (Table 13). Biggs (1976a,b) used the oxygen consumption rates of *Agalma okeni* to estimate the minimum ingestion needed to meet the energetic demands of metabolism and growth. Oxygen consumption (12 µl O₂/h), multiplied by an oxycaloric equivalent (4.9 cal/ml), gives 1.4 cal consumed/day by a specimen with 1 mg protein. J.E.P. has used metabolic rates measured by Biggs (1977b) (Table 11) for *Forskalia* spp., *Sulculeolaria quadrivalvis*, *Diphyes dispar*, *Stephanophyes superba*, and *Rosacea cymbiformis* (in Purcell, 1981c), and by Purcell and Kremer (1983) for *Sphaeronectes gracilis* to calculate ingestion in the same way (Table 13). Methods of collection and maintenance in the laboratory can affect the condition of the specimens. Metabolic rates can be used to estimate only

TABLE 12. DIGESTION AND ASSIMILATION RATES OF SIPHONOPHORES

Prey	Temperature (°C)	Digestion time (h)	Assimilation (%) carbon, nitrogen	Reference
<i>Physalia physalis</i>	fish larvae 15 mm	21 ± 1	—	Purcell, 1984a
<i>Rhizophysa eysemardti</i>	fish larvae 4–7 mm	23 ± 1	97.8	Purcell, 1981b
	8–12 mm			
	13–15 mm			
<i>Agalma okeni</i>	A	NA	3.6 ± 1.5 (15) 4.0 ± 1.0 (26) 5.1 ± 1.7 (3)	Biggs, 1977b
	shrimp, megalopa			
<i>Forskalia</i> spp.	C, 1.7–2.7 mm	21–22	4.1 ± 1.0 (50)	Purcell, 1983
	A	NA	2–3 (2), 3–6 (2)	Biggs, 1977b
<i>Diphyes dispar</i>	C, 1.7–2.7 mm	21–22	5.8 ± 1.4 (22)	Purcell, 1983
	A	NA	3–4 (3)	Biggs, 1977b
<i>Sphaeronectes gracilis</i>	C	13–14	—	Purcell and Kremer, 1983
	<0.4 mm	2–4		
	0.4–0.9 mm	4–6		
<i>Muggiaea atlantica</i>	C	8–10	—	Purcell, 1982
	0.1–0.35 mm	2–4		
	0.35–0.9 mm	4–6		
<i>Rosacea cymbiformis</i>	C, 1.7–2.7 mm	21–22	9.6 ± 2.9 (20)	Purcell, 1983
	A	NA	10–24 (1), 8–18 (1)	Biggs, 1977b
<i>Stephanophyes superba</i>	C, 1.7–2.7 mm	21–22	1.6 ± 0.5 (60)	Purcell, 1983
	A	NA	4–6 (2), 6–8 (1)	Biggs, 1977b

C = copepods; A = *Artemia nauplii*; NA = not available; numbers of measurements are in parentheses.

TABLE 13. INGESTION RATES OF SIPHONOPHORES CALCULATED BY THE METABOLIC RATE METHOD

	Feeding rate (per siphonophore/day)	Reference
<i>Rhizophysa eysenhardtii</i>	354.1 µg C*	Purcell, 1981b
6-7 cormidia	5.4 cal	
<i>Agalma okeni</i>	3-4 <i>Candacia</i> copepods	Biggs, 1976a,b
1 mg protein	91.8 µg C*	
	1.4 cal	
<i>Forskalia</i> spp.		
5 mg protein	590.2 µg C*	Smith, 1982
	9 cal	
10 mg protein	1128.5 µg C*	Biggs, 1977b
	17.6 cal*	
<i>Diphyes dispar</i>	300.9 µg C*	Biggs, 1977b
10 mg protein	4.7 cal*	
<i>Sphaeronectes gracilis</i>	5.3 µg C	Purcell and Kremer, 1983
6.7 ± 1.2 mg d.w. (2.8% C)	0.08 cal	
38.5 ± 9.6 gastrozooids		
<i>Muggiae atlantica</i>	2.9 µg C	Purcell, 1982
1.7 ± 0.6 mg d.w. (7.5% C)	0.04 cal	
av. 22 gastrozooids		
<i>Sulculeolaria quadrivalvis</i>	1600 µg C*	Biggs, 1977b
10 mg protein	25.0 cal*	
<i>Rosacea cymbiformis</i>	252 µg C*	Purcell, 1981c
av. 40 cormidia/colony	3.8 cal	
4 mg protein (= 72 mg C)		
<i>Stephanophyes superba</i>	1053 µg C*	Biggs, 1977b
10 mg protein	16.4 cal*	

* Calculated by J.E.P.

minimum ingestion, and do not necessarily reflect predation rates *in situ*.

Clearance rate method (Table 14). The number of prey consumed by siphonophores has been estimated by quantifying the prey density before and after the siphonophores have fed for a period of time in laboratory containers. Purcell (1982) and Smith (1982) presented *Muggiae atlantica* and *Forskalia edwardsi*, respectively, with copepod species and densities typical of the environment, and found that feeding increased linearly with prey density. The results of this type of experiment can be affected greatly by the types and sizes of prey offered (Purcell, 1982; Purcell and Kremer, 1983). The latter found that laboratory conditions reduced feeding rates, and Smith (1982) used large volume containers (177 l) in order to minimize that effect.

Gut content method (Table 15). Purcell (1981a,b, 1982, 1984b, unpublished) and Purcell and Kremer (1983) estimated ingestion rates from the number of prey in the gastrozooids divided by the time required for egestion of the prey (Table 12). It is important to consider diel feeding patterns (see p.

TABLE 14. INGESTION RATES OF SIPHONOPHORES CALCULATED BY THE CLEARANCE RATE METHOD

	Prey type and abundance	Feeding Rate (per siphonophore/d)	Reference
<i>Agalma okeni</i>	<i>Acartia</i>	2.6–2.9 l	Biggs, 1976a
	6000–8000/m ³	10.3–10.9 prey*	
	11,000/m ³	4.3–5.8 l	
		14.2–16.7 prey*	
<i>A. elegans</i>	<i>Pleuromama</i>	3.4 l	Biggs, 1976a
	5000/m ³	13.3 prey*	
	13,000/m ³	3.6–8.4 l	
		13.8–31.6 prey*	
<i>Forskalia</i> spp.	<i>Acartia</i>	4.6–8.2 l	Biggs, 1976a
	5000–6000/m ³	17.1–30.5 prey*	
	11,000–12,000/m ³	16.8–13.2 l	
	copepods 1–4 mm	50–63.8 prey*	
	51/m ³ †	no feeding	
	113/m ³ †	96 l, 10.8 prey*	
	226/m ³	3.2 cal*, 217 µg C*	
		96 l, 21.7 prey*	
	452/m ³	6.5 cal*, 434 µg C*	
		96 l, 43.4 prey*	
<i>Sphaeronectes gracilis</i>	<i>Acartia</i>	13 cal*, 868 µg C*	Smith, 1982
	250/m ³ calculated†	0.5 prey, 0.02 cal*, 1.1 µg C*	
	5,000/m ³	13.8 prey, 0.4 cal*, 29.4 µg C*	
	20,000/m ³	36.9 prey, 1.2 cal*, 78.6 µg C*	
<i>Muggiae atlantica</i>	nauplii and copepods <10,000/m ³		Purcell, 1982
	95.8%, 5.2%†	7 prey, 0.04 cal*, 3.3 µg C*	
	86.6%, 12.4%	17.8 prey	
	56.5%, 43.5%	22.8 prey	

* Calculated by J.E.P.

† Representative of densities *in situ* (Table 15).

l = Litres cleared.

227), but this is not always possible, and constant feeding often must be assumed. Specimens collected in nets yielded lower estimates of feeding than did specimens collected intact by divers (Purcell and Kremer, 1983). Digestion rates must be determined carefully at environmental temperatures using appropriate prey.

Comparison of the three methods shows that ingestion rates determined

TABLE 15. INGESTION RATES OF SIPHONOPHORES CALCULATED BY THE GUT CONTENT METHOD

Location	Prey type and abundance	Feeding rate (per siphonophore/d)	% prey population consumed daily	Reference
<i>Physalia physalis</i>	fish larvae 0.2/m ³	av 120 prey (94.1%)†	60	Purcell, 1984b
<i>Rhizopysa eysenhardtii</i> av 8 gastrozooids	fish larvae av 28/m ³	av 8.8 prey (100%)† 7300 µg C*	28	Purcell, 1981b
<i>Forskalia</i> spp. av 109 gastrozooids	copepods NA	107 cal 80 prey* (85.7%)† mean 1596.3 µg C* 25 cal*	—	Purcell, unpubl
<i>Diphyes dispar</i> av 128 gastrozooids	copepods av 852/m ³	547.2 prey* (89.7%)† mean 1580.7 µg C* 24.7 cal*	—	Purcell, unpubl
<i>Sphaeronectes gracilis</i> (as in Table 13)	copepods av 250/m ³	8.1–15.5 prey (100%)† 3.9–6.2 µg C 0.06–0.09 cal	2–4	Purcell and Kremer, 1983
<i>Muggiaea atlantica</i> (as in Table 13)	copepods av 9121/m ³	5.5–10.5 prey (100%)† 2.6–4.2 µg C 0.03–0.05 cal*	0.1–0.2	Purcell, 1982
<i>Sulculeolaria quadrivalvis</i> av 397 gastrozooids	copepods av 852/m ³	347* (93.4%)† mean 1449 µg C* 22.6 cal*	—	Purcell, unpubl
Gulf Stream av 180 gastrozooids	av 467/m ³	269 prey* mean 342.4 µg C*	—	Purcell, unpubl
<i>Rosacea cymbiformis</i> (as in Table 13)	copepods av 1495–1695/m ³	5.4 cal*	8*	Purcell, 1981c
<i>Stephanophyes superba</i> av 79 gastrozooids	copepods av 852/m ³	89.4 prey (75.4%)† 616–2068 µg C* 9.4–31.5 cal 397.5 prey* (100%)† 17,165 µg C* 268.3 cal*	—	Purcell, unpubl

* Calculated by J.E.P.

† Percentage of prey items in diet.

NA = Not available.

by gut contents, in many cases, were far greater than minimum ingestion calculated from metabolic demands, i.e. *Rhizophysa eysenhardtii* (19.8 times), *Forskalia* spp. (1.4–2.8 times), *Rosacea cymbiformis* (2.5–8.3 times), *Diphyes dispar* (5.2 times), and *Stephanophyes superba* (16.4 times) (Tables 13 and 15). This suggests that the siphonophores had much excess energy to devote to growth and reproduction (see below). Approximately equal ingestion rates were determined by metabolism and gut contents for the small species *Sphaeronectes gracilis* and *Muggiae atlantica*. At environmentally realistic prey densities, clearance rate experiments yielded lower rates than estimated from the other methods, possibly due to impaired feeding (as suggested for *S. gracilis* feeding at 250 copepods/m³), and high rates when high proportions of large active prey were used (as for *M. atlantica* feeding when the ratio of copepods to nauplii was increased, and for *S. gracilis*) (Table 14). Ingestion rates determined from gut contents probably are most accurate, because metabolic rates underestimate feeding *in situ*, and clearance rate experiments are highly subject to laboratory conditions.

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winter (8) c	4.1 ± 2.3	2.6 ± 2.1	3.4 ± 3.5	31.2 ± 53.8	
<i>Physalia physalis</i>	av 1/200 m ²	—	—	—	Purcell, 1984b
North Atlantic (No/10 000 m ³)		calycophorans			
temperate (4)	15.2 ± 24.5	27% d	14.2 ± 13.4	38.5 ± 31.9	grid
transitional (6)	6.2 ± 10.4	62% d	11.5 ± 9.7	24.7 ± 36.1	Biggs <i>et al.</i> , 1981
subtropical (7)	8.0 ± 4.5	90% d	2.6 ± 3.0	2.1 ± 3.2	
Bahamas (No/10 000 m ³)	total 8.3 ± 13.1	total 9.0 ± 7.8	52.3 ± 59.9	grid	Biggs <i>et al.</i> , 1981
Gulf of California <i>Rhizophysa eisenhardtii</i>	cove 0.9 ± 0.5/m ³	—	—	hoop	Purcell, 1981b
<i>Rosacea cymbiformis</i>	channel 40 ± 4/1000 m ³	—	—	hoop	Purcell, 1981c
Southern California (No/m ³)	eudoxids 8.3 ± 4.6	6.3 ± 5.4	4.6 ± 1.7	2.5 ± 1.5	net
<i>Sphaeronectes gracilis</i>	6.7 ± 3.7	17.3 ± 11.5	4.6 ± 1.7	2.5 ± 1.5	net
<i>Muggiae atlantica</i>	0.02 ± 0.02	—	0.06	0.05 ± 0.02	submersible
<i>Apolemia</i> sp. (450 m)	—	—	—	—	submersible
<i>Nanomia bijuga</i>	0.3	—	—	—	Barham, 1963

Strait of Georgia
(No./m³)

	<i>Muggiaea atlantica</i>	polygastric	eudoxids			
October		1.4 ± 0.8	8.0 ± 3.8	0.7 ± 0.5	0.1 ± 0.2	net
November		2.7 ± 1.8	7.2 ± 4.1	1.4	0.08	net
March		2.0 ± 2.6	common	2.9–10.5	0.8–5.5	submersible
June		0.03	0.27	1.3	0	net
	<i>Dimophyes artica</i>			11.6	2.9	net
November		0.2 ± 0.1	0.2 ± 0.1	1.4	0.08	net
		<0.2	few	2.9–10.5	0.8–5.5	submersible
	<i>Nanomia cara</i>					
November		0.04		1.4	0.08	net
Gulf of Maine				—	—	
	<i>Nanomia cara</i> (50–200 m)	<0.1–8/m ³		—	—	submersible
						Rogers <i>et al.</i> , 1978

a *Agalma*, *Physophora*; b *Forskalia*, *Agalma*, *Athorybia*, *Cordagaima*, *Rosacea*, *Stephanophyes*; c *Forskalia*, *Agalma*, *Nanomia*, *Cordagaima*; d *Diphyes*, *Chelophyes*, *Rosacea*; Numbers in parentheses are the number of SCUBA dives.

0.03/m³ to 24.5/m³ between March and June, 1983. Pugh and Boxshall (1984) report extremely high densities of *M. atlantica* polygastrics ($218 \pm 156/\text{m}^3$) and eudoxids ($1207 \pm 596/\text{m}^3$) off the north-west African coast in April.

At the ocean surface, the densities of *Physalia physalis* can be estimated by timing sightings within a predetermined distance from a ship underway at a constant speed (Purcell, 1984b). Kennedy (1972) used aerial sightings to estimate relative seasonal distribution and abundances. Beach strandings of *P. physalis* apparently are related to local current and wind patterns that vary seasonally along the Gulf coast of Texas. It is unclear if the strandings reflect seasonal changes in population abundance, or merely changes in wind and current patterns.

Observations from submersibles in the deep sea show that siphonophores can be very conspicuous members of the community (Barham, 1963, 1966; Rogers *et al.*, 1978; Youngbluth, 1984; Mackie, 1985; Pugh and Harbison, 1986, 1987). The gas-filled floats of the physonects contribute to the acoustic reflection from the deep-scattering layer (Barham, 1963, 1966).

2. Impact on prey populations

The estimates of feeding rates can be used to calculate the impact of siphonophores on prey populations when combined with accurate abundance estimates (Table 15). Purcell (1981b, 1984b) estimated that two cystonect species could have consumed 28 and 60% of the larval fishes daily in two locations. Cystonects can occur in extremely high numbers, and may be very important predators on larval fish populations. In contrast to this high predation impact on a relatively rare prey type, calycophoran species consumed only small percentages of their abundant copepod prey (Purcell, 1981c, 1982; Purcell and Kremer, 1983). Nonetheless, Purcell (1982) and Purcell and Kremer (1983) concluded that the siphonophores *Muggiaeatlantica* in Friday Harbor, Washington and *Sphaeronectes gracilis* off Catalina Island, California, respectively, were the most important soft-bodied consumers of copepods during the period of their studies. Siphonophores are found from the surface to the floor of the ocean, in neritic and oceanic waters, yet only recently has their importance as predators in planktonic communities become apparent.

Acknowledgements

Many people have helped in the preparation of this review and we thank them all. We thank also the referees for their constructive comments on the manuscript. In addition, M. V. Angel, D. C. Biggs, D. A. Hessinger and L. P. Madin made helpful suggestions on certain sections.

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Addendum

Since this article went to press, Freeman's findings on the distribution of photophores (p. 202) have been published (Freeman, G. (1987), Localization of bioluminescence in the siphonophore *Nanomia cara*, *Marine Biology* **93**, 535–541) and an account of the distribution of components of the physonectid nervous system showing FMRFamide-like immunoreactivity has also appeared (Grimmelikhuijzen, C. J. P., Spencer, A. N. and Carré, D. (1986), Organization of the nervous system of physonectid siphonophores, *Cell and Tissue Research* **246**, 463–479).