

VIII

Locomotion, Flotation, and Dispersal*

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I. INTRODUCTION

Cnidarians have populated all marine environments. The first animal brought up from the bottom of the Philippine trench (10,190 m) was a sea anemone (Bruun, 1956). Cnidarians are the dominant organisms of coral reefs, which alone would necessitate their recognition as a group of major ecological significance. They are also the dominant organisms of the marine pleuston, providing food or substrate for a variety of other invertebrates living at the air-water interface (Savilov, 1956,

* This chapter is dedicated to A. K. Totton.

without elaborate grasping organs, and without having to pursue their prey. It is doubtful if any other predators can obtain nourishment with such economy of effort. They are highly efficient animals and their structural and behavioral simplicity are part of their efficiency. They use locomotion for a variety of purposes, which are considered under four headings below, but pursuit of prey as such is never observed.

1. ESCAPE LOCOMOTION

The sea anemones *Stomphia* and *Actinostola* detach themselves from the substratum and swim when stimulated by direct contact with starfishes of the genera *Dermasterias* and *Hippasterias*, or with the nudibranch *Aeolidia papillosa* (reviews by Robson, 1966; Ross, 1967; D. M. Ross, this volume). *Gonactinia* shows a locomotory escape response to four species of nudibranchs (Robson, 1971). After prolonged photic, electrical, or mechanical stimulation, *Metridium* tends to walk away to new locations (Batham and Pantin, 1950) and *Bolocerooides* swims when given strong shocks (Josephson and March, 1966) but it is not known if these behavior patterns occur as escape responses in nature.

Horridge (in discussion following Barnes, 1966) reports that the cubomedusan *Charybdea* turns and swims downward away from shadows cast over it. The hydromedusae *Sarsia* (Passano *et al.*, 1967), *Polyorchis* (Gladfelter, 1970), *Spirocodon* (M. Yoshida, personal communication), and *Bougainvillea* (Singla, 1972) show light-off responses under laboratory conditions which might represent escape swimming in nature. *Eutonina* changes direction and swims downward away from a source of high frequency vibration (Horridge, 1966). Some medusae (e.g., *Aglantha*) swim vigorously in response to tactile stimulation of the umbrella, whereas others (e.g., *Sarsia*) show a protective "crumpling" response which does not involve swimming. The siphonophore *Nanomia* shows both forward and reverse escape swimming responses following sharp stimulation (see Section I,B,7,a,ii). In the majority of Cnidaria, however, escape responses take the form of protective retraction or closure rather than of locomotion.

2. LOCOMOTION IN RELATION TO SEX

Sagartia troglodytes is the only cnidarian known to copulate. In response to an unidentified pheromone in the genital secretion of the male, the females walk along the bottom and press their bases up against that of the male in such a way as to create an improvised external brood chamber in which the eggs are laid (Fig. 1). The copulatory position is maintained for 1 or 2 days. Nyholm (1943) suggests that the

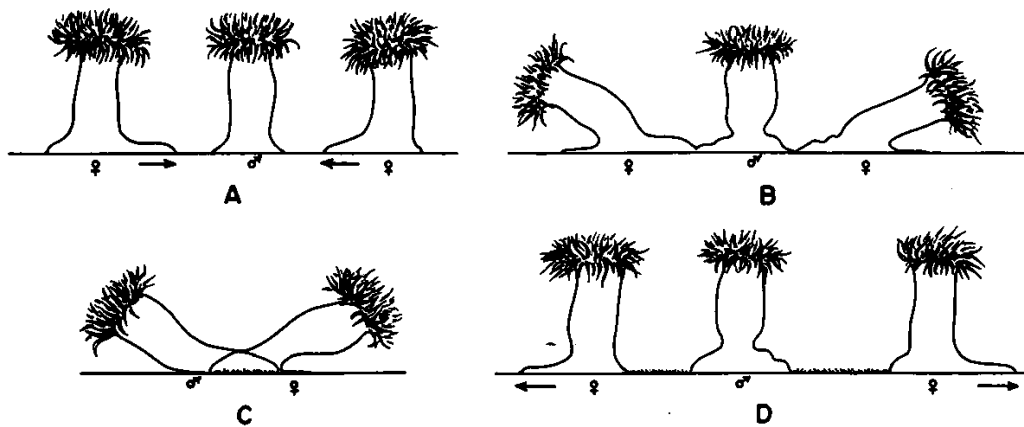


Fig. 1. Copulatory behavior in *Sagartia troglodytes*. (A) Males move toward female; (B) contact is made; (C) two specimens forming brood chamber between them; and (D) females migrate away on completion of mating act (Nyholm, 1943).

behavior represents an adaptation to life in regions of strong water currents. Jellyfish aggregations may likewise serve to promote fertilization, although no directed responses of the *Sagartia* type are known or likely in this case. *Linerges* is said to perform spawning migrations from deep water to the surface (E. G. Conklin, cited by Russell, 1970).

Sperm chemotaxis has been demonstrated in several hydroid groups (Miller, 1966). In *Campanularia*, sperm approaching the female gonangia turn toward the gonangia and show accelerated locomotion (Fig. 2A).

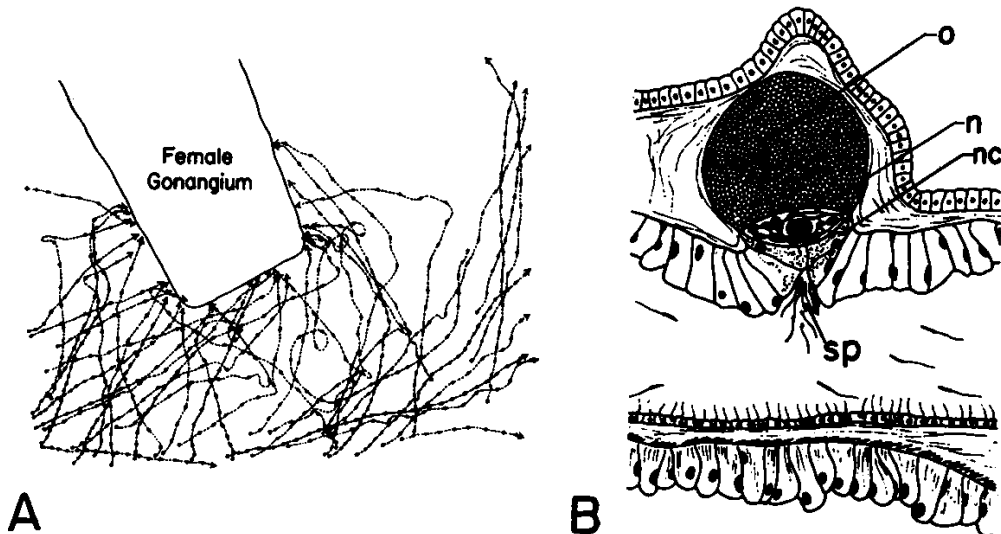


Fig. 2. Sperm chemotaxis. (A) Plot of sperm trails (*Campanularia flexuosa*). As the sperm approach the ♀ gonangium they turn toward it and accelerate (Miller, 1966). (B) Accumulation of sperm near a ripe oocyte in gastrogenital pouch of *Cyanea capillata*. The sperm are collecting in a pit formed by insinking of the nurse cells from their original epithelial location. n, Nucleus of oocyte; nc, nurse cell; o, oocyte; sp, sperm (Widersten, 1965).

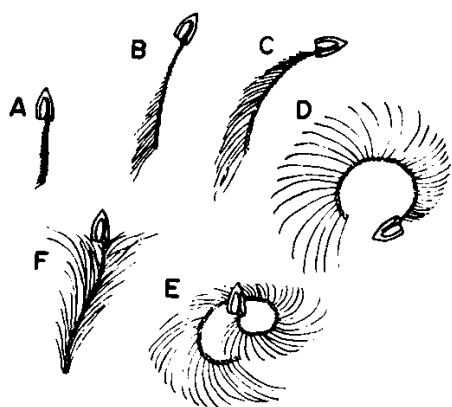


Fig. 3. *Muggiaea*, fishing behavior. The siphonophore starts swimming with its stem contracted (A, B), then releases the stem and tentacles and swims in a circle (D). Swimming stops, with the fishing lines extended (E). The stem sinks under its own weight (F), whereupon a new sequence commences (Mackie and Boag, 1963).

Casual observations on hydra (Brien, 1965) and *Cyanea* (Fig. 2B) suggest that sperm are attracted specifically to the eggs of these species.

3. LOCOMOTION RELATED TO FEEDING

The characteristic (nonescape) swimming activity of many siphonophores and medusae is best explained in ecological terms as a means of keeping the tentacles spread out and thus increasing the chances of plankton capture by random collision. An 11 cm long siphonophore can put out over 5 m of fishing filaments (Mackie and Boag, 1963). Occasional bouts of locomotion in which the fishing lines are contracted and then let out again appear to be part of normal behavior in *Nanomia* and also in smaller forms such as *Muggiaea* (Fig. 3).

The very long and numerous tentacles of *Cyanea* would tend to become tangled but for the continuous gentle swimming pulsations. The actual locomotory effect of swimming may be less significant than the tentacle-spreading role. In *Cassiopeia* which lies inverted on the bottom the "locomotory" movements appear to serve only to create feeding currents. Fraser's (1969) studies of *Aurelia* in the 20–50 mm size range indicate that they feed largely by filtering water through the tentacles while swimming (Fig. 4). For a specimen 50 mm in diameter, each

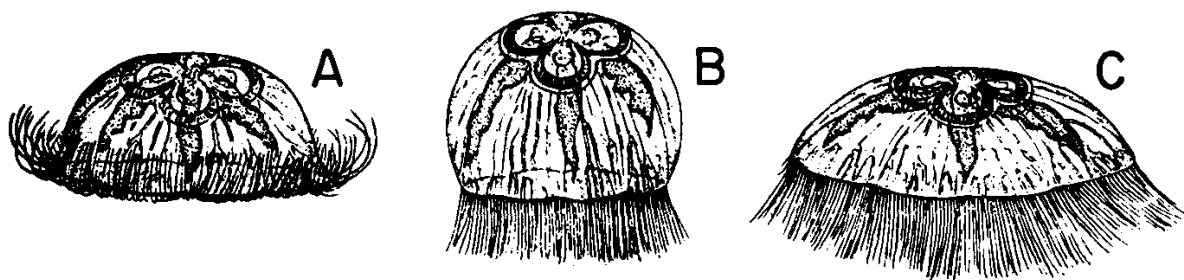


Fig. 4. Stages in pulsation of *Aurelia*. (A) Onset of contraction; (B) fully contracted; and (C) fully expanded. As the tentacles sweep down, food is trapped. One liter of water is filtered in 7½ minutes (Fraser, 1969).

swimming pulse filters about 22 ml of water. Older specimens are primarily ciliary-mucus feeders, but here too food capture would certainly be aided by locomotion.

The brown hydra *Hydra littoralis* are positively phototactic and starvation increases their rate of movement (Feldman and Lenhoff, 1960). Since their crustacean prey are often similarly phototactic, this behavior would tend to locate the hydra in good feeding positions. The diurnal vertical migrations of medusae and siphonophores probably help feeding and may be accomplished by swimming, although this is not certain (Barham, 1966). Coastal jellyfish tend to form swarms in regions of food abundance, and swarming may well be an active process involving swimming behavior (Zelickman *et al.*, 1969).

4. LOCOMOTION IN RELATION TO SUBSTRATE SELECTION

Many sea anemones can crawl along the bottom or climb upon preferred substrata such as mollusk shells. *Stomphia* will transfer from a tile or stone on which it has settled to a *Modiolus* shell placed in contact with its tentacles (Ross and Sutton, 1967). As with the preferential attachment of species living on shells inhabited by hermit crabs (reviewed by Ross, 1967), the anemone's response is to a chemical factor in the periostracum of the shell (see D. M. Ross, this volume).

Larvae of the hydroid *Sertularella miurensis* settle preferentially on *Sargassum tortile* (Nishihira, 1967a), and a high degree of substrate selectivity is known or may be assumed for a number of other species, especially commensal and parasitic forms. We do not know if the larvae swim actively toward preferred substrates or merely settle when they happen to come near them. Kawaguti (1941) shows that the tropisms of coral planulae, particularly their phototropisms, are such as would favor settlement of the larvae in suitable localities for adult growth (see also Harrigan, 1972). The responses of *Clava* planulae can also be logically explained in relation to site selection (Williams, 1965).

B. Mechanisms of Locomotion

1. CILIARY LOCOMOTION

With a few exceptions (e.g., *Corymorpha* and *Halcampa*) planula larvae are ciliated and can swim by ciliary action (Fig. 5A). Like ciliate protozoans, they often swim in spirals. Swimming velocities in the range 10–25 cm/minute are recorded for various species. Postplanula larvae, including pelagic forms, come to rely less on ciliary locomotion as they

get larger and their muscles develop. Young scyphistomae swim by ciliary action while older ones glide along the bottom (Spangenberg, 1964).

The sporosacs of *Dicoryne* are set free and swim by ciliary action, spreading genital products (Fig. 5B).

Halammohydra, a member of the interstitial fauna, moves around among the sand grains with the help of epidermal cilia. *Halammohydra vermiformis*, the most wormlike species, develops asymmetrically with one disproportionately large tentacle. Movement is in the oral direction with the large tentacle trailing (Fig. 5C) according to B. Swedmark (personal communication).

The locomotion of *Tubularia* sperm has been analyzed by Miller and Brokaw (1970), who show that chemotactic turning behavior is accomplished by an asymmetrical pattern of bending of the flagellum. The sperm can only make turns in one direction relative to their own bodies.

2. BURROWING

Burrowing anemones are elongated and wormlike, incapable of basal attachment, and equipped with powerful retractor muscles. Some such as *Halcampa* (Nyholm, 1949) can lean far out of their burrows to spawn. J. G. Spaulding (personal communication) installed *Peachia* in a tank and marked their positions; after the passage of one winter many of the anemones had changed their positions. Whether such migrations occur in nature is unknown. Burrowing anemones have not evolved the ability for horizontal subterranean locomotion shown, for example, by synaptid holothurians.

L. Faurot (cited by Stephenson, 1935) showed that burrowing in *Peachia* is accomplished by downward peristaltic waves acting against

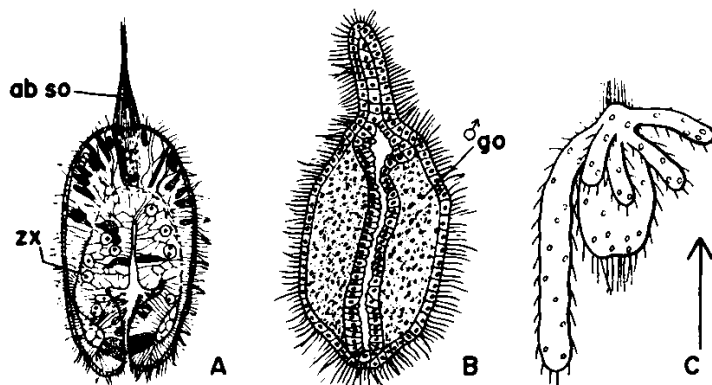


Fig. 5. Ciliary locomotion. (A) Planula larva of *Aiptasia*. ab so. Aboral sense organ; zx, zooxanthella (Widersten, 1968). (B) Free sporosac of *Dicoryne*. ♂ go, male gonad (Ashworth and Ritchie, 1915). (C) *Halammohydra vermiformis*. Arrow shows direction of locomotion (Swedmark and Teissier, 1957).

the fluid contents of the coelenteron. The circular constriction drives fluid to the base (physa), causing it to distend and to push the sand away in all directions. Ansell and Trueman (1968) confirm this general picture and show that the anemone is effectively anchored by a swollen part of its column just above the physa during physal eversion ("column anchor," Fig. 6A). The peristaltic waves occur roughly every $1\frac{1}{2}$ minutes. Once the anemone is firmly embedded in the sand, strong longitudinal contractions are found to accompany the cycle, occurring immediately after physal eversion and helping the anemone to pull itself strongly downward, anchored by the distended base ("physal anchor," Fig. 6B). Pressure changes in the fluid skeleton have not been recorded during burrowing but measurements on animals performing similar movements while lying flat on the sand show a rise in pressure from 1 to 3 mm of water during passage of the peristaltic waves, with pressures of 50 mm water during strong retractions of the column. According to Stephenson (1935), *Peachia* can bury itself in half an hour, although the process may take much longer.

The sea pen *Veretillum* burrows in a similar manner. Here, too, waves of peristalsis run down the elongated rachis, whose tip initially resembles a stiletto (Titschack, 1968) but swells into the shape of an ampoule

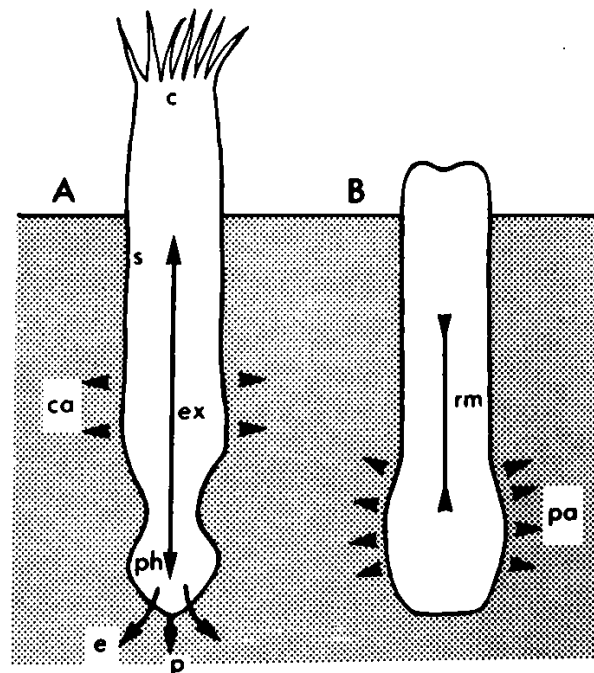


Fig. 6. Burrowing in *Peachia*. (A) Eversion of physa (e) with displacement of sand (arrows) and further penetration of the substratum (p); the anemone is held by the column anchor (ca, arrowheads) as extension (ex) follows retraction in B. c, capitulum; s, scaphus; ph, physa. (B) Tentacles infolded, physa swollen to form anchor (pa, arrowheads) which allows retractor muscles (rm) to pull anemone into sand (Ansell and Trueman, 1968).

(Buisson, 1971) during the anchorage phase. According to the size of the individual, *Veretillum* may take 1 to 3 hours to implant itself. Buisson's surgical experiments suggest that burrowing is controlled from a center in the proximal part of the peduncle.

Implantation of the rachis in *Pteroides* (G. S. Fraenkel, cited by Titschack, 1968) and of the holdfast in *Corymorpha* are believed to represent geotropisms. In *Corymorpha*, Campbell (1969) finds statocysts in the anchoring processes.

3. CRAWLING ON THE FOOT OR BODY SIDES

Slow pedal locomotion (1–2 mm/day) has been reported in stauro-medusans (Thiel, 1936) but is best developed in actinians, some of which are very mobile and can move several millimeters per minute (Stephenson, 1928; Robson, 1971). Some fungiid corals (*Cycloseris* and *Diaseris*) can creep slowly on the bottom (Goreau and Yonge, 1968). Phototactic locomotory behavior is described in *Anemonia* (J. Cotte, cited by Robson, 1965).

Pantin (1952) has analyzed the locomotory activity of *Metridium* using time-lapse cinematography. The muscular apparatus involved is essentially the same as that responsible for peristaltic waves in the column. In both types of activity, the circular ectodermal component is chiefly responsible. In locomotion a wave of contraction runs asymmetrically inward from the edge of the foot starting at the rear end, causing release from the substratum, and spreading around the sides. At the same time, downward peristalsis in the column forces water into the foot, making it expand and thus advancing the front edge of the foot after the pedal wave has traveled across it.

Aiptasia can release the foot and crawl on its side or climb using the adherent rugae of the column (Portmann, 1926; Stephenson, 1928). Locomotion involving muscular activity of the lateral body wall is described in the frustules (unciliated, asexual buds) of *Craspedacusta* (Dejdar, 1934). They detach from the parent polyp and move across the substratum to new locations (Fig. 7). One pole, probably the one which will attach, takes the lead. The benthonic larvae of *Halcampa* are unciliated and move in a vermiform manner, inserting themselves into crevices (Fig. 8).

4. TENTACULAR CREEPING

According to W. Seidentop (cited by Thiel, 1936) the preferred mode of locomotion in *Lucernaria* is by creeping on the arm tips following detachment of the peduncle, and this he describes in some detail.

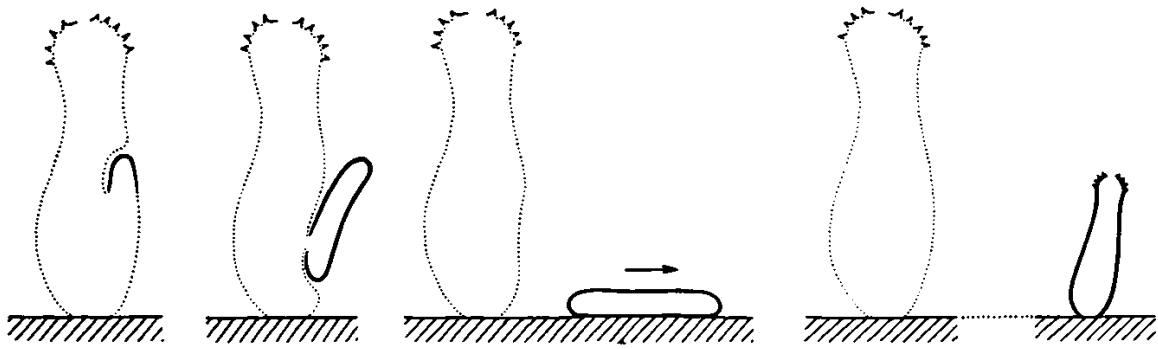


Fig. 7. Frustule formation, separation, and migration in *Craspedacusta* (Dejdar, 1934).



Fig. 8. *Halcampa* larvae are unciliated but on hatching creep on the bottom and insert themselves into the substrate (Nyholm, 1949).

Traction is typically generated by the shortening of an attached leading arm, with the other arms detached and following passively. Less often, lateral arms may be swung forward, appearing to assist forward motion. It is not known if nematocysts are involved in adhesion.

Some hydromedusae (*Cladonema* and *Eleutheria*) creep on their tentacles with the aid of adhesive pads (Fig. 9A). The parasitic hydrozoan *Polypodium* spends the winter as a stolon in the ovaries of sturgeons, but when the fish spawn in May, the stolons are liberated along with the eggs and subdivide forming mobile polyps which crawl around on their tentacle tips (Raikova, 1958) (Fig. 9B).

The coral *Diaseris* pulls itself along and climbs with its tentacles with the aid of a mucus float secreted on the aboral side (Hubbard, 1972).

5. COMBINED USE OF FOOT AND TENTACLES

The well-known looping and somersaulting movements of hydra, first described by A. Trembley, are not sharply distinguishable according to Ewer (1947b). The foot is lifted clear of the bottom and if it comes down on the same side of the attached tentacles as before it counts as looping, if on the other side as somersaulting. Ewer confirmed O. Toppe's observation that attachment of the tentacles during locomotion involves discharge of isorhizas and she was able to demonstrate them in the

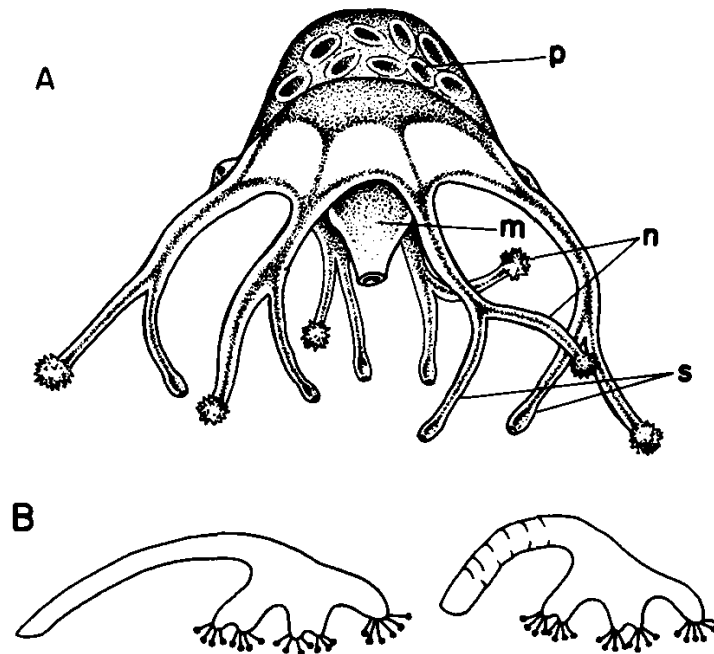


Fig. 9. (A) The medusa of *Eleutheria* creeps on its tentacles. m, Manubrium; n, nematocyst-bearing fork of tentacles; p, planulae in brood pouch; s, sucker-bearing fork of tentacle (from Hyman, 1940, after Hincks). (B) Looping locomotion in *Lucernaria*. The elongated polyp attaches by its arms. The foot is then drawn up, preparatory to a new step (from Thiel, 1936, after Seidentop).

stained "footprints" left by ambulant hydra on a glass slide. Passano and McCullough (1963) recorded a characteristic electrical pattern (attachment burst) associated with attachment of the tentacles during locomotion. Ewer (1947a) describes the negatively geotactic migration of newly detached hydra buds and of adults subjected to high CO_2 concentrations.

The movements made by sea anemones such as *Stomphia* and *Calliactis* in clambering onto shells are also accomplished by collaborative action of tentacles and foot, but nematocysts are here involved both in pedal attachment and in tentacular adhesion (see D. M. Ross, this volume). The looping locomotion of *Gonactinia* is analyzed in detail by Robson (1971). Another primitive anemone, *Protanthea*, is said to move like hydra with the help of its tentacles (Nyholm, 1959).

Some scyphopolyps can progress by looping and somersaulting (Fig. 9B) using their tentacle clusters alternately with the peduncular disk (W. Seidentop, cited by Thiel, 1936; Berrill, 1962).

6. SWIMMING MECHANISMS IN SEA ANEMONES

This topic has been the subject of detailed review by Robson (1966) and is further treated by D. M. Ross (this volume). We need only note

here that there are two fundamentally different swimming mechanisms in question, one involving coordinated tentacular flexions (e.g., *Gonactinia* and *Boloceroïdes*) and the other involving alternating side-to-side flexions of the whole body, brought about by activity of the endodermal muscles (*Stomphia* and *Actinostola*).

There is a striking parallel here with nudibranch mollusks, some of which (*Cumanotus*) swim by coordinated flexions of the long tentacle-like cerata (Farmer, 1969) while others (*Tritonia*) swim by alternating body flexions (Willows, 1967). Both sea anemones and nudibranchs are primarily adapted to life on the bottom and can only become water-borne by heroic, grotesque, and probably energetically wasteful exertions.

7. MEDUSAN SWIMMING

The reader should refer to Bullock and Horridge (1965) for a general account of medusan swimming, in particular its neural control. R. K. Josephson (this volume) covers more recent work on control mechanisms. In this chapter attention is directed toward the mechanical aspects of swimming.

a. Hydromedusae. i. MUSCULOMESOGLEAL RELATIONSHIPS IN THE UMBRELLA. The swimming muscles lie on the subumbrellar side and reduce its surface area when they contract, deforming the whole bell and expelling water from below. The muscles function purely in the systolic phase and are antagonized by elastic components in the mesoglea.

The problem of reducing the area of the subumbrellar surface in cylindrical medusae can be met by a relatively simple arrangement of circularly oriented muscle fibers. In wider, flatter forms the problem is potentially more complex, as the wide rim will tend to buckle unevenly during contraction (and does in some forms), calling for more elaborate muscular layout such as we see in *Obelia*. In hydromedusae, the swimming muscle does not, however, become subdivided into circular and radial components, as in scyphomedusae. Radial muscle may be present in the subumbrella and velum, but it does not appear to be directly involved in swimming. It serves to pull the margin inward in feeding behavior, in protective "crumpling," and possibly in steering.

In *Obelia*, the swimming muscle is arranged in two layers, neither of which is truly circular (Chapman, 1968). The fibers in the two layers are oriented obliquely with respect to the bell margin and run at right angles to one another (Fig. 10). Study of the system by optical and electron microscopy shows that both fiber layers are produced from a

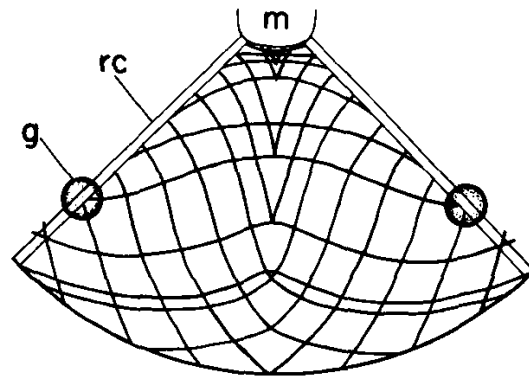


Fig. 10. *Obelia* subumbrellar muscle. General orientation of myofibrils in subumbrellar swimming muscle in one quadrant. g, Gonad; m, manubrium; rc, radial canal.

single layer of muscle cells. Any given muscle cell will give rise to fibers running in two different directions (see D. M. Chapman, this volume, Fig. 7). The fibers from different cells are abutted end to end in such a way that the composite fiber appears as a single long unit which can be followed for considerable distances over the subumbrella.

The way in which the mesogleal skeleton accommodates itself to and opposes muscular contraction during swimming has been studied by Gladfelter (1970, 1972a) in a large number of different medusae.

Contraction of the subumbrellar muscle tends to compress the mesoglea in the circular direction. Since the volume of the mesoglea cannot change, the bell must thicken to accommodate to this compression. As it thickens, radially arranged mesogleal fibers undergo stretching, and it is the potential energy built up in this component that provides the antagonizing and restorative force.

In a hypothetical cylindrically shaped medusa with mesoglea of homogeneous thickness and uniform fiber distribution, contraction of the subumbrellar muscle, if attached at all points, would cause symmetrical compression and thickening of the mesoglea. By contrast, the mesoglea of a form such as *Polyorchis* is not homogeneous and the thickening which occurs during contraction is not uniform, but results in the bell changing shape from a circular to an octagonal form, as seen in cross-section (Plate 1).

If the subumbrellar muscle were to contract by 44% the subumbrellar mesoglea in the hypothetical medusa would be compressed by 44%. In *Polyorchis* it is compressed by only 14% because it can fold outward away from the muscle sheet at eight adradial flexure points or joints (Plate 1, J Ar; Fig. 11). In the hypothetical model the resulting thickening of the bell mesoglea would be a uniform 46% but in *Polyorchis* the

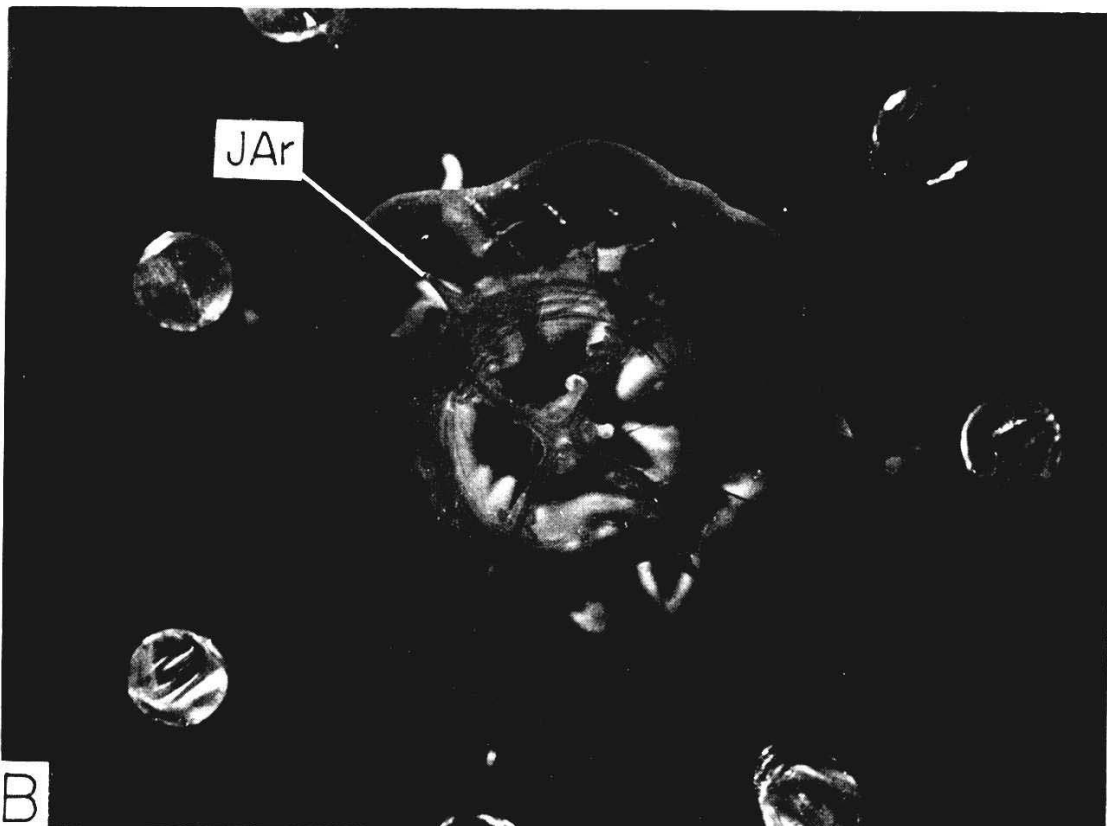
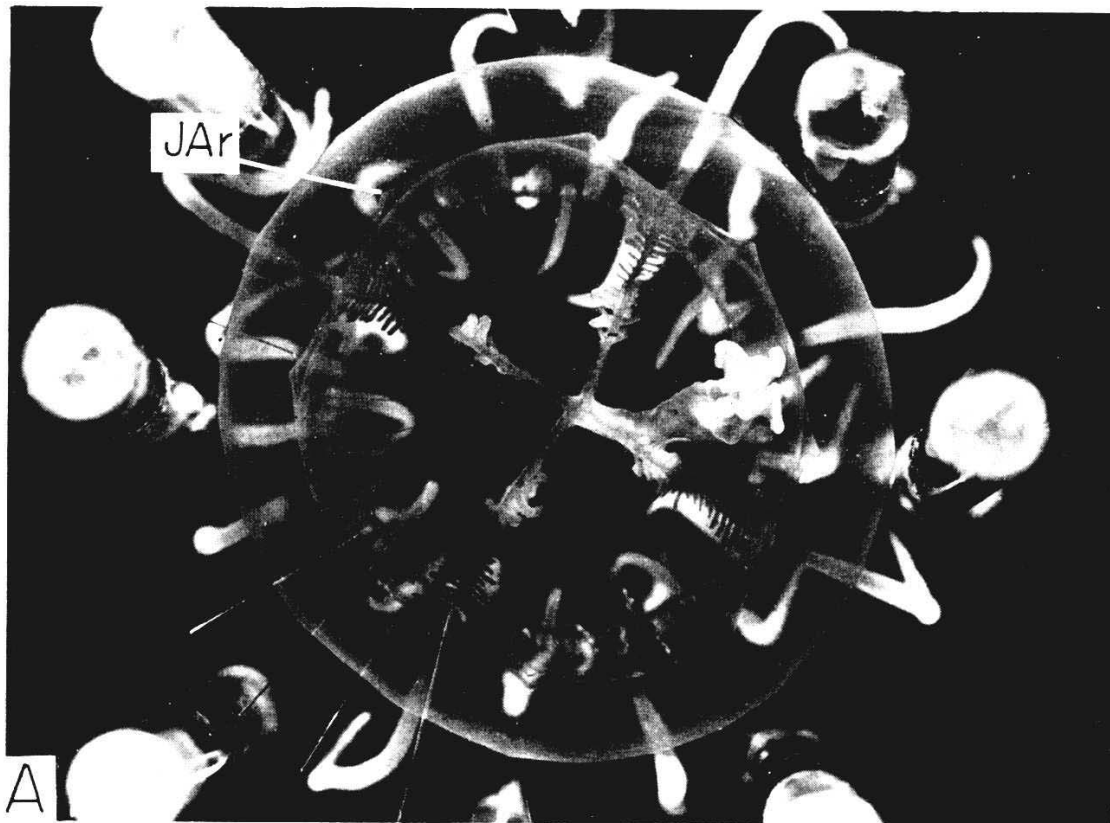


Plate 1. Axial views of *Polyorchis* (A) relaxed and (B) contracted in swimming pulsation. Fine glass needles serve as reference points. J Ar, Adradial joint (Gladfelter, 1972a).

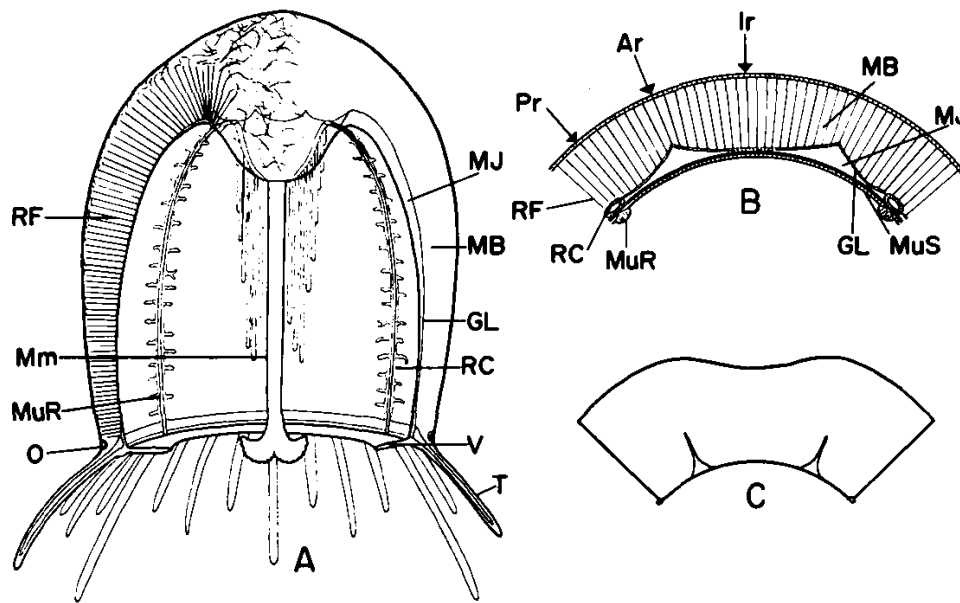


Fig. 11. *Polyorchis* bell architecture. (A) Longitudinal section passing interradially (left half), adradially (right). (B) Horizontal section through one quadrant at midbell. (C) The same in outline, to same scale, during contraction. Ar, adradius; GL, gastrodermal lamella; Ir, interradius; MB, bell mesoglea; MJ, joint mesoglea; Mm, manubrium; MuR, radial muscle; MuS, swimming muscle; O, ocellus; Pr, perradius; RC, radial canal; RF, radial mesogleal fiber; T, tentacle; V, velum (adapted from Gladfelter, 1972a).

increase amounts to only 34, 36, and 16% at the inter-, per- and adradial, respectively. A large part of the compressional deformation has been absorbed by the specialized joint mesoglea.

The joints consist of narrow columns, triangular in section, located between the gastrodermal lamella and the subumbrellar muscle sheet. They come together at the apex of each quadrant but are separate along the rest of their length. They are not only physically isolated from the bell mesoglea but are composed of a unique kind of mesoglea, lacking fibers and showing high deformability. Gladfelter notes that the joints may stretch radially by 200% during contraction.

Concentrations of springlike radial fibers in the main bell mesoglea converge on the joint regions, minimizing thickening of the bell mesoglea adjacent to the joints.

Presumably the absorption of a large part of the compressional deformation of the bell within the eight specialized joint regions permits the main mass of mesoglea to assume a firmer, less compliant consistency without this increasing the muscular energy required to reduce the subumbrellar surface by a given amount. *Polyorchis* is a bottom-living medusa and has the firm consistency needed to withstand some battering on occasion.

The *Polyorchis* system of internal joints is not universal among hydro-

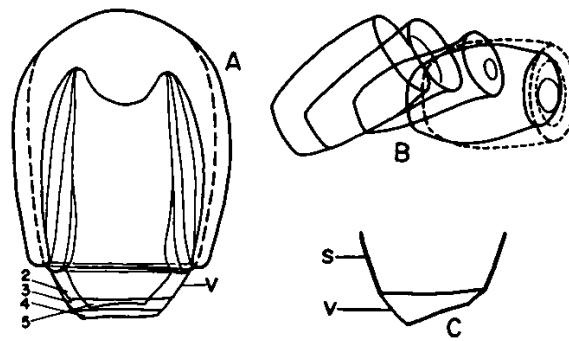


Fig. 12. *Polyorchis* swimming and turning. (A) Contraction profiles during a single contraction, traced from cinematographic sequences. Numbers indicate successive stages in velum (v). (B) Tracings of subumbrellar outline at $\frac{1}{8}$ -second intervals during turning, showing asymmetrical displacement of velum. The dotted outline shows the initial resting position. (C) Lateral view of velum (v) and adjacent subumbrella (s) during turning, from a movie sequence (adapted from Gladfelter, 1972a).

medusae. In *Aglantha* and the diphyid siphonophores for example the bell is quite rigid and there are permanent exumbrellar joints where flexion occurs, as in the arthropod exoskeleton.

ii. ROLE OF THE VELUM. The role of the velum is to narrow the orifice of the bell, increasing the velocity with which the water jet is emitted and thus increasing momentum (Gladfelter, 1972a). The velar circular muscles contract at the same time as the main swimming muscle but at a faster rate, so that the orifice is narrowed prior to the major water emission. The force of the effluent jet makes the velum bulge out as a cone-shaped structure (Fig. 12A). Following the contraction, it flops loosely inward as water is sucked into the subumbrellar cavity. Water entry will thus be at a lower velocity than water emission, and backward momentum will be decreased relative to forward. Removal of the velum drastically reduces swimming efficiency.

The velum functions somewhat like the siphon in squids (Packard, 1966). In both cases, swimming velocity varies according to size of the effluent orifice, on the one hand, and the mass of water expelled, on the other. If the velum were as solidly built as the siphon, there would be no disadvantage inherent in large size, but because of its delicate construction, the velum is less effective in containing larger masses of water. Large specimens of *Polyorchis* consequently swim more slowly in relation to their size than do small specimens. This may be an inherent size-limiting factor for hydromedusae generally. This observation also helps to explain the lack of a velum in typical scyphomedusae, most of which achieve much larger sizes than any hydromedusae.

Turning involves asymmetrical contraction of the velum and deflec-

tion of the water jet to one side (Figs. 12B and C). Velar deformation is the result of contraction of radial muscles in the ectoderm of the outer surface. These muscle fibers are undoubtedly homologous to the radial "fibers of Claus" which occur in the margins of the swimming bells of *Nanomia* and other physonectid siphonophores. The Claus' fibers in the latter, however, are not symmetrically distributed, but are concentrated in two groups at the two upper corners of the velum (Fig. 13). When they contract, they bring about a major deformation of the bell orifice such that the water jet is directed upward and the siphonophore swims downward. *Nanomia* does not appear to be able to direct the jet sideways, thus cannot swim laterally. However, *Nanomia* and its relatives are the only animals swimming by jet propulsion other than squids which are able to control the jet in such a way that they can swim either forward or in reverse (Mackie, 1964).

Gladfelter (1972a) and Singla (1972) note that turning is not a purely velar function but may involve deformation of the adjacent regions of the subumbrellar, indicating that radial muscles in that region may also be active. This is particularly the case in wider, flatter medusae. In *Nanomia*, electron microscope study (G. O. Mackie, unpublished) shows that the Claus' fibers of the velum are continuous through holes in the mesoglea with radial muscles fibers in the subumbrellar endoderm, and it is likely that this component helps bring about the marginal deformation during reverse locomotion, paralleling the arrangement in conventional hydromedusae.

b. Scyphomedusae. A striking parallel to the hydromedusan type of locomotion is shown by *Charybdea* (order Cubomedusae). Unlike typical scyphomedusae these jellyfish are tall and bell-shaped and have a horizontal annular flap or velarium which resembles a velum super-

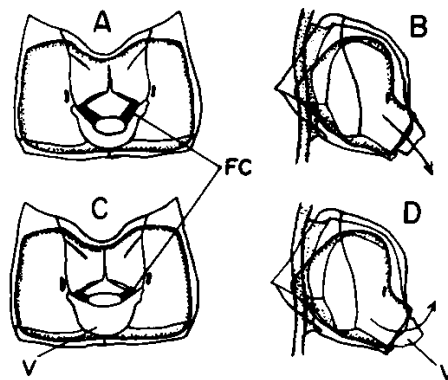


Fig. 13. Directional control in *Nanomia*. Swimming bells are shown full face in A and C, in profile in B and D. In forward swimming (A and B), water jet is emitted backward. In reverse swimming (C and D), Claus' fibers (FC) retract velum (V) asymmetrically directing jet forward (Mackie, 1963).

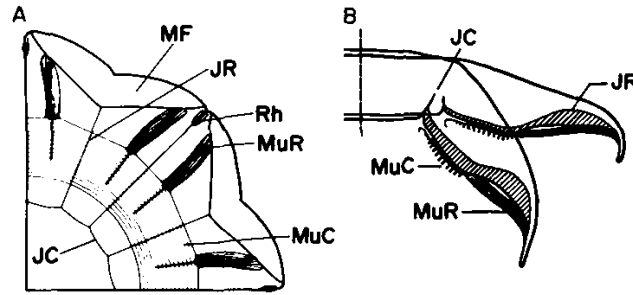


Fig. 14. *Cyanea* swimming components. (A) Oral view of one quadrant. (B) Lateral view, relaxed and contracted, from movie sequences. JC, Coronal joint; JR, radial joint; MF, marginal flap; MuC, coronal muscle; MuR, radial muscle; Rh, rhopalium (adapted from Gladfelter, 1970).

ficially and fulfills an equivalent role. Gladfelter (1970, 1972b) shows that turning is executed by asymmetrical contraction of the velarium. The pedalia, held to be responsible for turning by some writers, may have no such role.

In semaeostome medusae such as *Cyanea* the swimming contraction is a composite event involving both the circular (coronal) muscle and the eight pairs of likewise striated but radially oriented muscles (Fig. 14). The bell is hinged at a circular coronal joint proximal to the coronal muscle. Radial joints in the periphery of the bell allow the mesoglea to bend inward as this region becomes compressed in the later stages of the contraction. There is also some folding of the exumbrellar surface.

According to Gladfelter, the eight marginal flaps serve to increase leverage of the margin during the early stages of contraction and to increase the effective length of the subumbrellar cavity during the later stages. During recovery they flex inward, allowing water to stream past as the bell spreads out. In a general way, they fulfill a role similar to that fulfilled by the hydromedusan velum.

Turning in *Cyanea* as seen in righting behavior involves the two sides contracting sequentially at different rates and to slightly different degrees. The upper side contracts first with a powerful stroke causing the bell to shift sideways and then to tilt as the other side starts to contract. There is no parallel here to turning in hydromedusae.

According to Gutmann (1965), *Rhizostoma* shows a three-phase contraction sequence in which the inner coronal muscle contracts first, followed by the outer and then by the inner again (Fig. 15). This author also gives some information on mesogleal architecture, including the orientation of the elastic fibers.

From the studies cited above, particularly that of Gladfelter, it is becoming evident that the musculoskeletal system of jellyfish is just as highly developed as that of many animals having hard skeletons.

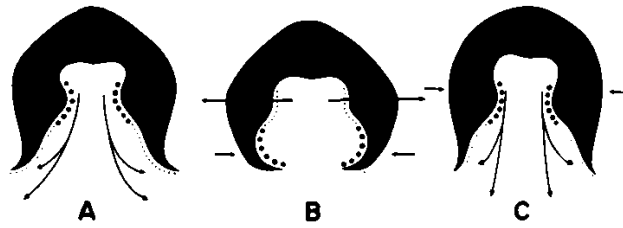


Fig. 15. Sequential shape changes in the bell of *Rhizostoma* during swimming. (A) Inner circular muscle contracts; (B) peripheral circular muscle contracts while the inner zone bulges outward elastically; and (C) the inner muscle contracts again (Gutmann, 1965).

III. FLOTATION

A. Use of Lipids to Aid Buoyancy

Lipid droplets apparently derived from the food are frequently seen moving around in the canals of medusae and siphonophores and they may coalesce to form prominent masses in certain regions, for instance, in the somatocyst ("oil holder") of calycophoran siphonophores (Fig. 16) and the palpon diverticulum in *Nanomia cara*. Some authors attribute a flotational role to these structures, but proof is lacking.

More credible is the suggestion that certain larvae which stay in the plankton for long times rely on their lipids for buoyancy. According to Nyholm (1943), *Pachycerianthus* blastulae float by means of their yolk reserves before any ectodermal ciliation is developed. Leloup (1929) attributes a flotational role to lipids in the conaria larvae of *Velella*,

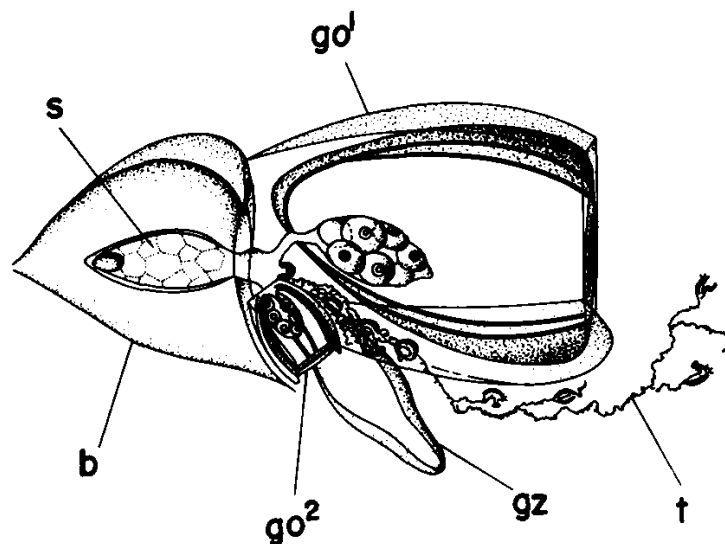


Fig. 16. Eudoxid of *Muggiæa*. b, Bract; go¹, go², gonophores; gz, gastrozoid; t, tentacle; s, somatocyst with oil drop (after Chun, 1897).

following Woltereck (1904). The so-called "nutritive yolk" (Nahrungsdotter) found inside *Cerianthus lloydii* larvae may be a flotational material, though not necessarily composed of lipids (Riemann-Zürneck, 1968).

B. Gas Bubbles and Gas-Filled Floats

Hydra are often seen with a gas bubble at the pedal end floating inverted at the surface. According to Lomnicki and Slobodkin (1966), food shortage induces flotation. Flotation may happen at any time of the day in brown hydra, but green hydra only float in the dark according to these authors. The nature of the gas is unknown; whether or not it is secreted or merely "captured" from the surface film is questionable. Kepner and Thomas (1928) and Kepner and Miller (1928) argued that the bubbles were secreted by specialized endodermal cells. According to their account, the gas is discharged into a sac of mucus which retains the bubble until the hydra reaches the surface, whereupon the bubble bursts and the hydra is left attached to the surface film by its mucus disk (Fig. 17). Scourfield (1901) made model hydra out of weighted

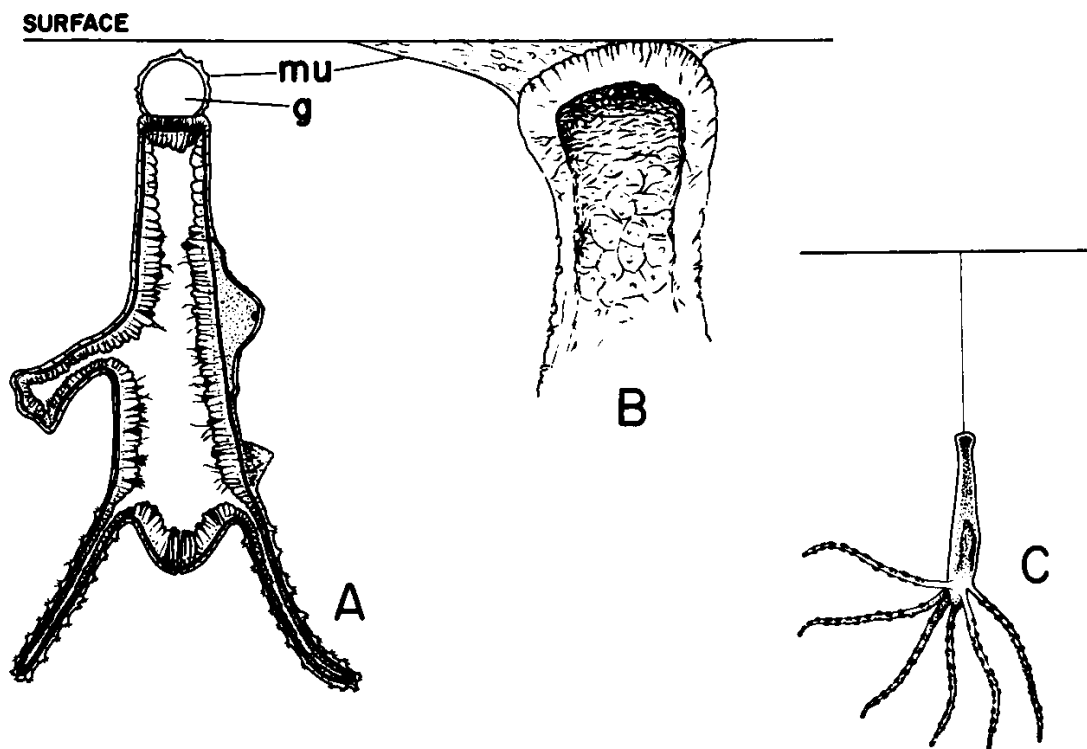


Fig. 17. Flotation in hydra. (A) Hydra suspended near surface by a gas bubble (g) contained in mucus (m) (after Kepner and Miller, 1928). (B) Base attached to surface film. (C) A specimen hanging from the surface by a mucus thread (B and C after Scourfield, 1901).

matchsticks and showed that even if heavier than water they would stay attached to the surface film if tipped with a water-repellent substance such as vaseline. Thus the gas is only necessary to get the animal to the surface.

A recent electron microscope study of the pedal disk (Philpott *et al.*, 1966) shows mucus-secreting cells in the ectoderm, but adds nothing to our understanding of gas secretion.

The sea anemone *Minyas* floats at the surface. According to Kästner (1967), "the pedal disc is modified as a gas float: deeply concave its borders meet to enclose a cavity that is filled with gas in a spongy matrix." Robson (1966) states that the float is "supposedly chitinous." Ross (1967) however cites observations by A. C. Haddon showing that the foot chamber secretes mucus, and that it is the mucus which enables the animal to float.

Porpita and *Velella* float at the surface by a combination of water-repellent mucus produced by glands around the mantle edge and a large central chitinous float. The float chambers are open to the air by aboral stigmata. Blind-ending tracheae run down into the soft tissues below the float. Rhythmical contractions of the underside of the float possibly serve to pump air in and out of the float by compressing the tracheae (Chun, 1897). Fields and Mackie (1971) appear receptive to the idea of *Velella* as an air-breathing cnidarian.

Leloup (1929) follows Woltereck (1904) in suggesting that the larvae which begin their development in fairly deep water (600–1000 m) rise to the surface by secreting gas into the float rudiment, but this suggestion requires confirmation. There is no evidence of gas-secreting tissue in the surface-living larvae and adults. It is quite possible that *Velella* rises to the surface by some nongaseous buoyancy mechanism, adheres by mucus to the surface film, and then loses water from the float by evaporation through the stigmata, becoming filled with air.

Physonectid and cystonectid siphonophores by contrast are definitely capable of gas secretion and some of them can regulate the gas volume in their floats and thus control their density. Jacobs (1935, 1937) reviews the older evidence and provides important original data for *Nanomia* (*Stephanomia*) *bijuga*. An apical pore is present at the tip of the float and gas bubbles are emitted through it. [In *Physophora*, the pore is at the base of the float (Leloup, 1941).] Elimination of gas involves peristalsis of the float wall. Replenishment of gas takes place in the gas gland and small bubbles can be seen arising in its vicinity in specimens which have had their floats emptied artificially (Fig. 18). Emptied floats fill again in about an hour (Pickwell *et al.*, 1964). In specimens observed in aquaria, it can be seen that the emission of a tiny air bubble may

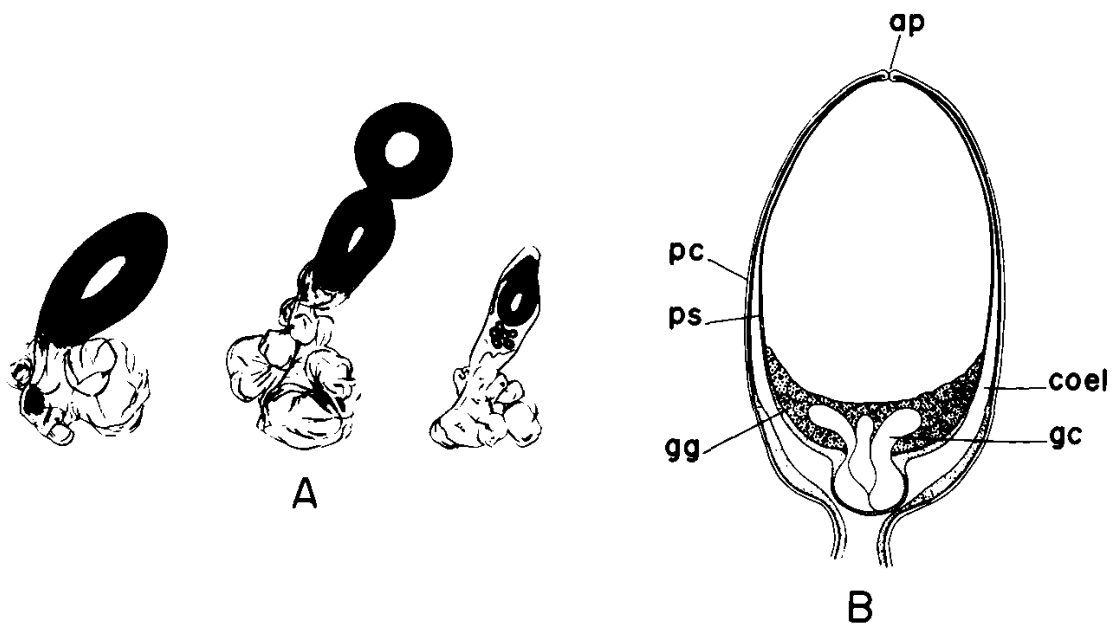


Fig. 18. (A) The float of *Nanomia* in three consecutive stages showing release of a gas bubble and resecretion of gas. (B) Longitudinal section through the float. ap, Apical pore; coel, coelenteron; gc, giant cell; gg, gas gland; pc, pneumatocodon; ps, pneumatosaccus (after Jacobs, 1954).

be enough to make a neutrally buoyant *Nanomia* start to sink. The colony is only slightly heavier than water without its float.

Analysis of float gases shows the principle ingredient to be carbon monoxide, which may constitute over 90% of total in *Nanomia* (Pickwell *et al.*, 1964). It is calculated that at the depth of 300 m, to which *Nanomia* regularly descend, the gas must be secreted and maintained in the float against a diffusion gradient of 30 atm or more. Other physonects live at much greater depths, for instance, *Stephalia* at 1800 m. Barham (1963, 1966) and Pickwell *et al.* (1964) give evidence associating *Nanomia* with sound-scattering layers. Gas contained in the floats or released bubbles would be responsible for the echo.

The presence of carbon monoxide in siphonophore floats was first demonstrated in *Physalia* (Wittenberg, 1958, 1960; Wittenberg *et al.*, 1962). *Physalia* lives at the surface and does not expel its gases or sink below the surface (Totton, 1960). Wittenberg, who found CO to comprise 0.5–13% of the total float gases, proposed that it was the gas secreted by the gas gland, and that diffusion resulted in its partial replacement by atmospheric gases. The substrate for CO formation proves to be L-serine. The gas gland is very rich in folic acid derivatives, and Wittenberg suggests that the CO may be formed by the dehydration of a coenzyme-bound formyl fragment. Hahn and Copeland (1966) find that the folic acid inhibitor aminopterin decreases production of CO in isolated gas glands maintained *in vitro*. Larimer and Ashby (1962)

found a maximum CO secretion rate of 120 $\mu\text{l}/\text{hour}$ per animal under experimental conditions. Since CO loss by diffusion through the float wall would exceed this rate of production, it may be assumed that the gas glands function more effectively *in vivo* than *in vitro*.

Having a higher surface-volume ratio and thinner float walls, small specimens of *Physalia* would be expected to lose CO quicker than large ones. Hahn and Copeland (1966) found the highest CO concentrations (18–28%) in small specimens, which suggests that the gas glands are indeed more active while the animal is young.

An electron microscope study of the *Physalia* gas gland has been carried out by Copeland (1968), who also reviews older histological evidence.

Some planktonic siphonophores, notably *Forskalia* and *Agalma*, have gas-filled floats but do not appear capable of liberating gases even when decompressed artificially. Possibly these forms are more restricted in their range of vertical migration than *Nanomia*.

C. Gelatinous Mesoglea and Ionic Regulation

Jacobs (1937) showed that the gelatinous parts of siphonophores, the bracts and nectophores, were lighter than other parts and often lighter than seawater and hence able to assist flotation of the colony as a whole (Fig. 19). In *Hippopodius* the larger, more gelatinous swimming bells are lighter than seawater, but all other parts are heavier. This species can regulate its density so as to sink slowly or to stay at the surface. The same is true of *Chelophyes*. In neither case is a gas-filled float present. The mechanism of density regulation is not understood, but might involve differential ionic adjustments. According to Bethe (1910) specific gravity adjustments occur over periods of 6 to 12 hours in *Solmaris* (*Aegineta*) *flavescens*.

In medusae there appear to be no exact studies correlating the amount of jelly with the animals specific gravity although it is apparent that the more gelatinous species such as *Solmissus* approach neutral buoyancy while less gelatinous forms (*Polyorchis* and *Gonionemus*) sink quite quickly if they stop swimming.

The tissues of medusae are isosmotic with their environment, but differ from seawater in their ionic composition. Denton and Shaw (1961) attribute the buoyancy of gelatinous marine animals to low sulfate ion content, SO_4^{2-} being a relatively heavy ion. Mackay's (1969) investigation of sulfate regulation in several hydromedusae makes it appear very probable that sulfate exclusion is an active process involving ionic pump-

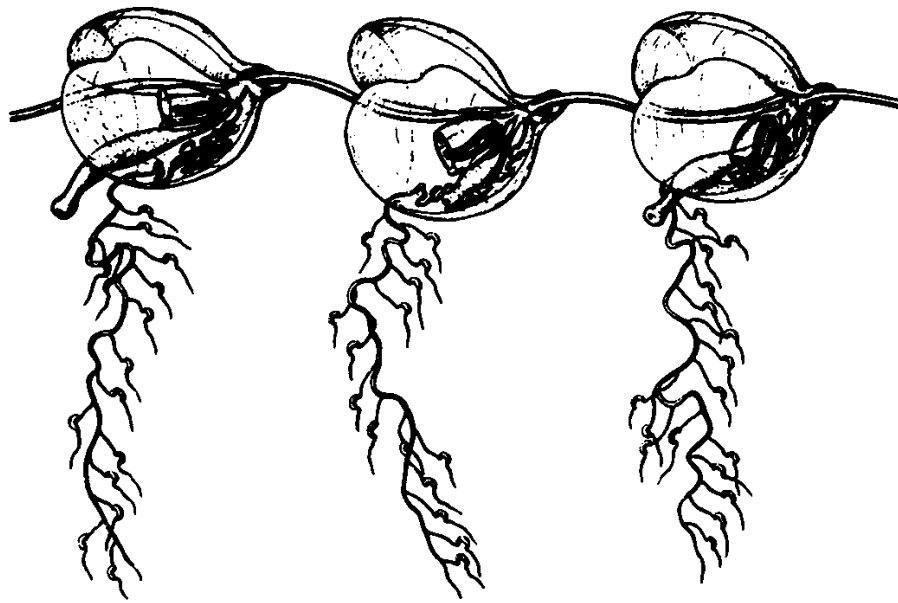


Fig. 19. The stem of the siphonophore *Sulculeolaria* (*Galeolaria*) floats horizontally due to the buoyancy of the gelatinous bracts (Jacobs, 1954).

ing by the covering epithelia. Whether or not medusae can adjust their buoyancy by ionic pumping and use this ability to perform vertical migrations is one of the major outstanding questions in jellyfish biology.

Ionic regulation possibly occurs in *Pelagohydra*. Pilgrim (1967) showed that this hydroid could suspend itself in seawaters of specific gravities from 1.0215 to 1.0255. Possibly the fluid filling the float cavities is subject to ion exchange.

IV. DISPERSAL

A. Pleustonic Species

The pleuston consists of organisms floating at the air-water interface. They should not be lumped in with the plankton, as they are a distinct ecological group, confined to life in this specialized niche. As Savilov (1958) points out, they are "typically bottom-living animals which in the process of evolution left the bottom and became adapted to life at the ocean surface." They include *Porpita*, *Velella*, and *Physalia*. In fact, these cnidarians dominate the oceanic pleuston, providing food or substrate for many other members of the community. The floating anemone *Minyas* is much less abundant.

Pleuston distribution is determined by movement of the top few centimeters of surface water and in some cases by the direct action of wind

on parts of the animal which project above the surface. *Velella* and *Physalia* have sails and are blown at an angle depending on the asymmetry of the superstructure. In both cases, the population is dimorphic, with some left-sailers and some right-sailers. Mirror-image dimorphism has apparently evolved independently in the two lines by a remarkable process of convergence (Mackie, 1962). *Porpita* lacks a sail and is distributed by surface water movement alone. However, surface currents are largely wind-induced.

In both *Velella* and *Physalia*, as in the bottom-living hydroids from which they presumably evolved, the sexual medusoid stage detaches and enters the plankton. The larvae are believed to develop at considerable depths before ascending to the surface, and it may well be that during this phase they undergo transport in currents running counter to surface currents, and so, on regaining the surface are able to repopulate areas from which the population has been expelled by wind action. Pleustonic cnidarians have dispersal problems closer to those of sessile hydroids than of holoplanktonic species and they can be regarded as a special case of the sessile mode of life with the air-water interface as their substrate.

1. SAILING AND DISPERSAL OF *Physalia*

The two dimorphic forms of *Physalia* are shown in Fig. 20. The tentacles and other appendages are budded from one side, and the whole float is asymmetrical. The crest on top of the float increases the area exposed to the wind and can be erected or collapsed according to changes in the muscular tonus of the float as a whole. Its curvature is also variable and there appears to be a characteristic "sailing posture" (Mackie, 1960). Woodcock (1971) gives evidence that the muscular

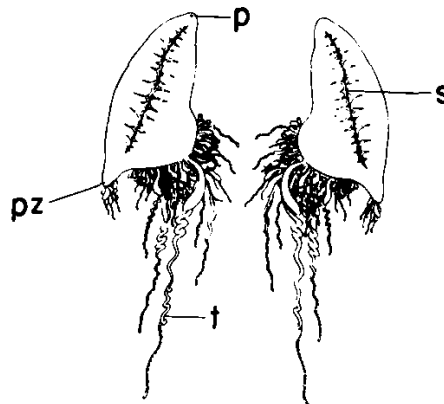


Fig. 20. Dimorphism in *Physalia*. The one on the left sails to the left, the one on the right to the right. p, Apical pore end of float; pz, protozoid end; s, sail or crest; t, tentacle (Tokioka, 1969).

contortions of the float which result in the much discussed rolling phenomenon are due to osmotic differences on the two sides caused by the higher evaporation rate on the windward side. Rolling would keep the float wet and prevent dessication. Other possibilities are discussed by Totton (1960).

Physalia are blown at angles up to about 45° to the left or right of the downwind direction (Fig. 21A). There is some evidence that sailing angles decrease in stronger winds. The curvature of the float, degree of crest erection, and degree of extension of the tentacles which act as a drogue anchor will affect sailing angles and velocities.

There is no direct evidence on how the dimorphism is produced and it is not known if the two forms are genetically or environmentally determined, whether they are produced in equal or unequal numbers, or whether indeed the two forms are part of the same interbreeding population, though this is assumed in calling them dimorphs. Because of these uncertainties, much of the debate which has gone on about the evolutionary significance of dimorphism appears to have been premature and will not be reviewed here.

One thing is clear: If the two sorts are truly capable of being produced within a single brood, the fact that they sail in different directions under the same wind will automatically ensure greater dispersal than if they all sailed in the same direction. Woodcock (1944) suggested that the adaptation had selective advantages in reducing entrapment in windrows of *Sargassum* weed which form at lines of convergence in parallel with the wind direction. The wind-induced vortex pairs which produce these lines of convergence differ subtly in the northern and southern hemispheres because of Coriolis forces, and Woodcock proposed that left-sailing *Physalia* functioned better in navigating through windrows in northern waters, right-sailers in southern waters. Later Woodcock (1956) and in the same year the present writer (cited by Mackie, 1960) commented on a wider aspect of dispersal in the two hemispheres, noting that because of the prevailing anticyclonic (clockwise) wind circulation in the northern hemisphere, left-sailers will tend to be carried peripherally, right-sailers toward the central parts of the oceans. In the southern hemisphere the reverse will apply. Thus in any ocean or wind circulation system, one sort will always sail outward toward the shores, the other inward away from them. This concept seems to be borne out by Savilov's data for *Velevella* and, less clearly, for *Physalia* and may be sufficient to account for the evolution of dimorphism without reference to *Sargassum* windrows or other local conditions.

Totton (1960) questions Woodcock's evidence (1944, 1956) that right-sailers are numerically predominant in the southern hemisphere,

but Savilov's data (1961) point to a similar conclusion. For the North Pacific, the two dimorphs are concentrated in different general areas but with considerable overlap. The ranges of left-sailers are more extensive and their populations larger than in the case of right-sailers, which would agree with Woodcock's expectations. Thus, present evidence indicates that while both sorts occur in all oceans, one dimorph (the outward sailing one) tends to predominate. Possibly, as Phillips (1971) argues for the Gulf of Mexico population, dimorphism is best explained on a genetic basis.

2. SAILING AND DISPERSAL OF *Velella* AND *Porpita*

Figure 21B shows a left-sailing *Velella*. Such a specimen is called "NW" by Savilov, which refers to the compass direction of the sail seen in relation to the longitudinal axis of the float as viewed from above. "SW" forms sail to the right. *Velella* unlike *Physalia* can rotate through 180° and continue sailing on the same tack. In strong winds they are believed to rotate more or less continuously. Sailing angles between 14° and 63° from the downwind direction were recorded for a group of left-sailing *Velella* under wind conditions ranging from Force 1 to Force 3 on the Beaufort scale (Mackie, 1962). Under Force 2 winds, a specimen on a 46° course traveled at 6.25 m/minute.

The chief lesson of importance arising from the extensive work of Soviet workers in the Pacific (Mednikov, 1957; Savilov, 1956, 1958, 1961) is that *Velella* and the biocoenosis it supports are distributed in distinct oceanic zones. Savilov (1958) discerned four *Velella* zones and a fifth dominated by *Porpita*. Work reported subsequently (Savilov, 1961) extends the data for the western half of the North Pacific (Fig. 22). It will be seen that in the case of the two northern Pacific *Velella* zones, right-sailers dominate the central zone and left-sailers the peripheral zone, as would be expected in an anticyclonic overall wind circula-

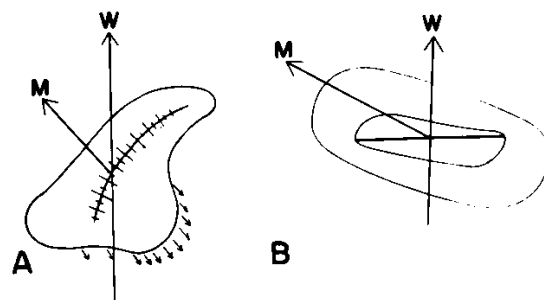


Fig. 21. Comparison of left sailing *Physalia* (A) and *Velella* (B) seen from above. M, direction of motion; W, wind direction. The small arrows in A represent direction of tentacular drag (A after Mackie, 1960; B after Mackie, 1962).

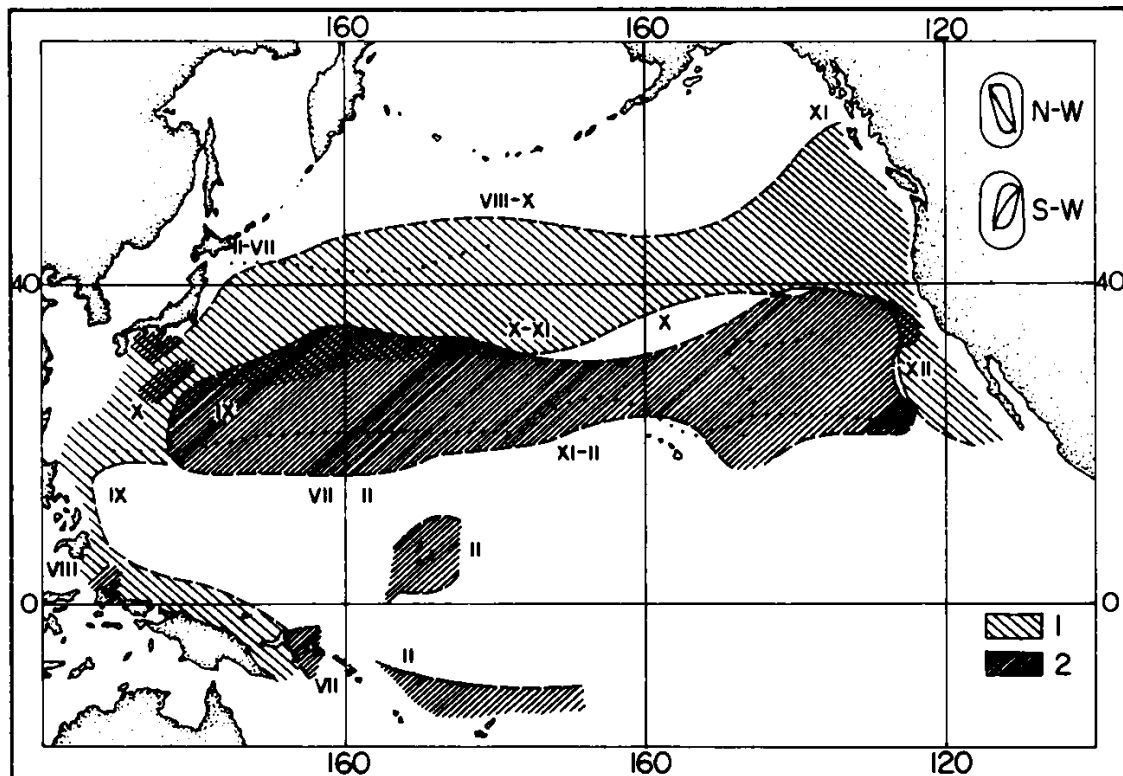


Fig. 22. Distribution of left-sailing (N-W, 1) and right-sailing (S-W, 2) *Velella* in North Pacific. Roman numerals represent months in which area boundaries were ascertained (Savilov, 1961).

tion. Edwards' (1966) data appears to support a similar construction for the North Atlantic. In the Mediterranean, which has an indigenous population of *Velella*, left-sailers appear to predominate heavily, but this may be because more collecting is done on the European side than on the North African side where right-sailers would be driven under the prevalent westerly winds. Alternatively, Edwards suggests that there may have been long-term selection for left-sailers in this population.

B. Benthonic and Meroplanktonic Species

There is a complete spectrum here between strictly benthonic species which have no pelagic stage in the life history and extremely limited dispersal capability through the large group of meroplanktonic species where sessile and pelagic forms are both conspicuous, finally to those where the pelagic stage predominates. Holoplanktonic species are considered in Section IV,C.

For purposes of this discussion, it will be assumed that any stage in the life history which is not attached to the bottom may serve for dispersal, so the initial task is to review cnidarians from the point of view of their potential mobility at different stages in the life history.

1. MOBILE LARVAE

Thorson (1946) classifies cnidarian larvae from the Danish Øresund according to the presence or absence of tentacles in the pelagic stage, overall size, duration of pelagic life, and mode of nutrition ("lecithotrophic" where yolk reserves are used, "planktotrophic" where food is obtained from the plankton). Both lecithotrophic larvae (*Tealia felina* and *Edwardsia beaumonti*) and planktotrophic (*Cerianthus lloydii*) may live for periods of several weeks in the plankton. *Cerianthus lloydii* may be carried around in the plankton for 3–4 months according to Nyholm (1943). The occurrence of zooxanthellae in many planula larvae (e.g., *Aiptasia*, Fig. 5A) suggests the possible need for the addition of a third category which could be called "autotrophic."

Like the larvae of most bottom-living invertebrates (Thorson, 1964), cnidarian planulae are usually photosensitive. Positive responses are more common than negative. All coral planulae are photopositive and all have zooxanthellae, but whether the larval response is causally related to the presence of zooxanthellae, as Kawaguti (1941) suggests, is still an open question.

From various accounts, reviewed by Nyholm (1949), it appears that most littoral actinians (e.g., *Sagartia*, Fig. 23A) live in the plankton for 8–10 days at most. Coral planulae are planktonic for 1–21 days. *Hal-campa* larvae are never planktonic, but disperse by creeping on the bottom (Figs. 8 and 23D). Rees (1957) notes that solitary hydroids generally brood their young to the actinula stage which settles rapidly, so there is virtually no pelagic stage in the life history. Most colonial athecate hydroids and medusae by contrast produce smaller, more numerous eggs which give rise to free planulae living 4–5 days in the plankton and offering better dispersal potential.

Peachia larvae attach to medusae such as *Phialidium* and are transported by them (Fig. 23C). Spaulding (1972) finds that the planulae are ingested by the host medusa and develop within the gastrovascular cavities as endoparasites. Later they move to the outside and feed on the gonads. They can transfer from one host to another, adhering by discharged nematocysts. The planulae have been cultured for up to a month in isolation, but apparently will not grow or differentiate unless they enter a host. Thus they seem to be obligate parasites. *Peachia* burrows in muddy bottoms and has virtually no powers of dispersal apart from its medusophilous larvae.

A number of actinians, e.g., *Urticina* (Fig. 23B) brood their larvae in the enteron, which would tend to limit dispersal. Even more strikingly,

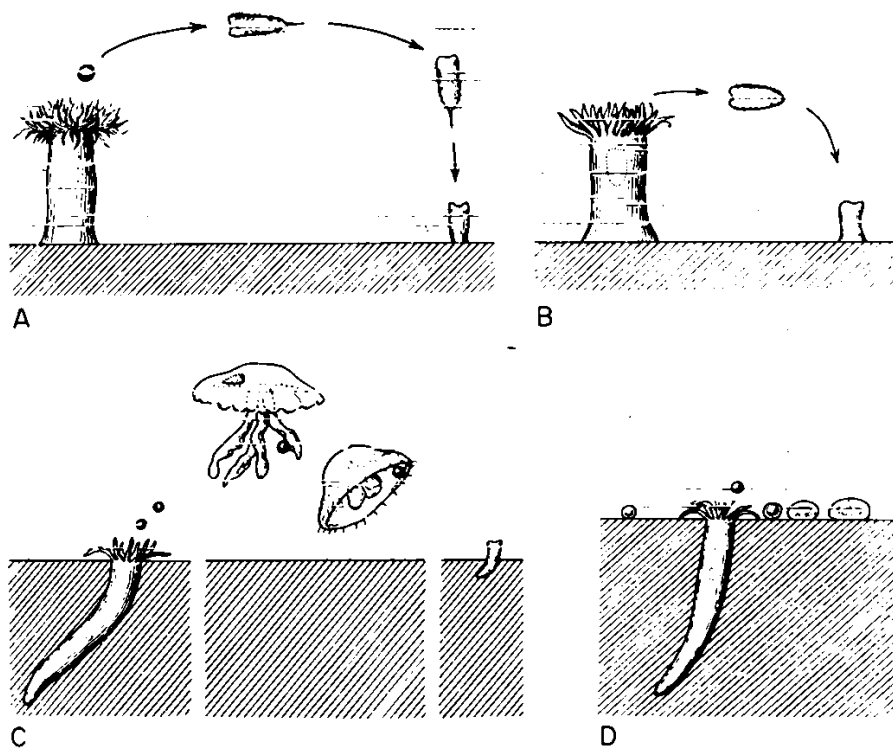


Fig. 23. Larval dispersal in four actinians. (A) *Sagartia*, eggs set free, planula settles after about 8 days; (B) *Urticina*, eggs develop to planula in female, short pelagic life; (C) *Peachia*, medusophilous larvae; and (D) *Halcampa*, unciliated benthonic larvae (Nyholm, 1949).

in *Actinia equina*, the evidence suggests that the planulae leave the parents for a period of planktonic life and then return and reenter the adults for a further period of incubation before metamorphosis and final release (Chia and Rostron, 1970). Such a life cycle would appear to expose the larvae to the nutritional advantages of planktonic life and would also favor the build up of high population densities in suitable areas, but it would hardly contribute to long-range dispersal of the species.

Sertularella miurensis typifies the type of hydroid with no medusa stage and larvae capable of dispersing only over very limited distances. The larvae settle preferentially on the alga *Sargassum tortile*. Nishihira (1967b) shows that settlement density on transposed algal fronds falls off very substantially even within 20 m from the main algal beds where the hydroids are concentrated. The pattern here would favor high settlement densities in the immediate area of the parent stock, with long-range dispersal possibly being accomplished by transport of hydroids on detached pieces of *Sargassum* weed.

Williams (1965) shows that the rate of dispersal of *Clava* planulae which move by crawling over the substratum is affected by the texture of the surface and is much higher over smooth surfaces than over rough.

2. FREE POLYPS

Some examples were given earlier of polyps with locomotory ability. It is doubtful if active movements of the kind described contribute much to dispersal in the usual sense. Passive transport is likely to be more significant.

Detached specimens of *Fungia* can creep and perform righting movements in spite of their heavy exoskeleton (Abe, 1939). In areas of strong tidal currents they are carried around passively with the tentacles spread out "like a ship's sail." Abe found that over a 6½ month period, 42 fungias moved into a 1 m² marked area. Portions of sessile hydroids (*Clytia johnstoni*, *Obelia dichotoma*, and *O. gelatinosa*) break off and are found floating in the plankton or along the shoreline as rounded pelagic colonies (J. Clare, personal communication). Detached spherical colonies of *Sarsia* and *Tubularia* are described by Clare *et al.* (1971), but such colonies may have been produced abnormally by the inhibiting effects of chemical pollutants on settlement of planulae. *Tubularia* shed their hydranths under certain ill-defined conditions. The detached hydranths are capable of living for up to 30 days (Rungger, 1969). Though heavier than water they may remain suspended and be carried around in the plankton for short periods. Sexually mature female hydranths would thus be able to spread actinulae around over a wide area.

Three athecate genera (*Margelopsis*, *Pelagohydra*, and *Climacodon*) have gone much further in invading the pelagosphere and their hydroids never settle. In *Margelopsis*, the hydroids and the medusae they bud off are both pelagic and may be found together in the plankton. During the summer, the eggs develop directly to pelagic hydroids without settling, but in the winter the eggs settle as blastulae and overwinter on the bottom, hatching to become pelagic hydroids in the spring (Werner, 1954). *Margelopsis* may represent a species on the way to becoming holoplanktonic.

It was noted earlier that hydra can detach and float to the surface. Liachov (1960) found hydra abundant in the plankton of the Volga during early June, when the spring floods were beginning to subside. With the advent of low water and reduced stream velocity, the hydra settle on the bottom. While evidence is lacking, hydra in lakes as well as in rivers might be expected to show seasonal pelagic excursions serving for dispersal, since detachment and flotation can be triggered by environmental factors likely to vary seasonally. Upstream dispersal of river-dwelling hydra presumably requires overland transport of zygotes in windblown dust or in mud attached to animals or other moving

objects. It seems likely that hydra evolved from marine ancestors via stages progressively adapted to increasingly less saline waters in marshy areas near the sea and eventually became tolerant enough of freshwater that they were able to disperse inland. The lack of a medusa stage is probably not an adaptation to freshwater life as such since other species which have invaded freshwater and brackish water have retained their medusae (e.g., *Moerisia*, *Ostroumovia*, *Limnognathia*, etc.). In any event, loss of medusae has occurred in many marine hydroid lines. The lack of free larval and medusan stages might severely limit dispersal in hydra were it not for the flotational and locomotory ability of the polyp.

3. POLYPS TRANSPORTED PASSIVELY ON FLOATING OR MOVING OBJECTS

Many anemones and hydroids are found on floating objects and some have probably achieved their present wide distribution largely by this means. To the extent that man has contributed to the amount of floating material in the water he has tended to aid dispersal of these forms. Millard (1959) found 14 species of hydroids attached to the hulls of vessels in Table Bay Harbor, Capetown. Many of the vessels had come from distant ports and some carried foreign species of hydroids. Tambs-Lyche (1964) reviews evidence suggesting that *Gonionemus vertens* has achieved its present world-wide distribution in recent historical times by transport of the hydroid stage on the hulls of wooden ships. Other well-documented examples are *Craspedacusta sowerbyi* (see Russell, 1953) and *Diadumene luciae* (Uchida, 1932). With the advent of plastics, a new floating substrate has become available, providing a means of dispersal for hydroids such as *Clytia* and *Gonothyrea* (Carpenter and Smith, 1972).

Prior to the advent of man-made boats and flotsam, floating objects such as detached algal fronds, bits of wood, etc., would have provided a steadily available means of long-range dispersal for many species capable of basal attachment to such objects. Eighty-one percent of the actinian species living in Bermuda are also found in the West Indies (Pax, 1925) and doubtless came to Bermuda via the Florida current, either as pelagic larvae or as adults attached to floating objects. As Nyholm (1949) points out, long-range dispersal of anemones on floating objects may involve long periods of starvation and salinity changes, so successful ocean crossings may be rare events.

A number of Leptomedusae and Anthomedusae have a truly oceanic distribution, occurring far out from land. Kramp (1959) suggests that such medusae have their hydroid stages on floating objects.

Epizoic, commensal, and parasitic cnidarians are often transported by

their hosts and we may presume that in some cases they achieve long-range dispersal by this means. Gudger (1928) reviews eight symbiotic relationships involving fishes and hydroids, ranging from forms like *Sertularia* (epizoic on dogfishes) to *Polypodium* (a freshwater endoparasite in sturgeon ovaries) and *Hydrichthyes* (a true endoparasite invading the flesh and blood vessels of several marine teleosts). Many hydroids and anemones are passively transported on or in mollusks on their shells (Rees, 1967). The coral *Heteropsammia* is transported by its sipunculid symbiont (Goreau and Yonge, 1968).

4. FREE MEDUSAE

Only two of the seven families of thecate hydroids listed by Naumov (1969) have species with free medusae, but these include some of the most familiar coastal jellyfish. Medusae are more common in athecate hydroids, including Limnohydrida, and in Scyphozoa. While all free medusae get dispersed to some extent, some bottom-living forms appear to resist transport by tidal currents by hanging on to submerged vegetation (e.g., *Gonionemus* and *Cladonema*).

In northern temperate waters where medusan life cycles have been studied the most, hydromedusae usually appear in the plankton in the spring or early summer as water temperature rises, disappearing gradually later in the year. Most authors have attributed the spring medusogenesis directly to rising temperature, and Werner's experiments seem to demonstrate this for *Coryne* (Werner, 1963). However, Roosen-Runge (1970) shows that medusogenesis in *Phialidium* is more likely to result from increased food uptake by the hydroid, which would occur in association with the spring plankton bloom. Temperature, food, and light may all affect medusogenesis in scyphomedusae (Russell, 1970).

Whatever the nature of the environmental trigger or triggers, coastal medusae tend to be produced in large numbers at particular times of the year. In the San Juan Islands in 1972, compact swarms of young *Aequorea* were found in early March at about 15 fathoms, near the bottom in places where the hydroid (*Campanulina*) grows (L. A. Fraser, personal communication). Not until May had they begun to appear at the surface. Later in the year, *Aequorea* are found in large numbers at the surface. Local concentrations of *Aequorea* found in July might represent the original swarms or they might be secondary accumulations created by eddies or resulting from the jellyfish actively swimming into the same zones in response to common environmental clues.

Zelickman *et al.* (1969) deny that hydrometeorological conditions could account for mass aggregations of jellyfish in Jarnyshnaya Fjord,

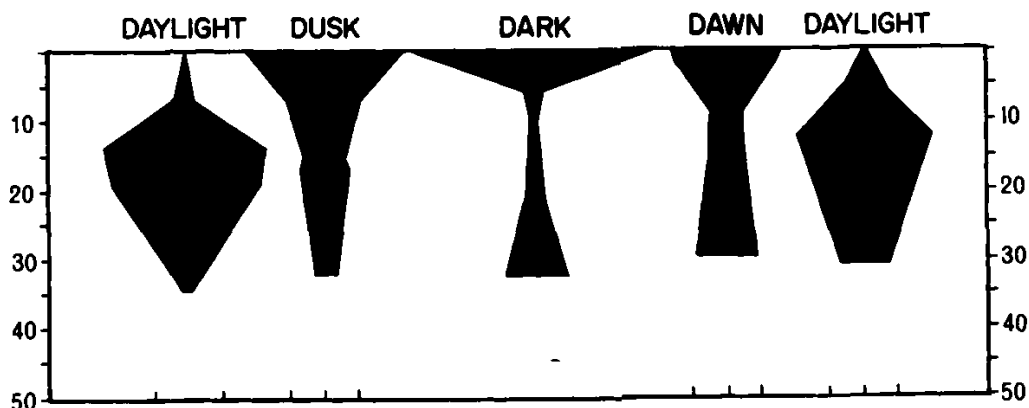


Fig. 24. Vertical distribution of *Leuckartiara octona* ("*Turris pileata*") over 24-hour period. Depths are shown in meters (Russell, 1925).

off the Barents Sea. They suggest that jellyfish concentrations are related to the distribution of their zooplankton prey, and that in forms like *Tiaropsis*, which have ocelli, photokinetic behavior is a factor in concentrating the population near the surface.

It would appear that medusan dispersal is not a random process, that the formation and maintenance of swarms may be in part active. This is further borne out by Arai's (1973) recent studies on *Sarsia* and *Phialidium*. These medusae aggregate actively at salinity discontinuity layers. Salinity differences as low as 2‰ can be detected.

Apart from possible trophic advantages, aggregation would promote fertilization of the eggs. A few species (e.g., *Linerger*) may actually carry out *en masse* spawning migrations to the surface.

Some coastal medusae perform definite migrations to the surface at night. Russell's (1925) most striking example was a species with ocelli, *Leuckartiara* (Fig. 24), but changes in vertical distribution over the 24-hour cycle were seen in a number of species lacking known photoreceptors (e.g., *Eutima*). Vertical migration is dealt with further in Section IV,C.

The importance of medusae in plankton ecology will sooner or later require much closer attention to questions of their population dynamics.

C. Holoplanktonic Species and Vertical Migration

All the siphonophores except for *Physalia* and all typical Narcomedusae and Trachymedusae are holoplanktonic, as are a few scyphomedusae.

While some holoplanktonic species are restricted to particular water masses (and can be used as indicators of these, Russell, 1953), other species are more tolerant. For example, in the Kurile Kamchatka region, *Aglantha digitale* is found in cold surface waters (50–200 m) and

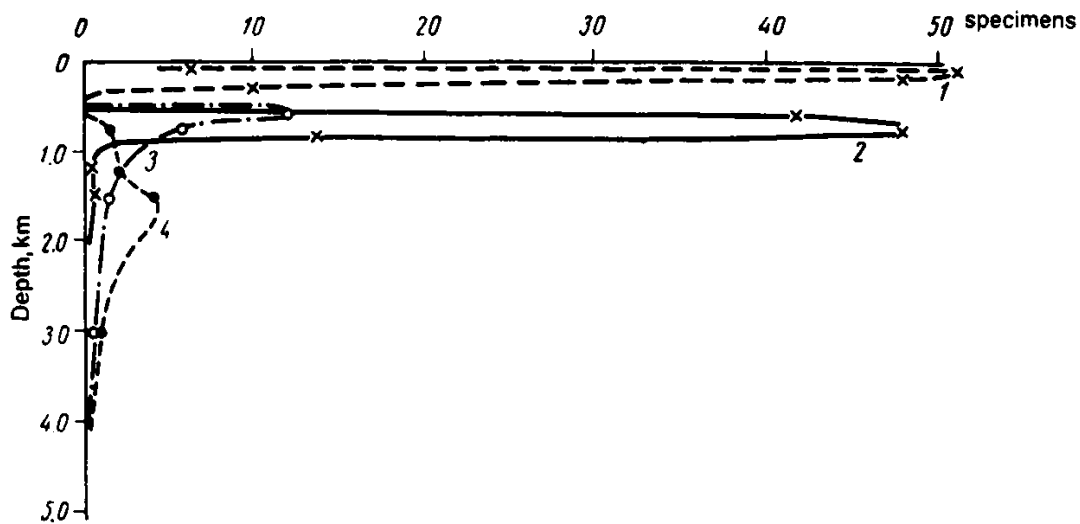


Fig. 25. Vertical distribution of four species of holoplanktonic medusae in the Kurile-Kamchatka Trench. 1. *Aglantha digitale* (species/40 m³), 2. *Crossota brunnea* (species/1000 m³), 3. *Pantachogon haeckeli* (species/1000 m³), 4. *Botrynema brucei* (species/1000 m³) (Vinogradov, 1970).

hardly ever penetrates the adjacent intermediate layers (300–500 m) (Fig. 25). Practically the whole population of *Crossota brunnea* is found at 500–1000 depths. The two other Trachymedusae shown have a much more extensive vertical distribution (Vinogradov, 1970).

Clearly for many species in the sea, dispersal will be subject to definite restrictions related to their tolerances for differences in salinity, temperature, density and pressure, their dependence on light, and their food preferences. Restriction within a given layer would permit greater biochemical specialization and physiological efficiency, but by preventing migration between different water layers, it might raise dispersal problems. Water masses in the sea are in the process of continual creation and dissolution. A water layer may resemble a river moving slowly from its point of formation and finally losing its identity by mixture with other waters. As in a river, upstream migration would challenge the dispersal powers of species living in it. If the species could reproduce rapidly enough to keep up with the flow, or if it could swim well enough to continually repopulate the head waters, there would be no problem. If not, and assuming it was relatively intolerant of waters other than the parent body, the species would tend to be lost downstream.

It seems likely that most species avoid this fate by being circulated in eddies around the borders of the parent water mass or by actively migrating into adjacent layers which are moving in a contrary direction. This however may necessitate some tolerance for waters of less than ideal composition.

Vertical migration between different water layers may occur seasonally, it may accompany ontogenetic changes in the animal's life, or it may be a regular diurnal event. As ontogenetic changes are often geared to seasonal changes, the first two categories tend to coincide.

Examples have already been noted of pleustonic and meroplanktonic species showing ontogenetic and seasonal differences in vertical distribution. While similar evidence exists for some holoplanktonic species, the importance of such migrations in terms of achieving or counteracting dispersal remains speculative. The eggs of holoplanktonic medusae develop directly, sometimes being brooded by the parent. Unless the young medusae have a vertical distribution notably different from that of the adults, there would appear to be no dispersal phase as such. Some siphonophores (e.g., *Hippopodius*) alternate between the free medusa and the polygastric phase, while others have eudoxids, which are free-living subcolonies strobilated off the end of the stem and carrying the sexual medusoids (Fig. 16). All siphonophores have free larval stages which could in theory serve a dispersal role.

With regard to diurnal vertical migrations, observations from manned submersibles in coastal waters off California with simultaneous tracking of scattering layers by echo sounding show that large populations of *Nanomia* undergo diurnal migration between the surface layer and about 300 m depth (Barham, 1963, 1966). Barham's observations from the bathyscaphe "Trieste" suggest that *Nanomia* reach population densities of 300/1000 m³ in scattering layers in San Diego Bay.

Off Cape San Lucas, Baja, California, Barham followed the scattering layers with a Cousteau "diving saucer" and again found physonectid siphonophores to be a major component of the migrating fauna (Fig. 26). Large and small siphonophores appeared responsible for different levels of the scattering layers either by themselves or in conjunction with myctophid fishes.

Barham saw *Nanomia* "actively swimming down at about a 45° angle" during the downward phase of migration and again "actively pumping" during ascent, but as the submersible's lights had to be turned on to make these observations, the behavior observed may have been light-induced. *Nanomia* respond to illumination by swimming (Mackie, 1964). Thus it is still uncertain whether vertical migrations are carried out by swimming or by density adjustments. The question applies to both medusae and siphonophores and is, perhaps, the least justifiable piece of ignorance in the whole field of jellyfish biology.

Diurnal vertical migration of the zooplankton may serve a variety of purposes unconnected with dispersal, and it is not possible to review

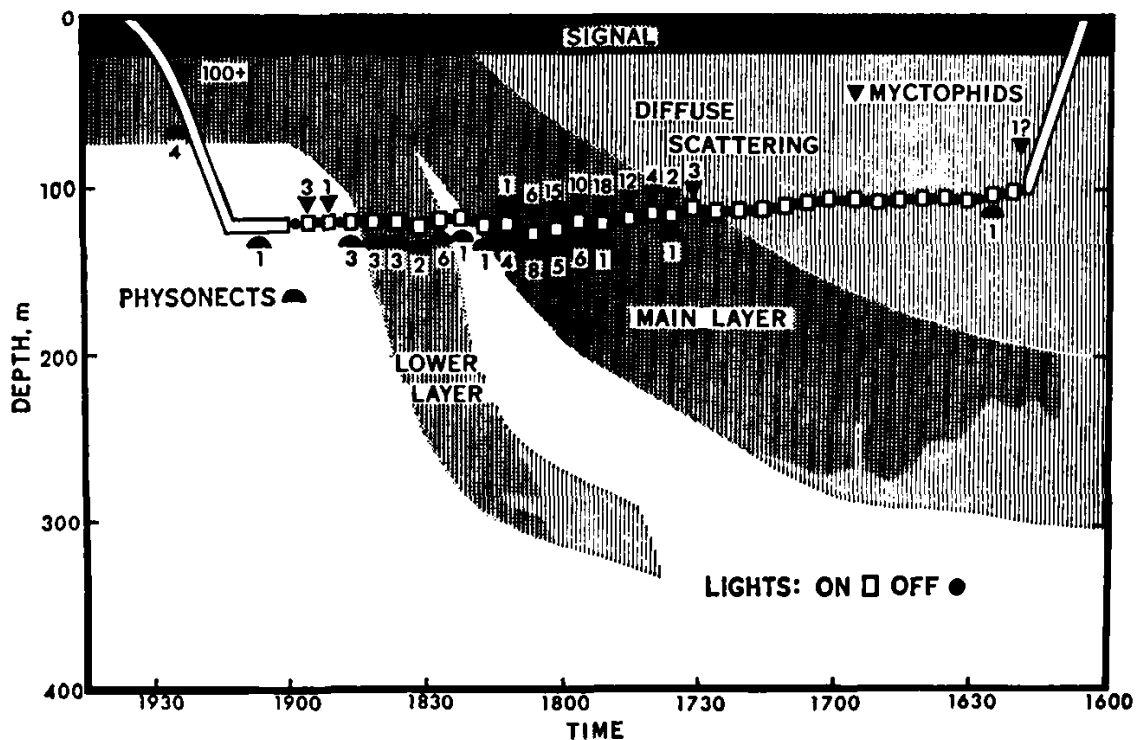


Fig. 26. Scattering layers correlated with physonectid siphonophores and myctophid fishes, observed from a diving saucer. Numbers along the depth course of the submersible represent individuals seen (Barham, 1966).

these broader questions here. Vinogradov (1970) provides a useful summary of the main theories.

D. Dispersal Strategies: Evolutionary Significance of Alternation of Generations

Many authors assume that where alternation of generations occurs, the significance of the medusa is that of a dispersal phase. Thus Werner (1966) writes: "A medusa is a polyp transformed by adaptation to pelagic life and set free for purposes of dispersion."

It is true that where medusae occur they bring about dispersal, but it should be noted that free medusae are lacking in the life cycles of the majority of cnidarians, that both larvae and polyp stages may be set free, and that where medusae are set free they sometimes aggregate in swarms instead of dispersing at random.

It would appear that there is a dispersal strategy appropriate for each species. Dispersal need not involve *long-range* dispersal. *Halcompa's* dispersal strategy is aimed at achieving high population densities in suitable bottoms where the adults can burrow and is limited by the

distance the bottom-living larvae can wriggle away from their parents. The spread of such a species from bay to bay around the coasts of the world would be a slow process. However, once established in suitable habitats, it would not easily be dislodged since it lives at a depth where conditions are stable. The selective advantage of having a free larval stage capable of long-range dispersal would have been overborne by the need to avoid loss of larvae in water currents and to settle them quickly in the home territory.

In *Sertularella* too, the strategy is directed toward maximal population of the substrate in the close vicinity of the parent stock rather than toward extension of the range.

In *Actinia* even more strikingly, although free larvae are produced, the evidence suggests that they return to a parent for a second period of incubation before finally being set free and settling locally. The foray into the plankton can hardly be explained by reference to dispersal, but must serve some other need, presumably related to nutrition.

Cases such as these cast doubt on the supposedly primary dispersal role of free larvae, polyps, and medusae and suggest that the free stage may be more significant as a period of nutritive uptake. The most productive area of the sea is the surface zone, and the greatest quantities of microplankton on which cnidarians typically feed are concentrated here. Possibly then the retention of medusae in metagenetic life cycles is related to the benefits to be obtained from access to surface plankton during peak productive periods. In Arctic and Antarctic waters, where plankton production is low, few hydroid species have free medusae (E. Stechow, cited by Werner, 1963). In warmer, more productive coastal waters free medusae are much more common.

Coastal waters in many regions are today highly productive because of upwelling and mixing of water layers and because of mineral run-off from the land. This was probably true in Palaeozoic times. The chemical composition of seawater has not changed greatly since the late Precambrian (Martin, 1970), and the basic biogeochemical cycles for nitrogen and phosphorus were probably established before the major metazoan groups appeared. With the paucity of life on land, mineral erosion and run-off were possibly greater than they are now and the fertilizing effect of rivers on coastal waters concomitantly higher.

Tentatively then we can envisage the warmer coastal waters as regions of phytoplankton abundance, offering good trophic opportunities for emerging metazoans. Species diversification is to be expected in highly productive zones given reasonable environmental stability or predictability in terms of seasonal change (Connell and Orias, 1964; Slobodkin and Sanders, 1969).

Considering cnidarians in this context, specifically the ancestors of hydrozoans and scyphozoans, it would seem that alternation of generations was adaptive in providing one stage (the medusa) capable of taking full advantage of the trophic opportunities offered by productive coastal surface waters and another stage (the polyp) able to attach itself to the bottom, thus ensuring retention of the population in suitable coastal waters despite seasonal loss of medusae through starvation and dispersal off the continental shelf into barren open ocean waters.

Alternation thus allowed the species to capitalize on seasonally available surface-living food organisms in the neritic plankton while retaining a home base from which to reinvade the plankton each year.

Over the course of time, as the total organic content of the sea increased, the benthos would have become richer and the sessile polyp phase would have come to predominate in some life cycles. At the same time, some species would have become holoplanktonic, losing their toe-hold on the bottom and invading the open ocean. (It would follow from these arguments that the direct development of Trachymedusae is a secondary feature, not an indication of primitiveness.)

We do not know what the ancestors of scyphozoans and hydrozoans were like but these arguments suggest that both sessile and planktonic phases existed in their life cycles. The sessile phase need not always have been a polyp. To keep a pied à terre in neritic waters a sessile winter egg like that of *Margelopsis* would have sufficed, with polyps evolving later. The important point is that rather than thinking of medusae as evolving "for dispersal" it may be better to think of them as evolving "for nutrition" and as polyps evolving essentially to *limit* dispersal.

The fact that the medusa carried the gonads could be related to the better opportunities for larval dispersal provided by the liberation of gametes or larvae from a floating parent. However, the primary significance of medusan sexuality, assuming that it is adaptive, probably lies in the heavy metabolic demands of gametogenesis which medusae, with their trophic opportunities, are best equipped to handle. Where polyps have found good trophic niches, medusae tend to be lost, and sexuality devolves on the polyp. In general, cnidarians seem to illustrate Istock's (1967) principle that complex life cycles are inherently unstable. Each phase tends to evolve independently, and unless the adaptation of the two proceeds at the same rate, the advantages of the original alternating cycle decrease with one stage tending to undergo reduction or loss. A species unable to adjust the balance between the two phases in this way would cease to be competitive. In spite of the potential handicap presented by their presumed origin from metagenetic ancestors,

cnidarians have evidently retained sufficient genetic flexibility to adjust their life cycles as required and thus have held their own in an increasingly competitive environment.

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