Underwater Observations of Gelatinous Zooplankton: Sampling Problems, Feeding Biology, and Behavior

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Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior[1]

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Abstract

Observations by SCUBA divers on the distribution and biology of gelatinous zooplankton have stimulated speculations about the structure of tropical oceanic ecosystems. The gelatinous group represents one of four apparent strategies for survival in pelagic animals. Conventional plankton collection probably does not sample these organisms accurately due to their patchy distribution, fragility, and escape responses. Many gelatinous plankters filter feed using mucous structures; these mechanisms are important because of their efficiency in collecting particulate material, and because mucus is a source of organic aggregates in the sea. Such aggregates are often large, irregularly distributed, and of complex composition; these properties are rarely discerned by conventional sampling gear. The aggregates contribute considerable spatial heterogeneity to a seemingly homogeneous environment. An entire category of pelagic animals lives in association with these floating substrates. The diversity and trophic complexity of epipelagic plankton communities have been underestimated by previous investigators.

During the past 5 years we have been collecting data on the natural history of various groups of gelatinous, transparent zooplankton. These observations on free-swimming, undisturbed animals were made by divers using SCUBA in the epipelagic blue water of several tropical water masses, the Florida Current, Sargasso Sea, North Pacific gyre, and Gulf of California. The logistics for this approach to biological oceanography are presented by Hamner

(1975). A photographic survey of the remarkably beautiful animals is available (Hamner 1974) as are several papers concerned with the biology of particular groups (Alldredge 1972; Alldredge and Jones 1973; Bé and Gilmer in press; Madin 1974a; Swanberg 1974). Here we offer some general observations on the biology of gelatinous zooplankters and the physical and trophic structure of the pelagic community, and we speculate on the importance of these observations. We have been asked repeatedly by colleagues what we think about various subjects of traditional interest when viewed from our perspective. We hope that our comments here will answer some of these questions and, more important, stimulate additional research.

The groups which we call gelatinous zooplankton are the Hydromedusae, Siphonophora, Scyphomedusae, Ctenophora, Heteropoda, Pteropoda, Thaliacea, and Ap-

pendicularia, as well as many meroplanktonic larvae. We have been concerned with these forms primarily because they are relatively large (> 1 mm) organisms that generally do not react to a diver unless physically disturbed. Consequently we have been able to observe undisturbed animals from all these groups at close range while diving in the upper sunlit regions of tropic seas. The fact that these organisms are large and do not avoid divers is convenient, but there are additional reasons to believe that we are dealing with a natural and important assemblage of tropical oceanic animals.

Gelatinous zooplankton comprises representatives of several phyla and spans two or three trophic levels. Notwithstanding this diversity, we consider this assemblage to be an ecological group on the basis of the predator-protection strategies which the animals have in common. The planktonic animals that inhabit the clear sunlit surface of tropic seas must avoid predators in an environment usually devoid of hiding places. They therefore possess a rather limited number of protective properties. We suggest that the organisms in our study area fall into one of four categories.

1. Animals that are too small to be seen by many predators (e.g. copepods).
2. Animals that are large but transparent and thereby invisible to many predators (e.g. ctenophores).
3. Animals that are large and readily visible but achieve protection either by aggregating in schools (e.g. herring) or by being very large, fast, and mean (e.g. sharks).
4. Animals that are nocturnal and seek cover by vertical diurnal migration (e.g. euphausids).

This scheme doubtless ignores many predator avoidance patterns, which operate within each of these assemblages, but we have found it useful and we believe it biologically reasonable to consider that the tropical, blue-water epipelagos has four basic predator avoidance systems.

We have directly observed each of these four assemblages. Members of the very small free-swimming zooplankton assemblage (< 1 mm) are visible but hard to follow. The gelatinous animals are perhaps the easiest to observe underwater, although some practice is necessary to locate the most transparent forms. Once we learned how to look for them we found that they are almost always present and easily studied.

We see small schools of fishes while diving, but only when they are pursued by some larger fish. Presumably we are perceived as large predators by these schooling fishes, and they avoid us whenever possible. Large predatory fishes—sharks, marlin, sailfish, and dolphin fishes—were rarely seen in midocean but were common in the Florida Current. They are curious and unafraid, but do not react to the gelatinous animals in the water around them. Although blue-fin tuna are reported to eat salps (Reintjes and King 1953), we have the impression that transparent animals are either invisible or of no interest to the large, visual predators in the pelagic fish assemblage.

Thus, we favor an ecological taxonomy for the creatures of the surface of the sea that divides pelagic animals into the four major assemblages listed above. We believe that the gelatinous-transparent assemblage is important and coequal with the three other groups but is much less well known.

Equally striking to us in the course of our underwater investigations have been the abundance, size, and complexity of organic aggregates ("marine snow"). Many of these aggregations appear to originate from mucous secretions of gelatinous zooplankton. Like those organisms, the aggregates are fragile and not accurately sampled with conventional gear. We feel that they too need to be better understood.

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Sampling

Among our most important motivations for studying gelatinous zooplankton by diving was the inadequacy of conventional plankton nets for collecting either intact specimens or reliable information on distribution and abundance. In the Florida Current, for example, we sampled regularly with meter nets for 15 months, but obtained only a few specimens of the common gelatinous forms and no specimens of others; yet we knew these animals were there because we saw them there almost every day while diving. Actually many were caught by the net, but then strained through the mesh and lost or damaged beyond recognition. Some of the gelatinous zooplankton are not only delicate but fast-swimming and can usually avoid nets. These observations convinced us that many previous estimates of the relative abundance of this fauna are incorrect.

By making direct observations in the sea we avoided many of these problems and at the same time saw some of the reasons why traditional methods of sampling fail for these large, gelatinous, and delicate organisms. For example, Gilmer (1974) has made in situ measurements of sinking and swimming rates of pteropods, which illustrate their capacity for avoiding nets. Pteropods are neutrally buoyant when they feed, but they are also extremely sensitive to turbulence and readily exhibit escape responses to local disturbances (Gilmer 1972, 1974). Pseudothecosomes (e.g. *Gleba, Corolla,* and *Cymbulia*) appear especially sensitive to turbulence; these pteropods are highly vulnerable to predators when feeding (Gilmer 1972), and they must be fast if they are to escape. They readily avoid capture by a diver, and it is therefore not

surprising to us that they have seldom been collected in large numbers (Chen and Bé 1964; Deevey 1971). Euthecosome species, on the other hand, are small, relatively slow, and encased in a hard shell; they are ideally suited to collection by nets.

The Gymnosomata, the shell-less opisthobranchs, also avoid nets. These fast swimming carnivores are found in all oceans. Although we rarely observed gymnosomes they were occasionally quite abundant, usually associated with the thecosomes on which they feed. Several genera, such as *Pneumodermopsis* and *Notobranchea,* are capable of swimming in excess of 1 m s^{-1}, or 2 knots (Gilmer unpublished observations); they too are seldom collected in nets.

Certainly most sampling techniques are biased; our own technique of collecting observational data misses things that are very small or very fast. But we believe also that in the case of the gelatinous zooplankton assemblage the sampling bias of traditional gear has been particularly misleading, and new approaches are necessary to understand the distribution and biology of these animals.

Filter feeding with mucous structures

Many aspects of animal behavior are dominated by trophic interactions; in the case of the gelatinous fauna we know very little about feeding biology. Of particular interest to us have been the filter-feeding mechanisms of pteropods, salps, and appendicularians. These animals collect, concentrate, and transport particulate organic matter using mucous sheets, nets, strands, and filters in conjunction with ciliated surfaces. The efficacy of these feeding mechanisms in collecting a broad size range of organic material is important to the organisms and to the ecosystem as a whole. While pteropods, salps, and appendicularians are particularly conspicuous mucous feeders, we have also observed mucous structures which appear to have a food collecting function in prosobranch veliger larvae (Gilmer unpublished observations) and polychaete larvae. The feeding mech-

anisms of some of these organisms have been described previously (*see* Jorgensen 1966 for general resume); we have added new information by direct observation (Gilmer 1972, 1974; Madin 1974*b*).

The mucous structures that we have seen may be classified as external or internal. One example of an external structure is the free-floating mucous webs produced by pseudothecosomatous pteropods (Gilmer 1972). These webs passively entrap suspended particles; the pteropods then draw portions of the mucous web into the mouth by ciliary action and ingest the material stuck on the mucus. Generally the mucous webs are much larger than the animals; we have seen webs more than 2 m across produced by an animal only 10 cm in diameter.

Appendicularian houses are doubtless the most complex and sophisticated external mucous structures; they are among the most complex external structures produced by any solitary animal. The structure and function of the house as a food collecting and concentrating apparatus was described by Lohmann (1909, 1933) and Körner (1952), but many details are still not clear. Field observations have enabled us to determine the morphology of several previously undescribed houses and to examine the functioning of the house in natural conditions (Alldredge unpublished observations).

An unusual external mucous feeding device is used by the larva of the polychaete *Poecilochaetus* sp. This worm secretes a 3-dimensional network of fine mucous strands. The larva is attached by its mouth to the threads and glides along them feeding on small adhering particles. In the field these threads ranged from 4 to 16 cm long; the worms are 0.5 to 1 cm long. *Poecilochaetus* larvae hand-collected in glass jars built threads in the laboratory, but only after the addition of a small amount of powdered milk to the water. *Poecilochaetus* occurred only rarely in the Florida Current, but animals were abundant when present. On one occasion about 58% of the larvae were feeding with their mucous threads (Alldredge unpublished observations).

Mucous secretions may serve a less direct feeding function. In the Gulf of California we observed another planktonic polychaete, the larva of *Loimia medusae*, which builds its own benthos about it. The larva secretes a clear, gelatinous barrel around itself and lies within the portable burrow with its prostomium and tentacles protruding from one of the open ends to filter particles. If disturbed it abandons the tube, swimming with rapid undulations. In the laboratory, one *Loimia* larva jettisoned its barrel and secreted another in 4 h. The completely transparent tube may provide the larva with some physical protection, but it is probably primarily a flotation device, allowing the larva to maintain its position while fully extending its tentacles to feed (P. Hamner and A. Alldredge unpublished observations).

Internal mucous feeding devices are best demonstrated by salps. In the Salpidae a conical mucous net within the cylindrical body strains particulate material from water which is actively pumped through the body. This water stream, with the aid of the ciliated tracts, moves the net continuously back from the oral opening, conveying trapped particles to the posterior esophagus. The mucus is ingested along with the collected food (Madin 1974*a*).

An important difference between collecting food with mucous structures and with rigid antennae or maxillae is that the size range of particles collected is often much greater for the mucous feeder. The lower size limit for setose filter feeders is determined by the minimum spacing between the rigid filter elements; the spacing sets a lower limit of 3–4 μ for most copepods (Gauld 1966; Poulet 1974). Mucous filters, however, can have extremely small pore sizes. The inner collecting filters of some appendicularian houses have a fibrillar structure with pores as small as 0.1 μm (Jorgensen 1966). Most appendicularians also have a coarse external filter that prevents large particles from entering and clogging the internal filter (Lohmann 1909). These animals can select a certain portion

of the available spectrum of particle sizes by constructing mucous filters with specific pore sizes.

The external mucous webs produced by pteropods have pores 20 μm or more across, capable of physically filtering only larger particles. But very small particles, 1–10 μm, are also trapped in these webs, evidently by adhering to the mucus on contact; such particles compose up to 50% of the food ingested (Gilmer 1972, 1974). This adhesive quality of mucus may be quite important, enabling mucous structures to retain small particles without possessing a very fine ultrastructure, which would be difficult to create and maintain in large mucous nets or sheets. Adhesion may also be responsible for the ability of salps to retain cells as small as 0.7 μm.

Although their efficiency must more than compensate, the energetic cost of producing these mucous feeding devices seems remarkably high. For example, appendicularians expend considerable material and energy in building their house, yet discard it entirely when it becomes clogged and build another. *Oikopleura dioica* builds as many as six houses per day (G. Paffenhöfer personal communication). Pteropods must also realize a substantial energetic return on their investment of mucus. Although they ingest the mucus along with the particles, much of the web material is lost, and, if disturbed, pteropods abandon the entire gigantic structure (Gilmer 1972).

Salps are more conservative of their mucus. Since the filtering net is inside the body, it is not as liable to accidental loss and is completely ingested. This recycling of the mucus may reduce energy loss and enable salps to feed effectively with a filter that is small relative to their body size. Appendicularians and pteropods do not recycle mucus effectively, and their filters are quite large relative to their body size. Thus there may be two approaches to obtaining an adequate net energy gain, one involving a small, efficient, recycled filter, the other a much larger, but less efficient and partly expendable structure.

Structure, distribution, and origin of organic aggregates

The amount of mucus produced by animals such as pteropods, gastropod larvae, salps, appendicularians, annelids, fish, and reef corals is considerable. Our own observations were limited to the upper 30 m of the water column, but Neumann (personal communication) has made numerous dives in the submersible *Alvin* in the Florida Current and has seen similar mucous structures down to 400 m. Although the original description of marine snow by Nishizawa et al. (1954) was also made from a submersible, most attempts since then to study this aggregated organic material have been made from surface vessels using water samplers. Unfortunately, blind sampling from the surface can provide neither correct estimates of the size and shape of the aggregates nor insight into the fine-scale spatial relationships within the water column.

There is now a wealth of indirect information on the distribution, origin, and significance of particulate organic material (*see* Riley 1970), but our direct observations suggest that some earlier generalizations are incorrect. While particles collected on filters almost never exceed 100 μm in diameter (Gordon 1970), larger particles may actually be abundant in the sea. Johannes (1967) and Suzuki and Kato (1953) observed particles up to 3 cm in diameter. In the Gulf Stream, we frequently dove among amorphous aggregates up to 30 cm in diameter, at densities of 2–3 m^{-3}. These aggregates contained algae, foraminifera, detritus, and small particulates in a mucous matrix.

Aggregates are quite variable in size, composition, and distribution. Determination of the actual amount of particulate matter per cubic meter of seawater can be confounded by this patchiness, as recently demonstrated by Wangersky (1974). By visually selecting patches of marine snow, we have measured concentrations of particulate organic carbon in water samples that change more than fourfold over a distance of 10 cm. Sampling from the surface may pro-

vide extreme and average values of particulate carbon concentration if enough samples are taken and unusually high values are not discarded as contamination, but indirect sampling has two major weaknesses. Large aggregates are often widely dispersed and can be collected only in a large sample volume: sampling for a *Gleba* web with a Niskin bottle is like sampling for trees with a trowel. Large aggregates are also very fragile; they can often be dispersed by the wave of a diver's hand and may disintegrate even when collected by hand. Turbulence from most standard samplers certainly disturbs these aggregates and changes the apparent particle sizes.

The problems of sampling these large organic aggregates are considerable. Hand collection and quantitative visual or photographic estimates of particle density in the field are possible approaches. Collection of aggregates in situ by freezing (Schubel and Schiemer 1972) or filtering (Marshall et al. 1972) may give a more accurate picture of the structure of the aggregates.

A truly representative sample of large aggregates would be of considerable importance for accurate measurement of particulate carbon or C : N ratios. Coles and Strathmann (1973) found coral mucus flocs to contain ten times as much particulate carbon and twenty times as much particulate organic nitrogen as particles filtered from a liter of the surrounding water; Benson and Muscatine (1974) found wax esters and triglycerides in coral mucus and observed that reef fish "avidly ingest it."

Fecal material, detritus, bacteria, and adsorption of dissolved organics on surfaces are probably all important sources of particulate organic matter (Baylor and Sutcliffe 1973; Barber 1966; Paerl 1973), but the mucous products of the gelatinous organisms discussed here may be equally important. Alldredge (1972) observed abandoned appendicularian houses ranging in size from a few millimeters to 3 cm at densities of up to 600 per cubic meter. The feeding webs of the pteropod *Gleba cordata* are flat sheets of mucus up to 2 m in

diameter; dispersion of these webs ranged from 10 m or more apart to a field of contiguous nets.

Not only is it produced in large amounts, but such mucus accumulates particles and smaller aggregates and may act as a surface for adsorption of dissolved substances. We do not know how much of the particulate organic material in the sea derives from mucus filter feeders, but the aggregates that we can visually identify (e.g. pteropod webs and appendicularian houses) have great significance in the organization of fine-scale community structure. Particulate organic carbon makes up only 1 to 10% of the total organic carbon present in the sea (Sharp 1973), but the small fraction tied up in aggregates may be of disproportionate importance as sources of food, surface microhabitats, or nuclei for the growth of larger aggregates. To understand the functional role of organic matter in the plankton community we must understand the origin, composition, and architecture of these macroscopic structures as well as of the microscopic particles. We feel that many previous discussions have missed the trophic and spatial importance of aggregates by focusing only on particles of 1–10 μm, a size range that is partially an artifact of the usual collection and filtration procedures (Strickland and Parsons 1968).

Utilization of surfaces in the plankton

Intuitively one conceives of the planktonic environment as a relatively homogeneous, fluid medium in which nutrients, phytoplankton, and most particles are invisibly small. Though zooplankters may attain macroscopic size, they too are thought of as adapted to a homogeneous fluid (Friedrich 1969).

Heterogeneity in this environment has been defined in terms of such physical parameters as microscale gradients (Gregg and Cox 1972; Gregg 1973), discrete oceanic or coastal water masses, current boundaries (Lovett 1968; Pingree et al. 1974), and thermo-, halo-, and pycnoclines (Harder 1968). However, the existence of actual

physical heterogeneity in the plankton environment resulting in a variety of microhabitats like those of a tropical rain forest or a coral reef has been considered only with regard to a few conspicuous examples like *Sargassum*, tar lumps (Butler 1975), or bacterial colonization of detritus (Jannasch 1973; Paerl 1973).

This image of a homogeneous planktonic environment does not coincide with our direct field observations. Pteropod feeding webs, coral mucus flocs (Johannes 1967), abandoned appendicularian houses, decomposing gelatinous animals, and other macroscopic particulates can produce a complex 3-dimensional pattern of discrete organic aggregates in an environment often considered unstructured.

Our observations indicate that many "planktonic" organisms depend heavily on the presence of discrete surfaces, both living and nonliving, in the pelagic environment. We have frequently observed hyperiid amphipods, copepods, ostracods, euphausid larvae, polyclad flatworms, and crab megalops resting on the surfaces of organic aggregates, on pteropod feeding webs, and especially on abandoned appendicularian houses. Feeding on houses was demonstrated in the laboratory for *Oncaea mediterranea* (Alldredge 1972). Zooplankters treat these surfaces as benthic organisms might treat a rock, moving about on them and scraping off particles. Such zooplankters are often morphologically adapted to benthic feeding methods. For example, the head and first thoracic appendages of the genus *Oncaea* appear better adapted to the scraping of surfaces than to filter feeding or grasping (A. Fleminger personal communication).

The frequent occurrence of feeding on floating surfaces indicates that it may be important in the trophic structure of the plankton community. About 11% of the abandoned appendicularian houses observed over a 7-month period in the Florida Current had organisms visible on their surfaces. In the Gulf of California, the occurrence of organisms on the surfaces of ap-

pendicularian houses approached 80%. These surfaces provide highly concentrated energy packets in an environment where food normally is thinly dispersed. Nannoplankton and microorganisms too small for most adult crustaceans to obtain by filter feeding are readily available on abandoned appendicularian house filters and organic aggregates.

The living bodies of various species serve as more or less stable habitats for other organisms. Bacteria and protozoa can also use most organic aggregates as microhabitats (Pomeroy and Johannes 1968; Paerl 1973). Three species of planktonic dinoflagellates utilize the pelagic foraminiferan *Hastigerina pelagica* as a surface habitat in the Florida Current (Alldredge and Jones 1973). Hyperiid amphipods use living surfaces (medusae, salps, siphonophores, ctenophores, and tornaria larvae) as both microhabitats and sources of food (Madin 1974*b*). Our observations so far confirm the hypothesis of Pirlot (1932) that hyperiid amphipods have conquered the pelagic space by attaching themselves as inquilines or parasites of the macroplankton.

Planktonic microhabitats are of particular interest as they relate to the origin and maintenance of diversity in planktonic animals. Attempts to resolve the "paradox of the plankton" (Hutchinson 1961) have taken several forms (e.g. *see* Harding and Tebble 1963; Richerson et al. 1970). The presence of heterogeneous microhabitats in the sea, with specific associated biota, may help.

Our direct field observations demonstrate that the planktonic environment contains considerable physical spatial heterogeneity in the form of macroscopic surfaces of a variety of sizes and shapes. We propose that the structure of this environment has two important characteristics not found in other habitats:

1. Constantly changing spatial relationships: Drifting aggregates are constantly changing relative to each other, due to the action of currents, microgradients of density, and the activity of animals. Organisms

remaining on specific surfaces are relatively unaffected by this motion, but organisms using these surfaces for feeding must develop suitable means of locating particles.

2. Small habitat size per unit animal: Many of the surfaces are only slightly larger than most of the organisms that utilize them, and thus the number of interacting animals per aggregate is probably much smaller than in other communities.

Predator-prey relationships

In situ observations and collections are particularly useful for investigating predation among planktonic animals. Events of predation and escape were seen in the sea and could often be recreated in aquaria with undamaged animals. Among the most active and effective predators we have observed are medusae, siphonophores, ctenophores, and heteropods.

The heteropod *Cardiapoda placenta* was observed on 38 occasions. On five of these, we saw *Cardiapoda* eating *Salpa cylindrica*; on seven other occasions the contents of the gut could be identified as *Salpa*. Time from ingestion to release of feces varies from 4.5 to 6.5 h, depending apparently on the relative size of predator and prey. In the laboratory, other prey were taken, including the pelagic nudibranch *Phyllirhoe atlanticum*, various fish larvae, and the heteropod *Firoloidea desmaresti*. The maximum time of digestion was never more than 7 h.

The attack behavior of *Cardiapoda* was observed once in the field and twice in the lab; it was initiated by the heteropod when the prey was as much as 60 cm away. In each case, the prey was above the heteropod (which swims on its back) suggesting that the silhouette of the prey can be seen by *Cardiapoda* from considerable distances. *Cardiapoda* swims rapidly to its prey (up to 40 cm s^{-1}), seizing it initially with the buccal cones. The entire prey is pulled into the esophagus by the combined action of the radula, buccal cones, and peristalsis of the proboscis. On one occasion, a heteropod attacked a salp twice its size, and after half was ingested severed the remainder

with its radula. Ingestion in all cases took about 10 min. Previous estimates of digestion times for net-collected specimens of *Carinaria japonica*, a close relative of *Cardiapoda* (Seapy 1970) averaged between 1.5 and 2.5 days, with some prey requiring up to 4 days to be digested. Compaction in the cod end of the net probably damages these organisms. Only a few percent of Seapy's specimens were healthy enough for observation in the lab, and the digestion times recorded were very likely affected by net damage.

Another heteropod, *Pterotrachaea coronuta*, was seen in the sea 27 times and on five occasions was eating physonect siphonophore bracts. No other prey items were observed underwater, nor would *Pterotrachea* feed on salps, ctenophores, or pteropods in the laboratory. Digestion times ranged from 6 to 8 h for the siphonophore bracts.

In the field (though not in the laboratory) these two heteropods swam actively only when attacking a prey item or avoiding capture by divers. Otherwise, they were rolled into a loose ball, with the posterior section of the tail in contact with the buccal region. The animal floats in this manner apparently as a neutrally buoyant mass; we could not detect any sinking.

We saw dramatic predation on salps by the hydromedusa *Aequorea* sp. Large *Aequorea*, with tentacles trailing 2 m or more, caught and ingested large salps by the dozen in one particularly dense swarm of *S. cylindrica*; the salps were apparently digested rapidly.

The tentaculate ctenophore *Lampetia* was generally no larger than its salp prey. On encountering a salp, the ctenophore opened its mouth and flattened itself over the surface of the prey (*see* Hyman 1940), eventually engulfing the salp.

The predatory behavior of *Beroe ovata* on other ctenophores, such as *Bolinopsis*, has been described by Swanberg (1974). *Beroe* maximizes the energetic gain in each encounter with its prey by eating as much of *Bolinopsis* as possible, either engulfing

small ones whole or biting substantial portions out of larger ones with specialized ciliary "teeth." *Aequorea* also feeds on these ctenophores in aquaria. The tentacles of the medusae slice through the tissue of *Bolinopsis* and the individual pieces are eaten.

The pomocentrid fish *Abudefduf saxatilis* were seen in shallow waters of the Gulf of California feeding extensively on appendicularians in their houses (*see also* Shelbourne 1962). Nutritional utilization of the algae-clogged house as well as of the appendicularians would increase the caloric gain for these fish and shorten the food chain considerably, making nannoplankton directly available to upper trophic levels (Alldredge unpublished observations). Predation by fish on salps may also constitute a trophic shortcut from small primary producers to large consumers (Madin 1974a).

Our observations of the gelatinous zooplankton show that predation ranges from visually oriented and highly specific patterns, as in *P. coronuta*, to nonvisual and rather indiscriminate modes, as in *Aequorea*. Between these extremes many sorts of predatory feeding are undoubtedly important to the trophic and diversity structures of the zooplankton community. Most of these patterns will be discernible only by in situ observations.

The principal defense strategy against predation within this assemblage as we have defined it is transparency (Greze 1963). However, in addition, virtually all the animals we have seen exhibited behavior patterns, usually in response to the proximity of a diver, which seemed to be escape responses. Commonly the animals swam away in the normal or a different swimming mode when approached at a certain distance. Nonvisually oriented animals responded only to physical contact or local turbulence.

Heteropods abandon their enrolled postures and pteropods their feeding webs to swim away at remarkable speeds when approached. Some appendicularians have elaborate escape responses, retreating out

through an escape hatch in the house when disturbed physically by a diver, or, as once observed, by a chaetognath. This hatch evidently serves as an exit port both when the house filters are clogged and to escape predation. Free-swimming appendicularians are extremely fast; we saw *Oikopleura longicauda* swimming at 30–50 cm s^{-1} over short distances. But this response is not universal. Other species remain within the house despite continued prodding by a diver, and their responses to an actual predator are unknown.

Salps respond to touch on the posterior end by swimming faster for a few seconds; they sometimes stop or reverse when touched on the anterior end. Siphonophores, spread in the fishing position, contract rapidly to a fraction of their extended length and swim away in response to turbulence or contact with a tentacle. Medusae respond to a touch on the bell by contracting the tentacles and swimming somewhat more rapidly.

Ctenophores are also responsive to touch. *Pleurobrachia* rapidly contracts its tentacles when touched and swims away. *Ocyropsis* swims powerfully with its muscular lobes when disturbed. *Cestum* switches from swimming as a rigid wing propelled by cilia to a fast undulating pattern that moves it at right angles to its previous course. Presumably these animals can differentiate between potential predators and prey items by the intensity or extent of the contact. In most cases the prey items are much smaller than the predators. Food or foe may also be identified chemically. In every case, rapid escape swimming persists only for a few seconds, moving the animal a meter or two away, and is followed by reversion to the normal speed or pattern.

A more complex response was seen in the ctenophore *Eurhamphea vexilligera* and several alciopid polychaetes that released reddish-brown streamers of pigment as they swam away; the secretion of *Eurhamphea* is also luminescent, producing a shower of green sparks in the water. This appears to be an "ink-cloud" escape behavior like that of cephalopods and bespeaks

unexpected sophistication on the part of these plankters. These defenses may be effective only against visually oriented predators; the secretion of *Eurhamphea* seemed not to deter predation by the chemotactically oriented *Beroe* (Swanberg 1974). The diversity of predators and feeding behaviors among planktonic animals suggests that these instances are only a few of many escape responses that have arisen to deal with specific pressures.

We feel that our observations on the biology of the gelatinous zooplankton community amply demonstrate the utility of SCUBA diving in the open ocean as an investigative tool to complement conventional zooplankton methods. We hope that the thoughts presented here will stimulate additional study of the gelatinous macroplankton.

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