

## GELATINOUS ZOOPLANKTON - THE FORGOTTEN FAUNA

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### ABSTRACT

For the past 100 years nets have been used extensively in an attempt to make quantitative estimates of the depth and geographical distribution of zooplankton in the World's oceans. However, with the introduction of in situ studies, by SCUBA diving and from submersibles, it has become increasingly obvious that there are other, very important, populations of planktonic animals that, because of their fragility, are not sampled adequately, if at all, by nets. These animals form part of the so-called 'gelatinous zooplankton', whose representatives are drawn from a wide variety of invertebrate taxa, particularly the pelagic coelenterates, ctenophores ("comb jellies"), and tunicates. The importance of these various groups of gelatinous zooplankton is reviewed briefly and illustrated by means of video recordings made during submersible dives.

### INTRODUCTION

During the nineteenth century many eminent marine biologists placed great emphasis on studies of the systematics, life histories and behaviour of planktonic animals. Many of the animals they collected were fragile gelatinous forms, yet detailed and beautifully illustrated descriptions of many new species were produced because the animals were being carefully collected from just below the sea surface, using dip nets or collecting jars. However, many of the animals so described have remained unrecorded or little known for most of the present century, and have caused many, more recent researchers

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to conclude that either the animals are extremely rare or that the original descriptions were very dubious. Yet, once SCUBA divers began to look into the open ocean it became clear that not only were some of these species relatively common at shallow depths in the ocean, often with widespread distributions, but that the original descriptions and illustrations were extremely accurate.

The reason why so many planktonic animals disappeared from notice is that for the past 100 years remote-sampling techniques, particularly the use of towed nets, have dominated our research efforts and that interest has been centred on attempts to make quantitative estimates of the depth and geographical distribution of zooplankton. The inception of this methodology aroused much controversy, as reviewed by Harbison (1983), with particular emphasis on the fact that, although nets could be used to study large-scale distribution patterns, the small-scale patterns and the interactions between the individual species became totally obscured. Thus net sampling 'proved' the paramouncy of the crustacean zooplankton, at least in their numerical abundance, but totally ignored the already established fact that representatives of this group, i.e. certain amphipods, had been found to associate with other animals, implying that any studies of the distributional patterns of the amphipods in isolation were meaningless. It was only when in situ studies were carried out that the importance and specificity of these associations began to be fully appreciated. Nonetheless, it is apparent that no single sampling technique is appropriate at all space scales, nor can it give a full picture of the composition of a plankton community, and it remains a major problem as to how these separate data sets can be interrelated. However, here we will simply consider some of the aspects of the biology of those animals that nets have failed to catch.

This forgotten fauna is collectively known as the 'gelatinous zooplankton', whose representatives are often so fragile that they are totally destroyed by nets, and sometimes, even if collected, they dissolve in the preservative leaving an amorphous 'goo' in the sample. However, with the introduction in recent years of in situ observation and collecting techniques, such as SCUBA and submersibles, it has become increasingly obvious that this fauna is not only ubiquitous, but also can be the most abundant component of the oceanic community. In fact, over 50 years ago William Beebe, during pioneering dives in his bathysphere, observed that the plankton world revealed before his eyes was totally different

from that collected during his extensive net sampling programmes in the same area (Beebe, 1934). In particular he drew attention to the abundance of many large gelatinous organisms.

Representatives of the 'gelatinous zooplankton' are drawn from a diverse and heterogenous assemblage of invertebrate taxa, spanning at least seven phyla, including protozoans, particularly radiolarians; cnidarians (coelenterates), such as hydromedusae, scyphomedusae and siphonophores; ctenophores ("comb jellies"); annelids, e.g. polychaete worms; molluscs, such as heteropods, thecosome pteropods, and even squid; chaetognaths (arrow worms); and pelagic tunicates, such as salps, doliolids, pyrosomes and appendicularians (larvaceans). Even though there is such a diverse assemblage of gelatinous zooplankton, which spans three trophic levels from herbivory to secondary carnivory, there are many similarities between them. Most forms are characterized by the absence of any hard parts and their high water content (>95%) means that their specific gravity is close to that of water, rendering them neutrally buoyant. However, the inclusion of certain shelled molluscs may seem surprising, but their feeding behaviour, using large mucous webs (see Gilmer and Harbison, 1986), means that they have much in common with other forms, particularly the appendicularians. Most gelatinous forms, be they herbivores or carnivores, have feeding rates that show no lower threshold or upper limit, as is the usual case with copepods. Because of their generally high assimilation efficiencies, they have the ability for rapid growth, and a high fecundity in association with a short generation time means that they can react quickly to a potential food source.

Allredge (1984) recently has given a detailed account of the significance of gelatinous zooplankton in the marine ecosystem, with particular emphasis on their abundance and impact as pelagic consumers. Much of the information she discussed has been derived from observations made, in near-surface waters, by SCUBA divers, and subsequent experimentation on the animals collected intact in hand-held jars, or retained undisturbed in enclosures. It is not necessary to repeat that information nor, in the limited space available, is it possible to provide a comprehensive review of all the types of gelatinous zooplankton. Instead attention will be focussed on three groups of midwater gelatinous zooplankton that reflect the various scales of the problem in interpreting data from net or in situ collections. Particular emphasis is given to the new and exciting observations that

have been made in recent times using submersibles to study midwater zooplankton communities.

## **SUBMERSIBLES**

In situ midwater studies have almost exclusively been carried out using American submersibles, such as 'Alvin' or 'Johnson-Sea-Link', together with the use of the WASP Atmospheric Diving Suit and, recently, the one-man submersible 'Deep Rover'. I have been fortunate to become involved in some of these activities thanks to the benevolence of Dr. Richard Harbison of the Harbor Branch Oceanographic Institution, which operates the submersibles 'Johnson-Sea-Link' I and II. These latter submersibles are remarkable in that the forward compartment is a 1.7 m diameter, 10 cm thick, acrylic sphere that allows both the pilot and the observer the same, almost panoramic, view of the surrounding water. Although these submersibles have a depth limitation of 1000 m, this still allows plenty of scope for making studies on the midwater zooplankton.

One of the early problems associated with the use of submersibles was the inability to capture any of the spectacular animals that were observed, such that many of Beebe's visual descriptions of fish remain to be verified. However, the 'Johnson-Sea-Link' submersibles are exceptionally well equipped with sampling devices allowing even the most delicate and fragile animals to be collected individually. However, another major problem in making in situ observations is that we have to use the submersible's light in order to see the animals, and it is apparent, as is shown in the video, that lights can have a great affect on some animals. Some fish simply are dazzled and dart about erratically, while others appear to take absolutely no notice whatsoever. The lights attract vast swarms of certain animals, particularly euphausiids and amphipods, to our vicinity, and on one memorable occasion the submersible was swamped by thousands of polychaete worms. Squid are often seen hovering in the distance, before swooping in to capture some tasty morsel that we had been studying. Amphipods, particularly Thermisto sp., also use the opportunity of our lights to attack virtually anything in sight. Even the gelatinous zooplankton themselves, without sophisticated eyes, are affected by the lights of, or perhaps the turbulence generated by, the submersible. Many siphonophores and ctenophores remain unidentifiable because they simply disintegrate 'before your very eyes', leaving nothing that can be studied. Others appear robust at depth, but fall apart once they have been captured

and returned to the laboratory, even if kept at the ambient temperature of their capture depth.

## MEDUSAE

Jellyfish, in general, are amongst the most robust of the gelatinous zooplankton forms, with at least the main body (bell) of the animal frequently being found in net collections. There they are often the most important contributor to the catch, particularly in temperate waters. Nonetheless, it is apparent from out in situ studies that there are still many, more fragile, medusan species that are new to science. We have also found that many other species, of which we have only a fragmentary knowledge, are relatively common in midwater, and complete animals have now been collected. Although, as mentioned above, it is potentially difficult to study associations in the deep ocean, because of our lights, some have still been discovered. For instance, recently we found a rare amphipod, previously thought to be free-living, sitting atop the bell of the medusa, Atolla. We have also observed active predation on the same species of medusan by a large decapod shrimp, Notostomus. This decapod was so intent on enjoying its meal that it failed to heed the warning of our presence, and both animals were collected together.

Even though many medusans may be well known from net collections, their fishing behaviour and general ethology is not. For instance, in the descriptions of Atolla it had been noted that one of the tentacles was much larger than the others. Observations show that this tentacle in fact is much longer than the others and is trailed for a considerable distance behind the animal. We have yet to discover the reason for this phenomenon, and similarly we do not know why another common scyphomedusan, Periphylla periphylla, holds its tentacles rigidly in front of its bell while swimming actively (Fig. 1, A).

On one occasion we collected another Periphylla to which was clinging a pycnogonid. Although pycnogonids are usually benthic, some have been collected in midwater and it had been suggested previously, without direct evidence, that they may have been sitting on medusae. In situ observations have provided conclusive proof for this supposition. In addition, on closer examination it was found that two juvenile pycnogonids were parasitizing the same jellyfish. This raises the interesting question as to how the host is found, and a possible explanation may lie in observations of specimens of

Periphylla resting, or perhaps feeding, on the sea bed. Why the medusae behave in such a way is another mystery, but it would appear to facilitate the parasitism.

## SIPHONOPHORES

Siphonophores, which are my particular speciality, are highly polymorphic animals that occur in a bewildering variety of shapes and sizes. The most famous representative is Physalia physalis, the Portuguese Man O'War, that 'sails' over the surface of the oceans with its deadly tentacles stretching down many tens of meters into the waters below. However, almost all siphonophore species are holoplanktonic, the only other exceptions being a small group that have attached themselves to the sea bed, like tethered air-balloons (Pugh, 1983). The biology of siphonophores has been reviewed recently by Mackie et al., (1987).

Siphonophores can be split into two basic groups depending on the presence (physonects and cystonects) or absence (calycophorans) of an apical float, or pneumatophore. Of the ca. 160 known species, approximately two-thirds are calycophorans (without floats). This group, in general, has a simpler structural organization than the physonects and many species are robust enough to be caught by nets. Although in the open ocean they rarely reach abundances of greater than  $0.1 \text{ animals m}^{-3}$ , neritic species, such as Muggiaea atlantica, can occur in numbers exceeding  $200 \text{ animals m}^{-3}$ . Nonetheless the oceanic species are amongst the most abundant macrozooplankton forms and frequently dominate net catches. In contrast, physonect species, because of their fragility and more complex structure, are usually destroyed by nets and the myriad pieces lost. Even if recognizable pieces were to be collected it is virtually impossible to ascertain the number of animals that had been sampled. Our in situ studies, however, indicate that physonect species are very common and up to  $8 \text{ specimens m}^{-3}$  of Nanomia cara have been observed, which is a considerable abundance when one considers that these animals can measure up to 4 m in length.

In contrast to net collections, where calycophoran species predominate, over 60% of the siphonophore species and 70% of the specimens collected during our limited submersible studies are physonects. A mitigating factor may be that the small calycophoran species may have been overlooked as it would take a keen eye to spot them, whereas the larger physonects are often brightly coloured and their spectacular appearance quickly draws one's attention to their presence. But it is

clear that only with a combination of in situ and net collection techniques can the significance of the entire spectrum of siphonophore species be appreciated. However, the in situ observations of the abundance of physonect species can only enhance the already established fact, from net collections of calyphoran species, that siphonophores play an important role in the marine ecosystem.

A further revelation of these in situ submersible studies is that over half of the physonect, and a quarter of the calyphoran, species collected have proved to be new to science. However, even the previously known species have proved to have many surprises in store. For instance, during a cruise to the Bahamas, we found that the commonest siphonophore species was the physonect Lychnagalma utricularia (Fig. 1, B) (Pugh and Harbison, 1986). This species was described originally in 1879, from the Straits of Messina in the Mediterranean, but until we collected it, there had been no other substantiated records. Subsequently we have collected it at various other sites in the western North Atlantic, indicating that not only is it a common species but it has a widespread distribution.

All siphonophores are carnivores and capture prey using their tentacles, which usually have side branches, or tentilla, that are strongly armed with nematocysts. Each tentacle is attached to a gastrozoid, or stomach, and these usually are arranged in a linear series along the stem of the siphonophore. In situ studies have enabled us to discover that many siphonophore species are highly selective in their feeding, with the type of prey captured depending on certain morphological and behavioural characteristics of the individual species (see Mackie et al., 1987). These characteristics include the size and number of gastrozooids and tentacles borne on the stem; the types of nematocysts present; and the specific fishing behaviour. Unlike many medusae, whose prey is captured while the tentacles are pulled, or pushed, through the water during active swimming periods, siphonophores are passive feeders, setting tentacular nets that often can form complex patterns. In the simplest case, the main body of the siphonophore is held horizontal and the tentacles hang down, often for some considerable distance, forming a vertical curtain. Species using this configuration tend to spend long periods 'fishing', and have large gastrozooids that can engulf larger prey items. Thus these animals have adopted a sit-in-wait strategy, expending little energy in fishing, and relying on the fact that crustacean swimming speeds generally increase with their size, such that

the chances of encountering a suitably size prey item are increased purely on the basis of the latter's activity.

The greater energy expenditure in these activities is offset by the fact that these smaller species tend to be more active and have adopted a different feeding strategy, alternating between short bursts of swimming and fishing. During the former the stem and tentacles are contracted, but as this phase ends the animals swim in a particular fashion, whilst relaxing the stem and tentacles, so that the tentacles are spread out in an often complex, three-dimensional arrangement. Once the tentacular net has been set it is common for the animals to sink slowly, thereby allowing a greater volume of water to be searched for prey. The greater energy expenditure of these activities is offset by the fact that these smaller species have smaller, more numerous gastrozooids and that they feed on the smaller, more abundant zooplankton, particularly copepods. The siphonophore species that have adopted these various feeding strategies have different patterns of geographical and vertical distribution and Pugh (1986) has speculated on the probability that these species have evolved in a response to the particular distributions of their preferred prey items.

Although the basic methods of 'fishing' are passive, relying on the potential prey items becoming ensnared in the tentacular trap through their own activity, in situ studies have shown that some siphonophores have other tricks up their sleeves. Some species periodically contract and relax their tentilla in a manner reminiscent of 'squid-jigging' or fly-fishing, whilst others have adopted more subtle techniques, through aggressive mimicry, by evolving tentilla that resemble small planktonic animals to lure in their prey. Thus some tentilla can resemble small copepods (Agalma), jellyfish (Lychnagalma), fish larvae (Athorybia), or can be vibrated in a way reminiscent of the swimming of chaetognaths (arrow worms) (Eretna).

While many species eat a wide variety of crustacean prey, dependent only on its size, others are much more selective, for instance the hippopodiids that feed exclusively on ostracods. All these animals ensnare their prey in a plethora of Lilliputian ropes that are discharged from the nematocysts. However, some species have nematocysts that can penetrate into soft-bodied animals and inject a deadly toxin. The latter species mainly capture small fish, but one (Apolemia) is known to feed on other gelatinous organisms. In situ observations have revealed that Apolemia species can reach many tens of



metres in length, which when we can make accurate measurements should qualify them for the 'Guinness Book of Records' as truly the longest animals in the world. These animals also have been observed to have a distinct fauna of fish associated with them. Presumably the fish are gaining some protection from predation as well as feeding on the siphonophores' potential predators, such as amphipods. Other associations between fish and siphonophores also have been observed.

## CTENOPHORES

Ctenophores, or comb-jellies, of all the types of gelatinous zooplankton, are the most difficult to study because of their extreme fragility. In some cases even the slightest turbulence in the water can destroy them; others fall apart after collection; and even the most robust forms usually cannot be preserved, simply dissolving in the preservative to form the amorphous 'goo' that characterizes many net collections. Nonetheless, their presence in vast numbers in coastal and inshore waters has long been known and, as Alldredge (1984) reviewed, they are often the most important predator present, having a considerable impact on the balance of the ecosystem. An instance of this, and an example of the false story that nets can tell, lies in direct comparisons, using nets and in situ observations, of the abundance of the ctenophore Velamen, a close relative of the famous Venus' Girdle. Whereas SCUBA divers estimated populations of between 10 and 305 animals  $m^{-3}$ , the nets 'caught' no specimens at all!

In contrast to the considerable volume of information on the importance of neritic ctenophores, a survey of the literature for this century reveals little or no information on the oceanic species of these animals, with almost all records being for near-surface dwelling forms. Thus, oceanic ctenophores usually have been dismissed as being irrelevant in the ecology of the seas. In fact, until recently, only three species of ctenophore had been described as being truly deep-water forms, one of which was the well-known Beroë. This is one of the few forms that can be preserved, although not without some considerable shrinkage. However, it was established last century that Beroë species feed almost exclusively on other ctenophores and, thus, it was apparent to the earlier researchers that there must be a large population of deep-water ctenophores in order to sustain this diet. But this fauna remained unknown until recent in situ observations from submersibles showed that, indeed, there was an abundance of ctenophores at midwater depths. These observations have shown that oceanic ctenophores are important and widely

distributed predators in the open ocean, and, perhaps not surprisingly, that about three-quarters of the species collected were new to science, or have been described only recently, e.g. Thalassocalyce inconstans (Fig. 1, C).

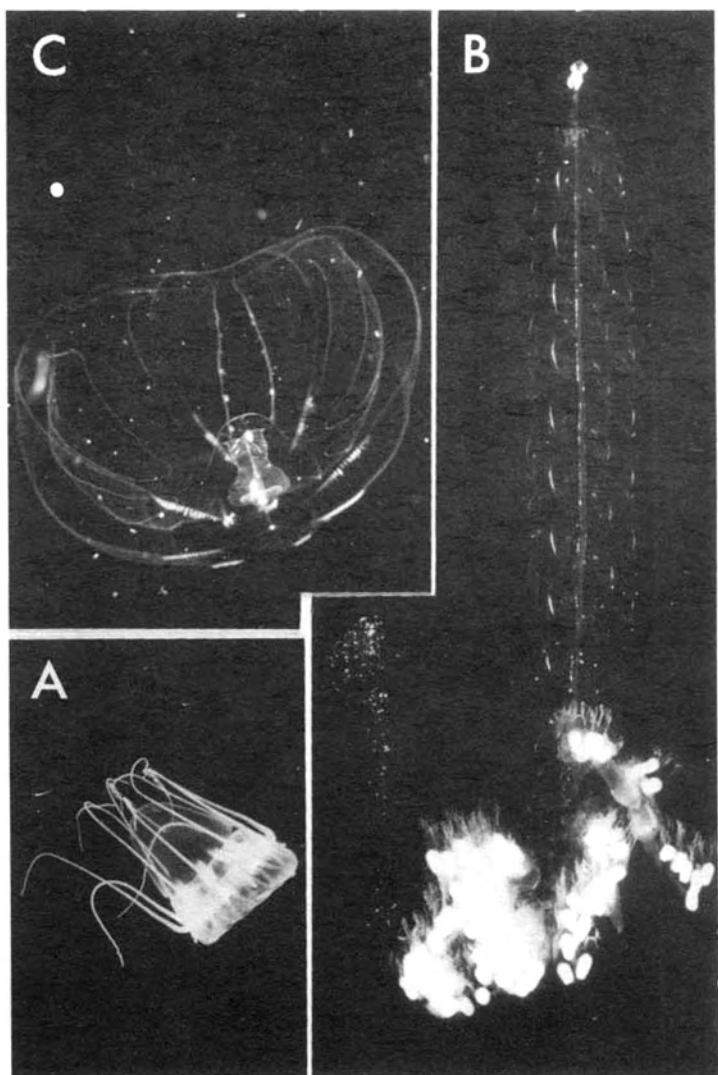
Ctenophores are carnivores and many, like siphonophores, are sit-in-wait predators, while others utilize slow swimming movements and ciliary water circulation over their lobes to optimise prey encounters. Similarly, the different species have adopted a variety of feeding strategies in order to optimise the capture of their preferred prey. These strategies have been reviewed by Harbison et al. (1978). Some species have long tentacles covered all over by sticky colloblasts, and sometimes these colloblasts are grouped together, in a way analogous to the nematocyst batteries of siphonophores, so that the species can probably capture larger prey animals. Other species use their sticky oral lobes as 'fly-paper', although some have no mucous and, like a Venus Fly Trap, enfold any animal that comes into contact with them. However, it has been observed that many prey, captured by whatever means, quickly cease to struggle suggesting that a poison or anaesthetic is secreted by the ctenophore. This may also be a sort of chemoattractant enabling Beroë to home in on other ctenophores, which, with its enormous mouth, it engulfs or 'bites' large chunks from.

## CONCLUSIONS

'Gelatinous zooplankton' are relatively abundant and ubiquitous in the World's oceans, despite the story that net collections appear to tell. These animals have the potential to exploit potential food sources rapidly, and in situ studies, particularly using SCUBA diving techniques, have allowed some assessment of their importance in the marine ecosystem. However, such studies in deep water, using submersibles, are only at preliminary stages and, in many cases, we have yet to pass the descriptive phase, particularly as so many of the animals have proved to be new to science. Gelatinous zooplankton have yet to be incorporated properly into ecosystem models, although their importance is beginning to be recognised. As Alldrege (1984) concluded "our present knowledge ... of gelatinous zooplankton ... serves only as a titillating introduction to the possible trophic interactions and ecological significance of this ubiquitous, diverse and poorly understood group of marine consumers". Clearly, we have a long way to go before we can begin to understand, let alone model, the oceanic ecosystem.

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**Figure 1.** A. *Periphylla periphylla*, a scyphomedusan with a bell height of up to 20 cm; B. *Lychnagalma utricularia*, a physonect siphonophore reaching 2-3 m in length, when fishing; C. *Thalassocalyce inconstans*, a ctenophore up to 15 cm in width.