

Scuba Diving in Blue Water: A Window on Ecology and Evolution in the Epipelagic Ocean

*Laurence P. Madin, William M. Hamner, Steven H. D. Haddock,
and George I. Matsumoto*

ABSTRACT. Conventional methods of zooplankton sampling have serious limitations for the study of soft-bodied gelatinous animals, which are easily damaged or destroyed in nets and trawls. An alternative approach is scuba diving in the upper waters of the open ocean to make observations, measurements, and collections in situ. With appropriate safety measures, this method has proved highly effective in revealing natural behavior of a variety of animals, as well as in allowing collection of live specimens for experimental work or detailed taxonomic examination. Simple precautions and protocols have allowed blue-water diving to be conducted safely and productively for the last 40 years. It has provided insight into both the biology of individual species and the structure and functioning of epipelagic communities in tropical, temperate, and polar oceans. It has further revealed the occurrence and effects of nonliving material like marine snow, as well as the microstructure created by density layers and convergences. The direct experience of the water column environment that blue-water diving can provide is a valuable key to understanding the lives of its inhabitants.

INTRODUCTION

The study of zooplankton has been based historically on the results of pulling nets of various configurations through the water column and taking what was collected as representative of the zooplankton community. It is obvious, though frequently ignored, that different nets capture different categories of organisms depending on their mouth diameter, mesh size, bridle configuration, and towing speed. Crustaceans are usually well represented in net samples, along with other small- to medium-sized animals with hard bodies and slow swimming speeds. Trawls with very large mouth openings and coarse mesh size capture faster and larger epipelagic animals, such as fish and squid. Other sampling devices, like Niskin bottles, retrieve an intact water sample with everything in it, and in principle provide a comprehensive picture of all planktonic organisms present. But the necessarily small sample size of a water bottle (typically 1–30 L) with its small opening (centimeters in diameter) makes it unlikely to catch anything that is rare or large, or that would avoid a bottle moving through the water on a wire. With nets or water samplers, it is possible to get a fairly representative sample of small organisms ranging from microbes, phytoplankton, and protozoa up through the smaller crustaceans and other mesozooplankton. What is typically missing from these samples are alert, fast-swimming animals like euphausiid and decapod crustaceans, squid, and fish, and also the

Laurence P. Madin, Woods Hole Oceanographic Institution, 266 Woods Hole Road, Woods Hole, Massachusetts 02543, USA. *William M. Hamner*, University of California, Los Angeles, Department of Ecology and Evolutionary Biology, Box 951606, Los Angeles, California 90095-1606, USA. *Steven H. D. Haddock and George I. Matsumoto*, Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, California 95039, USA. *Correspondence:* L. Madin, lmadin@whoi.edu.

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gelatinous animals that are often sparsely distributed, relatively large and fragile, and usually damaged or destroyed by plankton nets and trawls.

Many oceanographers and marine biologists unfortunately still think of the upper water column of the open ocean as a biological desert, a misconception related to the fact that most epipelagic zooplankton are effectively invisible, either transparent or too small to be seen. Nonetheless, net zooplankton are always present in blue, seemingly empty surface waters. One need only tow a net for five to ten minutes to collect a valid sample of net zooplankton, but short net tows grossly undersample rare species, and small-diameter nets underestimate the abundance of larger taxa, most of which are gelatinous and transparent. As blue-water diving research has shown, epipelagic waters contain a rich spectrum of larger gelatinous zooplankton that is rarely represented in net collections.

BLUE-WATER SCUBA DIVING

We know now that many aspects of animal biology are best understood by observing undisturbed animals in the environments where they live and evolve. Terrestrial biologists are not constrained physiologically from conducting most field investigations, but comparable field studies of undisturbed oceanic animals are surprisingly recent because humans are not adapted for underwater work. William Beebe used hard-hat surface-supplied air to observe fish and zooplankton under water in 1926 (Beebe, 1926), and he later used a bathysphere a half-mile down (Beebe, 1935) to observe midwater fish and invertebrates. Although the aqualung was invented in 1943, publications about underwater behavior of fish did not appear until the 1960s (Randall and Randall, 1960; Hobson, 1963, 1965). Use of scuba to investigate demersal fish and invertebrates is now routine (see other chapters herein), with long-term in situ investigations possible under water day after day at the exact same site, often on the same individual organisms. In the open sea, however, one cannot return day after day to investigate the same individuals or population of pelagic animals because zooplankton drift and pelagic fishes swim away. According to Haddock (2004:553), “With the exception of pioneers like Bieri (1966) and Ceccaldi (1972), few people attempted to observe plankton in their natural environment before Hamner and students pioneered the technique of blue-water scuba diving (Hamner, 1975; Hamner et al., 1975).” Subsequently, many biologists have spent thousands of hours using scuba in blue water to observe undisturbed, mostly gelatinous animals in their own environment. It is important to emphasize that our review of discoveries about epipelagic animals via use of scuba since 1972 is concerned with only those creatures that are found routinely in the upper 40 m of the water column. Many gelatinous animals occur also in much deeper water where they have been investigated via bathysphere, research submersible, and remotely operated vehicles (ROVs) (Beebe, 1935; Nishizawa et al., 1954; Mills et al., 1996; Johnsen, 2001; Haddock, 2004; Robison, 2004).

Blue-water scuba diving was formalized during a research program in 1971–1972 in the Florida Current near Bimini in the Bahamas (Hamner, 1974; Hamner et al., 1975). Although primarily a scuba-oriented exercise, the work also included sampling of zooplankton with 30-cm-diameter nets every month for 15 months. Specimens of only the most common gelatinous species were captured with nets, although gelatinous animals were clearly present in the water column because they were observed almost every day by scuba divers. Ctenophores were often strained through the mesh of the net or damaged almost beyond recognition. Other gelatinous taxa, delicate but also fast-swimming, actively avoided nets. For example, the pseudotoxosome mollusks *Gleba*, *Corolla*, and *Cymbulia* are especially sensitive to turbulence. They are vulnerable to predators when feeding motionless with mucus structures, and they swim away rapidly when disturbed by the bridle of a plankton net (Gilmer, 1972). Planktonic mollusks sometimes even evade capture by divers and it is not surprising that they had not been collected previously in large numbers (Gilmer, 1974). However, given good visibility, a group of divers can examine thousands of cubic meters during a dive, locating individuals of many of the larger gelatinous animals within that volume.

The gelatinous zooplankton studied via scuba in the Florida Current were, at that time, poorly known taxa such as foraminifera, radiolarians, hydromedusae, siphonophores, scyphomedusae, ctenophores, heteropods, pteropods, salps, and appendicularians (Hamner et al., 1975). Most of these gelatinous zooplankton have evolved convergent attributes: they are all mostly transparent, delicate, relatively large (>1 cm), neutrally buoyant, slow-swimming, tactile, and nonvisual. Most do not react to scuba divers unless physically disturbed, enabling scuba divers to observe undisturbed, undamaged specimens from all these taxonomic groups at very close range in the upper sunlit regions of tropical seas. Though many gelatinous taxa are transparent and hard to see against a uniform blue background, there are ways to enhance their contrast by looking at them from certain angles relative to down-welling sunlight and, with practice, divers sometimes can spot and identify species from meters away. Like birdwatchers who recognize a species from a flash of color or movement, experienced blue-water divers can often identify animals by their characteristic swimming attitudes or motions or a gestalt impression, even without a clear, close-up view.

Plankton nets and trawls damage or destroy gelatinous zooplankton, so scuba divers collect individual, undamaged animals by hand in wide-mouthed jars for subsequent identification and laboratory study. Oceanic zooplankton live in the water column away from the sea floor, rarely encounter the seabed or shallow reefs, and have not evolved behavioral responses for avoiding rigid surfaces. In standard rectangular laboratory aquaria, therefore, these animals often sink to the bottom and become trapped in the corners, or are embolized by air bubbles. Some taxa can be cultured or maintained in the laboratory via use of circular planktonkreisels (Hamner, 1990) or other taxon-specific aquaria (Raskoff et al., 2003), but it is difficult to know how much

physical confinement alters their behavior. Blue-water diving is without question the best way to learn how undisturbed pelagic animals behave naturally (Hamner, 1985; Haddock, 2004).

Different sampling procedures can mislead, but they can also corroborate and confirm the nature of biodiversity in a marine community. Thus, in a study of the western Mediterranean Sea (Mills et al., 1996), use of scuba in blue water generated a list of gelatinous organisms that was as rich in species as the taxa collected with the *Johnson Sea Link* submersible, yet few of these species are ever present in plankton tows in the same waters. Many new gelatinous species are yet to be described; some, such as the ctenophores *Tinerfe cyanea* (Chun, 1889) and *Deiopea kaloktenota* (Chun, 1879), not seen since the nineteenth century, were recently “rediscovered” in the Mediterranean by blue-water divers.

Studies of bio-optical properties of open-ocean animals have benefitted greatly from blue-water collections by scuba divers. Blue-water collections of individual, undamaged, hand-collected specimens are especially critical for studies of physiology and bioluminescence. A series of recent papers has cataloged the distribution and physical properties of transparency of scuba-collected specimens (e.g., Johnsen and Widder, 1998, 1999, 2001; Johnsen, 2001). Examinations of bio-optical properties of these species have included luminescence spectra (Haddock and Case, 1999) and the discovery and cloning of a green-fluorescent protein from a ctenophore (Haddock et al., 2010).

LOGISTICS AND SAFETY AT SEA

Blue-water divers are neutrally buoyant in a featureless open sea. There are no landmarks for orientation, the sea floor is far below and out of sight, and it is possible to become disoriented and drift too far from other divers or descend too deep. To avoid these potential hazards and ensure the safety and productivity of blue-water diving, simple operational procedures for use of scuba at sea have been employed (Hamner, 1975; Haddock and Heine, 2005).

Blue-water divers usually work at sea from a small boat launched from a mother ship or driven offshore from a marine lab. At the research location, the divers tie a surface float to the boat with a 10 m line. A weighted (1–2 kg) 30–40 m down-line with a small trapeze is suspended from the surface float. One person acts as a safety diver and stays close to the trapeze, which is a central hub for organizing the divers’ lines. Lightly weighted 10 m safety lines (tethers) slide up and down through clips on the trapeze, and each diver attaches the free end of a tether to his or her buoyancy vest. With tethers attached to the trapeze, the divers descend, moving the trapeze to the desired working depth, where they are then free to search for animals within a 10 m radius from the down-line without danger of drifting away or going too deep.

Blue-water dives typically last from 30 to 60 minutes. Maximum dive depths depend on the certification levels of the divers but rarely exceed 40 m (130 ft), with dive time dependent on

water temperature, the depth at which the divers work, and how hard they swim. Usually no-decompression diving is practiced, with mandatory safety stops as the divers ascend. As with other types of scuba diving, dive computers help determine dive parameters. Enriched air nitrox gas has been used, and GPS technology allows divers to make accurate records of their dive location and drift rate when landmarks are not available. Specialized blue-water diving methods have been adapted for use at night and also for operations under Antarctic ice (Hamner, 1982).

TROPICAL AND TEMPORATE EPIPELAGIC ECOLOGY

PHYSICAL CHARACTERISTICS OF A LIQUID THREE-DIMENSIONAL WORLD

The waters of the world’s oceans are the largest known living space in the solar system: at over 1.37 billion km³ and extending to an average depth of 3.7 km, they comprise 98% of all the water on Earth. The open ocean stretches from the surface to the bottom—a vast, three-dimensional, fluid environment that presents some extreme challenges for all inhabitants. The organisms that occupy this vast space are among the most numerous of Earth’s creatures but also some of the most unfamiliar to us land-dwellers; they are sometimes called “aliens from inner space.” This liquid environment has permitted the evolution of organisms quite unlike any terrestrial species, which are restricted by gravity to life primarily in two dimensions. Blue-water diving allows humans to briefly experience what life in the upper waters of the largest biome of Earth is like, enhancing our understanding of the open ocean environment and the daily lives of its inhabitants.

The liquid, three-dimensional nature of the water column is perhaps its most significant difference from terrestrial environments. Reduced gravity has allowed for the evolution of the largest animal on Earth, the blue whale, and gelatinous zooplankton with bizarre shapes and without rigid support structures. Pelagic organisms are released from the physical constraints imposed by gravity on terrestrial animals, swimming or floating neutrally buoyant in the ocean. The opportunity to observe the beauty and grace of gelatinous invertebrates is a splendid reward for those scientists fortunate enough to have dived in blue water.

The water column is divided by subtle yet important vertical gradients and discontinuities that affect the distribution, behavior, and life histories of the organisms that inhabit it. Temperature is an important structuring gradient in the open ocean. In the blue water of the tropics and subtropics, heating from the sun often creates a thin, very warm layer of water just below the surface, which can be a unique habitat for small animals like radiolarians, ctenophores, and calycophoran siphonophores. An upper, mixed layer of uniform temperature is usually bounded by a lower thermocline where temperature changes several degrees over a few meters or less. This sharp boundary creates a density difference, or pycnocline, that often is within diving

range. Organisms sensitive to the temperature difference may be restricted to above or below the thermocline. Food particles, grazers, and their predators often accumulate at the pycnocline between lighter and denser water masses (Hamner et al., 1987). Particulates like marine snow and clumps of inorganic and organic materials are also sometimes trapped within density layers. Sometimes multiple layers of water with different densities can occur within the top tens of meters, creating a layer-cake structure that sorts organisms according to size, density, and behavior. These discontinuities can be visible to divers, whether through a difference in refractive index, which is seen as a shimmering or hazy layer, or through the presence of dense phytoplankton layers that visually indicate the subsurface chlorophyll maximum, which is typically measured by oceanographers through its fluorescence.

A second pervasive gradient throughout the water column is hydrostatic pressure. The monotonic increase in pressure with depth is almost certainly of ecological significance to organisms in the water column and may be an important sensory cue regulating depth distributions and diel or ontogenetic migrations, but little is known about mechanisms of pressure sensitivity in zooplankton.

Light is strongest at the surface and the photosynthetic zone typically extends to about 200 m. However, some light penetrates to about 1,000 m at intensities that allow animals to detect the difference between day and night. This mesopelagic zone is home to a wide variety of predatory and scavenging animals, most of them bioluminescent, and with many that make daily vertical migrations. At night in the open ocean the gradients of temperature, density, and pressure remain, but light is gone and the composition and activity of the biological community in the epipelagic zone often change dramatically, with the arrival of diel migrators and an increased level of feeding. Use of scuba at night in the open sea has begun to provide insight into the behavior and ecology of midwater migratory animals (Graham et al., 2009).

The movement of water in the open ocean also creates horizontal as well as vertical discontinuities and boundaries. Fronts between water masses, such as the west wall of the Gulf Stream, can create distinct barriers that separate adjacent horizontal water masses and accumulate large and small organisms at the interface. Wind-driven down-welling structures like Langmuir cells can also concentrate passively and actively swimming organisms, as can areas of shear at the boundaries between different currents (Rakow and Graham, 2006). The scale of these discontinuities is sometimes small enough to be observable by divers.

THE NATURE OF COVER IN OPEN WATER

Recent textbooks on biological oceanography assume that pelagic ecosystems are controlled almost exclusively by the flow of materials and energy and microbial processes. Alternately, 40 years of blue-water diving have shown us that although epipelagic communities are affected on a daily and seasonal basis by flows of energy and materials and by microbial processes, over

geological time these communities have been shaped primarily by convergent evolution related to the attenuation and diurnal pattern of sunlight, an absence of cover in the open sea, and predation.

Charles Elton (1939:336) noted that terrestrial animals use the presence of cover on land as a refuge from predators, but that refuge can be achieved also through the “influence of the physical qualities and behavior of the prey, such as size, speed, color, and quickness of sense,” as well as nocturnal behavior, camouflage, running, and flying. Thus, according to Elton (1939), there are a limited number of broad but nonetheless discrete categories of terrestrial animals that hide, burrow, fly, or run quickly; that are large, aggressive, nocturnal, small, or dangerous; or that aggregate for protection as in herds, flocks, and schools. All of these attributes are part of Elton’s (1939:334) “protective system of the prey.” We recognize a similar ecological taxonomy for the creatures of the surface of the sea (Hamner et al., 1975; Hamner, 1995; see also Zaret, 1975, for freshwater). Epipelagic animals cluster due to convergent evolution into seven major oceanic assemblages based on the absence of cover at sea and the necessity for refuge from predators. We describe these categories of adaptation below.

Plants on land are large and rooted in the soil, they structure the ambient light environment through foliage density and shade, and they provide lots of cover where animals can hide from predators. In the epipelagic ocean, however, the primary producers are phytoplankton, single-celled algae. Phytoplankton cannot provide cover for oceanic animals because they are too small, and in the water column there are no rocks beneath which animals can hide nor soils into which they can burrow. In the epipelagic zone light is attenuated primarily by the absorption spectrum of water rather than by shade from the primary producers. In the open ocean, quite simply, there is no place to hide from predators.

In the absence of cover, species interactions are governed dramatically by predators, as we learned for ourselves when our University of California (UC), Davis, research group began blue-water diving in Bimini, Bahamas, in 1972. As we observed and collected many types of gelatinous zooplankton in the surface waters of the Gulf Stream, suspended in clear blue water over a sea floor thousands of feet below, we felt vulnerable to large predators. Our first three weeks of blue-water diving were uneventful, but then one morning a large shark suddenly appeared. None of the scuba divers reacted calmly, but instead everyone tried unsuccessfully to get into the boat at once. We subsequently developed better protocols for responding to the presence of sharks.

Just as noted by Elton (1939) for terrestrial animals, a surprisingly limited number of effective antipredatory evolutionary options are also available for oceanic animals. In the open sea there has been convergent evolution for

1. transparency: relatively large (0.5–20 cm), slow, nonvisual, gelatinous animals (e.g., medusae, ctenophores, siphonophores, salps, and pteropods);

2. small size: below visual resolution of the vertebrate eye (less than 0.2 mm; e.g., copepods, appendicularians, fish eggs, and invertebrate larvae);
3. schooling behavior: individuals identical in size and color (2–20 cm, fast and silvery) in schools (e.g., clupeid fishes, small squid, and krill);
4. nekton: fast swimming, large size (20 cm–20 m), and aggressive (e.g., tuna, billfish, sharks, penguins, and seals and other mammals);
5. vertical diurnal migration: relatively fast swimmers, micronekton, intermediate in size (2–10 cm; e.g., euphausiids, midwater fish, and squid);
6. neuston: sea-surface dwellers (e.g., *Physalia* and *Velella*); and
7. “cheaters”: 20–200 cm, slow, conspicuous, armored or tricky (e.g., turtles, *Mola mola*, remoras, and flying fish).

The epipelagic ocean is therefore a rich mixture of transparent zooplankton, microplankton, schooling species, nekton, vertical diurnal migrators, and neuston, but transparent gelatinous animals are by far the easiest group of animals for blue-water divers to study because humans are poorly designed to keep pace with faster swimming animals. Many taxa of relatively large, slow, gelatinous invertebrates are almost always present in blue water near the sea surface. They are protected from fast-swimming predators during the day because most visual predators cannot see them. Blue-water scuba divers can see these creatures by hovering in place, focusing for close-up vision, and looking upward to enhance side- and back-lighting of the organisms against the sea surface. Excellent vision is required to collect effectively in blue-water research. Since many gelatinous zooplankton are unrelated genetically, it is certain that tissue transparency is a highly selected feature and has evolved quite independently in many taxonomic groups via convergent evolution. In the future, we anticipate that additional cladograms similar to that constructed by Johnsen (2001) for tissue transparency will demonstrate that epipelagic transparent animals also have converged evolutionarily for relatively large body size, slow swimming speeds, and reduction of sense organs.

FOOD RESOURCES AND TROPHIC STRUCTURES

In situ scuba observations of feeding behavior and mechanisms have provided many new insights into how epipelagic animals obtain food. Some animals such as thecosome and pseudothecosome pteropods (Gilmer, 1972, 1974) and some medusae, siphonophores, and ctenophores (Swanberg, 1974; Harbison et al., 1978; Matsumoto and Hamner, 1988; Haddock, 2007) can be observed only in situ because they do not behave normally in captivity. Even animals that can be used in lab experiments, such as salps and some medusae and ctenophores, give the best results when collected by divers (Madin, 1974; Hamner et al., 1975 [for prey selection and avoidance], 1987 [for ctenophores]; Matsumoto and Harbison, 1993; Madin and Deibel, 1998). Information on the potentially important role that the

“jelly web” might play in oceanic trophic structure was provided by Robison (2004) and Condon et al. (2011). It should be noted that both laboratory and in situ observations are often required to determine the full suite of feeding behavior. There are behaviors observed in the field that are not typically seen in the laboratory, and if actually observed in the laboratory, they could not have been understood without corroborative field evidence (e.g., foraging behavior); but there also are behaviors observed in the laboratory that are never or infrequently observed in open sea. Recent advances in technology have elicited some very detailed water flow mechanics used for feeding both in the field (Dabiri et al., 2005) and in the laboratory (Colin et al., 2010).

Our observations of epipelagic gelatinous zooplankton using blue-water scuba in the Florida Current and the Gulf of California showed us three trophic levels: grazer-herbivores, primary carnivores, and secondary carnivores (Hamner et al., 1975). These zooplankton constitute a distinct evolutionary assemblage based on shared, convergent attributes of large size, neutral buoyancy, tissue transparency, slow swimming speeds, and tactile sensory abilities, but they also constitute an ecological assemblage that exchanges nutrient resources via competition and predation (Alldredge and Madin, 1982). One of our most unexpected early findings regarding trophic relationships was that, in contrast to a rigidly layered trophic pyramid wherein small herbivorous crustaceans use tiny appendages and fine setae to select and capture a narrowly restricted size of phytoplankton, large gelatinous grazers instead use mucus structures to capture and consume a broad range of sizes and types of food particles across different trophic levels, including algae, live net zooplankton, and detritus. We observed for the first time how mucus sheets, nets, and strands were used to collect, concentrate, and transport food particles by pteropods (Gilmer, 1972, 1974; Lalli and Gilmer, 1989), thaliaceans (salps, doliolids, and pyrosomes; Madin, 1974), prosobranch veliger larvae (R. Gilmer, UCLA, unpub. observation), polychaete larvae (Hamner et al., 1975), and free-swimming appendicularians (Alldredge, 1972, 1976a). These large gelatinous grazers filter commensurately large volumes of water. For example, a single chain of a large oceanic salp, *Pegea confoederata*, composed of 200 individual zooids filters as much water per minute as 90,000 copepods/1,000 m³ (Harbison and Gilmer, 1976). Thus, although not nearly as abundant numerically as net zooplankton, large gelatinous animals are disproportionately effective grazers and predators in the water column.

The use of mucus for food capture by epipelagic grazers, along with phytoplankton aggregations, produces copious quantities of marine snow, a primary mechanism for carbon flux (Alldredge, 1972; Wangersky, 1974; Hamner et al., 1975; Silver et al., 1978; Alldredge and Silver, 1988). Feeding filters and mucus webs become clogged, discarded, and heavy with unwanted materials and feeding wastes, and this material sinks rapidly away from surface waters. These macroparticles can be collected by hand in syringes by divers and used in a variety of studies (Silver et al., 1978; Villareal et al., 1999). The constituents of the marine snow

and associated microbial or invertebrate populations may also be observed. During the 38 years since our description of marine snow in the blue waters of the Florida Current, we have learned much about how microbes process particulate and dissolved organic carbon and transparent exopolymer particles (Allredge, 1989; Allredge et al., 1993). There are more than 1,600 literature entries for marine snow in ISI Web of Science since 1975, but none prior to this, not even the unfortunately ignored initial description of marine snow by Nishizawa et al. (1954).

Recently we have learned that salp-mucus feeding webs can capture an even greater size-range of particulates than we thought initially, including submicrometer particles. According to Sutherland et al. (2010:15129), “Although particles larger than 1 μm (e.g., flagellates, small diatoms) represent a larger carbon pool, smaller particles in the 0.1- to 1- μm range (e.g., bacteria, *Prochlorococcus*) may be more quickly digestible because they present more surface area, and we find that particles smaller than the mesh size (1.4 μm) can fully satisfy salp energetic needs” (see Figure 1). Epipelagic offshore waters are frequently dominated by microplankton that are too small to be captured by mechanical sieving (Riisgård and Larsen, 2010), yet salps apparently can fulfill their entire energetic requirements through an exclusive diet of submicrometer particles, including viruses, bacteria, and colloids. It was known that small copepods are size-specific herbivores, and we knew from observations made while blue-water diving (Hamner et al., 1975) that the much larger salps and pteropods were generalized grazers that fed on particulates that sometimes

differed in size by two to three orders of magnitude, thereby blurring the distinctiveness of discrete trophic levels. We learn now, however, from controlled laboratory and field experiments that “salps and other pelagic tunicates remove particles that are four to five orders of magnitude smaller than themselves, thereby bypassing several trophic levels” (Sutherland et al., 2010:15132).

Direct observations under water have provided exciting and previously unknown details of parasitic or commensal relationships. One of the most common involves hyperiid amphipods and some copepods living on or in a variety of gelatinous hosts (Harbison et al., 1977; Madin and Harbison, 1977; Laval, 1980), and that often rear their broods on the bodies of gelatinous animals (Gasca and Haddock, 2004). These associations rarely are apparent in net-collected samples, yet constitute an important ecological niche occupied by major groups of otherwise nonpelagic crustaceans. Similar behavior is also seen in some juvenile cephalopods and fishes.

There are also many kinds of predatory gelatinous zooplankton in the water column. In our initial blue-water publications from Bimini we described predation by medusae, siphonophores, ctenophores, heteropods, pteropods, and chaetognaths (Hamner et al., 1975). Medusae, siphonophores, and ctenophores feed directly on small copepods via tentacles with nematocysts and colloblasts; some siphonophores consume surprisingly large prey (Pagès and Madin, 2010). Narcomedusae and ctenophores can also specialize, capturing specific types of gelatinous prey, including other ctenophores, medusae, appendicularians, or salps (Harbison et al., 1978; Madin, 1988; Haddock, 2007). In many simple oceanic food pyramids or linear food chains, herbivorous copepods are directly preyed upon by primary carnivores. But chaetognaths also eat copepods, and many medusae, siphonophores, and ctenophores eat chaetognaths, thus feeding as secondary carnivores higher on the food chain. Tuna, flying fish, cod, sea turtles, and albatross (Madin, 1974) sometimes eat salps, and salps capture and consume copepods along with diatoms, yet salps apparently can also consume viruses, colloids, and bacteria (Sutherland et al., 2010). Consequently it is often difficult to assess trophic status at any given time without simultaneous analysis of gut contents.

During the past 38 years we have learned an enormous amount about predatory relationships within the gelatinous epipelagic assemblage beyond our initial observations in the Gulf Stream and Gulf of California (Madin, 1988). It is now clear that the gelatinous assemblage of blue-water zooplankton is not a “dead end” to the flow of energy and materials in the open sea, but instead is a complex, often-changing food web, with surprising and strange trophic interactions and links to everything from the microbial web to fish, whales, turtles, and birds. Gelatinous grazers and predators can sometimes unexpectedly overwhelm entire pelagic ecosystems and become keystone species, such as when a single species of introduced ctenophore ate all the fish larvae in the Black Sea, eliminating most commercial fishing (Kideys, 2002; Ghabooli et al., 2011). Recently it has been shown that blooms of medusa and ctenophores also

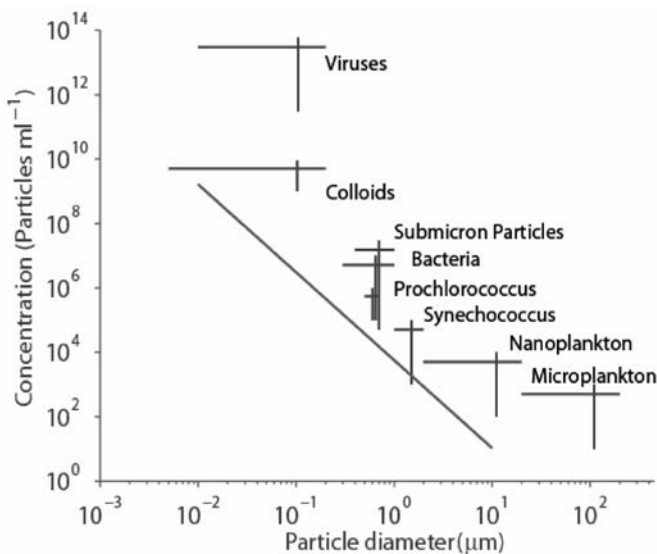


FIGURE 1. Size distribution of living and nonliving particles in the upper ocean, including viruses, colloids, submicron particles, bacteria, *Prochlorococcus*, *Synechococcus*, nanoplankton, and microplankton. Diagonal line is regression of microphytoplankton concentration versus cell diameter.

produce large quantities of dissolved and colloidal organic material that both stimulates and alters the composition of the microbial community, potentially with broad consequences for the biogeochemistry of entire habitats (Condon et al., 2011).

BEHAVIOR

Blue-water diving allows observation of many aspects of behavior, one of the most obvious of which is locomotion. Although the word plankton means “drifting,” in fact zooplankton, including most gelatinous taxa, can swim by various means. Swimming behavior can be difficult to study in the laboratory because confined tank volumes and the delicate construction of many species often lead to artifacts of behavior and misleading observations or measurements. Constraining animals with tethers and other devices to restrict their movements, while effective for small, hard-bodied forms like copepods, is usually impractical with larger gelatinous animals and can create problems with natural fluid flow. Tanks large enough to minimize these effects make it hard to observe animals closely.

Direct observations by divers at sea are preferred to ensure accurate documentation of swimming behavior, but these can be difficult to obtain under uncontrolled field conditions. The tethered-diver safety system for blue-water scuba allows divers to maintain good visual distance and continuous visual contact with a subject animal without disturbing them, but this is only effective for fairly large and slow-swimming species. Besides by direct visual observation, behavior can be recorded on video and fluid flow visualized with dye tracers (Madin, 1990; Sutherland and Madin, 2010). Estimates of swimming speed in situ have been made by timing the transit of animals over known distances, measured with depth gauges or by marking start and end points with dye and measuring distance (Madin, 1990); fluid flow patterns and rates can be measured from video of dye traces (Sutherland and Madin, 2010). Recently the development of a Self-Contained Underwater Velocimetry Apparatus (SCUVA; Katija and Dabiri, 2008) makes possible in situ digital particle image velocimetry measurements that provide information on swimming energetics.

Medusae were thought to swim by jet propulsion but work by Costello, Colin, and colleagues (Colin et al., 2003; Costello et al., 2008) has shown that there are different modes of fluid manipulation by different species that combine jetting with swimming and feeding currents created by the “rowing” action of the bell margin. Early studies of siphonophore locomotion (Mackie, 1964) were made in aquaria, with subsequent lab and field studies by Purcell (1980, 1981). Swimming of ctenophores has also been studied in tanks, but the size and fragility of many lobates and cestids makes in situ observations critical (Harbison et al., 1978; Matsumoto and Hamner, 1988; Matsumoto and Harbison, 1993). While some early studies of swimming by salps were done only in lab tanks (Bone, 1984), later studies combined lab and field observations and measurements to observe both small- and large-scale aspects of swimming behavior by single salps and

chains of various species (Madin, 1990; Sutherland and Madin, 2010). Blue-water diving also enables study of complex swimming behavior of animals relative to their environment or in schools or swarms.

Complex behavior of the moon jellyfish (*Aurelia aurita*) was investigated using scuba in Saanich Inlet, Vancouver Island, British Columbia, Canada (Strand and Hamner, 1988; Hamner et al., 1994). Dense swarms of *Aurelia* can be found in Saanich Inlet in late summer. Jellyfish dispersed across Saanich Inlet at night via tidal currents, but when direct sunlight hit the water in the morning the medusae began to swim horizontally at the surface and directionally to the southeast, producing massive swarms along the southeastern sides of the fjord in the afternoon. Jellyfish that had greater distances to swim also swam directionally southeast in the afternoon, demonstrating that horizontal navigation is controlled by a time-compensated sun compass. When the jellyfish reached the sides of the fjord, they ceased swimming horizontally and instead swam vertically, and thereafter male medusae released sperm strands into the water column. The dense swarms of *Aurelia* in Saanich Inlet, therefore, are breeding aggregations, something that could only have been determined from direct observations via use of scuba. Similar swarms of moon jellies with trailing sperm strands have been seen in the waters off California (G. Matsumoto, Monterey Bay Aquarium Research Institute, pers. obs.).

TAXON-SPECIFIC OBSERVATIONS

A broad diversity of organisms have become gelatinous as they evolved to live suspended in the water column. These span a taxonomic range from single-celled organisms to large jellies and colonies of tunicates. Many larvae of fish, worms, mollusks, and others also spend a portion of the life cycle as semitransparent meroplankton.

Macroscopic protists, such as radiolarians and foraminifera, and other protists, such as the giant dinoflagellate *Noctiluca*, can reach high numbers in surface waters. Radiolarians and foraminifera are amoeboid but bear siliceous (radiolaria) or calcareous (foraminifera) “shells” or spicules. Some of these feed by snagging marine snow on spicule tips, where it is enveloped by the cell membrane. Inactive particles and live microzooplankton also adhere to the sticky surface of the cell membrane. *Noctiluca* feeds with an external mucus web (Omori and Hamner, 1982). Shallow polycystine radiolarians contain algal symbionts, and while their molecular phylogeny has been examined (Amaral Zettler et al., 1997), little is known of their ecological impact (Swanberg, 1983). Some species are small enough to be collected with syringes, while other colonial forms (often mistaken for egg masses) may reach a meter in length. These gelatinous colonies trap small zooplankton like copepods on their surfaces, and digest them within vacuoles. Yet at the same time, hyperiid amphipods of similar size roam freely over the colonies as commensals. The observation and collection of these colonial radiolarian in situ has only been possible with blue-water diving. Foraminifera

are important indicators of past climate change. Their shells hold a record of the isotopic composition of the seawater in which they were formed, and thus they are of great interest to paleo-oceanographers. Divers have collected live forams in snap-cap vials so they can be cultured and studied in the laboratory (Spero et al., 1997).

Many planktonic cnidarians, principally hydromedusae, have been investigated in the field, collected using scuba, and studied further in the laboratory (Colin et al., 2003; Costello et al., 2008). Siphonophores, fragile colonial forms that are rarely seen intact, are especially suitable for blue-water collection (Biggs et al., 1986) and have contributed to a recent molecular phylogeny of this group (Dunn et al., 2005). Hydromedusae, smaller scyphomedusae, and cubozoans are all readily collected in jars; larval anemones (particularly cerianthid larvae) and larval corals may be encountered.

Comb jellies are among the most fragile gelatinous zooplankton. Only the hardiest species, such as *Pleurobrachia* and *Beroe*, could be found in plankton net collections or were figured in older textbooks. Scuba divers, however, now collect even the most fragile of lobate and cestid ctenophores by hand in individual jars, and ctenophores collected through blue-water diving have revealed new facets of their ecology (Swanberg, 1974; Harbison et al., 1978) and molecular phylogenetics (Podar et al., 2001). Rarely seen forms sometimes appear common to blue-water divers; many new species have been discovered in surface waters (Madin and Harbison, 1978; Matsumoto, 1988).

Pelagic tunicates (salps, doliolids, pyrosomes, and appendicularians) feed directly at low trophic levels, demonstrate rapid population explosions, and form an important component of many highly productive food webs (Madin, 1974; Alldredge, 1977). While many salps are hardy enough to be enumerated from plankton tows, their physiology and ecology is difficult to study without in situ observation and hand-collected live specimens for laboratory experiments. Doliolids are even more fragile and difficult to maintain in the laboratory (Madin and Deibel, 1998). Appendicularians (also called larvaceans) build elaborate feeding webs (or “houses”) that, until recently, could only be observed in situ (Alldredge, 1976b; Deibel, 1986). A few species of appendicularians have been successfully cultured (Paffenhöfer, 1973; Fenaux et al., 1986), but the great majority of species are poorly known and not amenable to laboratory observation.

Pelagic mollusks, such as pteropods, heteropods, and nudibranchs, have been investigated using blue-water scuba techniques. Pteropods (*Limacina*, *Corolla*, and *Clione*) may occur in large numbers, along with diverse species of heteropods and other pelagic mollusks (Lalli and Gilmer, 1989). Holoplanktonic nudibranchs such as *Phylliroe* prey on planktonic cnidaria. Ommastrephid squid may occasionally be observed with their large gelatinous egg masses (Staaf et al., 2008).

Arrow worms (phylum Chaetognatha) are sometimes large enough to be observed by divers. They are among the most important net zooplankton predators, feeding particularly on copepods. A diverse array of polychaetes are found both free-living

and in association with other gelatinous plankton. Alciopid polychaetes, for example, are often predators or parasites of ctenophores.

Open-ocean adult fish, such as the sunfish *Mola mola*, as well as sharks, billfish, and some schooling pelagic species, can be occasional, charismatic visitors during scuba dives in blue water; larval fish are frequently encountered at night. In addition, some pelagic fish hide behind the veil of large gelatinous species such as scyphomedusae or the siphonophore *Physalia*.

EPIPELAGIC POLAR OCEANS

In polar regions, the light regime of the epipelagic zone differs from that in all other parts of the ocean. Instead of experiencing a diurnal light/dark regime, surface waters at high latitudes remain sunlit for most or all of a 24-hour day in summer, and the opposite in winter. Polar oceans are also unique in that sea ice provides cover for epipelagic organisms, year-round in the Arctic and seasonally in the Antarctic. We have used blue-water scuba extensively in the open sea in the Antarctic, Arctic, and subpolar oceans to investigate epipelagic euphausiids, salps, ctenophores, and medusae, but we have been able to study euphausiids near the sea surface during the day only in polar oceans. “In polar oceans in summer, diurnal vertical migration [is not necessarily advantageous] . . . for an herbivore such as *Euphausia superba* because all phytoplankton production occurs quite near the surface and pelagic herbivores either feed there or they starve. Rather than swimming down into deep water to evade predators, *Euphausia superba* engages in schooling behavior in the epipelagic zone, . . . electing a modal survival strategy that is quite different from the diurnal vertical migratory solution so effective for most tropical euphausiids. Thus, when the temporal periodicity of the 24-hour light environment changes, so must the nature of the convergent adaptive solutions change to permit survival in an illuminated, three-dimensional environment devoid of cover” (Hamner, 1995:75).

For behavioral research on Antarctic krill *Euphausia superba* near the Antarctic Peninsula, we used tethered, blue-water scuba protocols modified for dry-suit diving (Hamner, 1982). In most parts of the world euphausiids are vertical diurnal migrants, near the surface only at night, but surface schools of Antarctic krill had been seen previously in summer at the surface by Hardy and Gunther (1935) around the docks at South Georgia Island and by Marr (1962) from aboard ship; density of krill in schools was estimated at about 64,000/m³ (1 krill/in³), which was later confirmed photographically under water via scuba by Raguin (1969), Hamner and colleagues (Hamner et al., 1983; Hamner, 1984a), and O’Brien (1987). These observations of schooling behavior by Antarctic krill are of central importance for understanding the ecology of the entire Antarctic water column (Hamner et al., 1983; Hamner, 1984b; Hamner and Hamner, 2000).

The behavior of *Euphausia superba* changes during ontogeny from a dispersed solitary larva to larvae clumped within

swarms and then to uniformly polarized furciliae close-packed into schools. We directly observed this behavioral transition for krill larvae in the Gerlache Strait, Antarctica, while blue-water diving (Hamner et al., 1989). In open ocean without sea ice, isolated furciliae at the surface were at very low densities (0.003/m³). In the presence of sea ice, individual, free-swimming furciliae were more abundant (0.3/m³), but tiny schools of furciliae also were found below the sea ice at densities of about 3 × 10⁹/m³. Sea ice provides larval krill with concentrated epontic algal food and protection from predators, and it facilitates formation first of swarms of nonpolarized individuals and then of small, ice-oriented polarized schools. “*Euphausia superba* makes an abrupt behavioral transition after the last larval molt from an individualistic, planktonic lifestyle to that of a highly social, nektonic juvenile. Then and throughout the rest of its life, most aspects of krill behavior are expressed within the context of highly organized, polarized schools” (Hamner and Hamner, 2000:192).

The large cydippid Antarctic ctenophore *Callianira antarctica* captures and digests Antarctic krill. Near the Antarctic Peninsula we saw ctenophores with feeding tentacles fully extended and with partly digested krill in their guts, but only when there were no krill schools in the immediate vicinity, although krill were clearly nearby as evidenced by krill acoustic signatures and krill fecal pellets and molts in the water column (Hamner and Hamner, 2000). When *C. antarctica* was seen within krill schools, ctenophore guts were empty and fishing tentacles were completely retracted. *Callianira antarctica* captures prey with colloblasts and stretchy tentacles that reel in prey one at a time, which often takes several minutes. Schooling, therefore, protects most krill from *C. antarctica* because it is physically impossible for cydippid ctenophores to fish with delicate, extended tentacles within schools of tens of thousands of krill/m³.

At least one large lobate ctenophore, probably a new species in the genus *Eurhamphaea*, has been observed and collected by blue-water divers in the Antarctic. This species also appears to be a predator on krill or their larvae. Also present is *Beroe cucumis*, the species that preys on other ctenophores and attains a size of 25 cm in the Antarctic. In the Arctic, the cydippid *Mertensia ovum* occupies a similar niche to *Eurhamphaea*'s, but preys on large copepods as well as krill (e.g., Matsumoto, 1991; Swanberg and Bamstedt, 1991). *Mertensia ovum* appears to store lipids derived from crustacean prey in numerous droplets contained within the mesoglea, presumably as an energy store (Larson and Harbison, 1989). Other ctenophores observed by diving in the Arctic include *Bolinopsis infundibulum*, which attains a size of 20 cm or more, *Beroe cucumis*, and *Dryodora* (Purcell et al., 2010).

Pelagic tunicates have an unusual asymmetric distribution in polar seas. While appendicularians are common in the Arctic, salps are absent (Deibel and Daly, 2007), yet salps are extremely abundant in the Southern Ocean where they often alternate with krill as the dominant grazing species (Loeb et al., 1997; Atkinson et al., 2004). The dominant species of salps in most of the Southern Ocean is *Salpa thompsoni*, with smaller populations of the very similar *S. gerlachei* reported nearer the Antarctic continent.

Two other species, *Ihlea racovitzai* and *I. magalhanica* also occur in the region, but usually in smaller numbers. Three of these species appear restricted in distribution to south of the Antarctic Convergence, with *I. magalhanica* found in the vicinity of the Falkland Islands. Blue-water divers have provided material for studies of salp energetics and fecal pellet production (Phillips et al., 2009).

CONCLUSIONS

Although study of gelatinous animals of the plankton began in the nineteenth century when naturalists like Chun, Mayer, and Bigelow dipped specimens from the sea, major progress in understanding the functional morphology, behavior, and ecological roles of these organisms has depended on the ability afforded by blue-water diving to observe and collect gelatinous fauna from their natural oceanic environment. Blue-water diving is simply field biology carried out in a field that has become accessible with scuba in the last four decades. It has allowed biologists to do the kind of research that was done a century ago on land, but in one of the largest and least known habitats on Earth, populated by diverse, abundant, and largely unknown animals. While the method has clear limitations, it is a powerful complement to other approaches to the study of open-ocean organisms, and deserves to be more widely used by a new generation of oceanographers. In addition to its value as a means of observing, collecting, and experimenting with planktonic animals in situ, blue-water diving gives oceanographers and marine biologists a personal, immersive experience of the nature of the open ocean environment that cannot be achieved by towing nets, looking at instrument readouts, or even watching video from an ROV. We believe this is a valuable experience for all ocean scientists.

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