

Deep pelagic biology

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Abstract

The deep pelagic habitat is a vast volume of cold, dark water where food is scarce and bioluminescence is the principal source of light and communication. Understanding the adaptations that allow animals to successfully inhabit this daunting realm has been a difficult challenge because investigators have had to conduct their work remotely. Research in the deep water column is going through an essential transformation from indirect to direct methods as undersea vehicles provide unprecedented access, new capabilities, and new perspectives. Traditional methods have accurately documented the meso- and macro-scale zoogeographic patterns of micronekton and zooplankton, as well as their distribution and migration patterns in the vertical plane. The new in situ technologies have enabled advances in studies of behavior, physiology, and in particular, the role of gelatinous animals in deep pelagic ecology. These discoveries reveal a deep-water fauna that is complex and diverse and still very poorly known.

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1. Introduction: the habitat

The waters that fill the ocean basins constitute the largest living space on Earth. This vast habitat is home to the largest animal communities on the planet—largest in terms of biomass, in numbers of individuals, and in areal extent. Despite its obvious significance to the biosphere, and more than a century after the return of the Challenger Expedition, the ocean's deep interior remains an unexplored frontier, more than a billion cubic kilometers of living space “that we have barely looked at and do not understand” (Kunzig, 2003). Within this volume there may be a million undescribed species, with biological adaptations and ecological mechanisms that we cannot yet imagine.

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The physical and chemical properties of the oceanic water column show considerable variability within the upper kilometer but at greater depths they remain relatively constant. Conditions in the horizontal plane are spatially homogeneous and have been very stable over time. Patterns of seasonal and latitudinal variability seen at the surface are usually dampened with increasing depth.

The near-surface wind-mixed upper layer of the ocean is thickest at low latitudes and diminishes toward the poles. Below the mixed layer, temperature drops sharply and the great majority of the deep water column is very cold, typically between 0 and 6 °C. Likewise, salinity ranges only from 34.6 to 34.8 psu throughout most of the deep habitat. Hydrostatic pressure increases linearly with depth and, among other effects, it influences the solubility of gases. At depths below about 1 km pressure begins to affect the ability of animals to extract carbon dioxide for making calcium carbonate. Increased pressure also makes it more difficult to extract oxygen for respiration. Enzyme activity is probably affected by increasing pressure as well.

Oxygen content decreases below the mixed layer and it shows considerable geographic and sometimes seasonal variability. In upwelling regions such as the eastern tropical Pacific, the Arabian Sea, and the eastern tropical Atlantic, high productivity at the surface leads to elevated levels of organic carbon at depth, where microbial respiration removes the oxygen. Oxygen concentrations can drop to less than 2% of saturation in these layers, which may extend to depths of 1 km or more. Oxygen depleted zones have dramatic effects on the horizontal and vertical distributions of most midwater species, and some support only a highly specialized fauna.

At night, the light regime of the entire deep pelagic habitat is limited exclusively to bioluminescence. During the day, sunlight decreases exponentially with depth and by the time it reaches 150 m, more than 99% of the light entering the surface has been scattered and absorbed. Only the blue wavelengths penetrate to this level. As depth increases the axis of illumination becomes more vertical and the remaining light becomes highly directional. Scattering makes the dim light at depth diffuse, softening the edges of images and reducing contrast. Despite the profound darkness of the habitat, light is an important factor in structuring vertical zonation and in communication. Deception and visual trickery are common at depth among predators and prey alike.

Particles of marine snow are widespread throughout the water column in most of the geographical regions that have been examined, with overall abundance clearly correlated with surface productivity. While much of the material is refractory, a significant portion harbors populations of luminous bacteria that produce light upon mechanical stimulation. The result is that movement in these depths may trigger bioluminescence in the surrounding water that could give away the location of a moving animal. This may be a factor selecting for reduced activity at depths where sunlight is substantially diminished. Particle density (but not bioluminescence) increases in the boundary layer near the sea floor, largely due to re-suspension of sedimented material.

In general, biomass in the deep water column reflects the annual level of productivity at the surface. Primary productivity, and thus deep pelagic biomass, varies geographically with continental margins and upwelling areas the richest, and central gyres the poorest. Seasonal variability increases with increasing latitude. In any region, biomass decreases with depth as the supply lines to the base of the food web get longer. Species diversity also

decreases with depth and, in the horizontal plane, diversity decreases with increasing productivity (Angel, 2003).

2. Methods: a brief history

What we know about something is usually a function of how we learned it, and the evolution of our understanding of deep pelagic biology is strongly linked to the technologies that have been employed to investigate this difficult habitat. During the Challenger Expedition midwater animals were collected by benthic sampling gear as it traversed the water column on its way to and from the deep seafloor. At the time there was little recognition that a separate, deep pelagic fauna existed and even Charles Wyville Thomson, the Expedition's leader, opined that "there is every reason to believe that the fauna of deep water is confined principally to two belts, one at and near the surface and the other on and near the bottom; leaving an intermediate zone in which larger animals, vertebrate and invertebrate, are nearly or entirely absent" (Kunzig, 2003).

Subsequent expeditions sampled the ocean's interior with modified benthic gear such as otter trawls or with plankton-sampling ring nets. In 1951 the Isaacs–Kidd midwater trawl was introduced and it quickly became the standard collecting tool for midwater animals. The desire for discrete-depth samples led to the development of mouth-closing nets like the Tucker Trawl and Rectangular Midwater Trawls, which evolved into multiple net systems like the MOCNESS. Trawling gear samples the water column selectively, with a bias for firm-bodied fauna like micronektonic fishes and crustaceans. The condition of specimens collected by trawling and their suitability for physiological and behavioral studies after capture was greatly enhanced by the advent of closing cod ends (Childress et al., 1978). These devices are typically activated by the closing of the net mouth and they insulate the catch from light, turbulence, and temperature change during retrieval.

The vertical resolution of most closing nets is about 5 m and they have served well to determine the vertical range, distribution, and migration patterns of micronekton and crustacean zooplankton, thus revealing much of the basic spatial arrangement of midwater communities in the vertical plane. In contrast, midwater trawls integrate samples in the horizontal plane so their resolution is seldom less than a kilometer, which obscures patchiness and interspecific associations. However, accumulated trawling data reveals that on an ocean basin scale, the distribution of individual species and communities of midwater animals conform to the boundaries of the principal oceanic water masses (Backus et al., 1977).

After the Second World War, sonar became available as a tool for profiling biological targets in the water column. Shipboard acoustics provide sound scattering density data as a horizontal series of vertical slices through the water column. Thus its resolution of relative biomass in both the horizontal and vertical planes is quite good. However, acoustic methods typically lack the ability to enumerate individual animals or to distinguish between most species. Different species and even different individuals of the same species may require distinct frequencies to provide reliable target data. Together, nets and sonar show that diel vertical migrations by zooplankton and micronekton are global-scale, mass feeding forays into the productive euphotic layers when the sun is down (Pearcy et al., 1977).

Trawling and acoustic methods complement each other and when used in conjunction they can provide reliable data on horizontal and vertical, microscale distribution patterns. When multiple frequency acoustic systems are integrated with nets and with optical systems, it is possible to resolve zooplankton biomass and their patch-scale, three-dimensional distribution patterns with great precision (Greene et al., 1998; Benfield et al., 1998).

The most significant technological advance in deep pelagic research since the advent of sonar has been the development of undersea vehicles capable of working freely in the water column. The first research submersible was the Bathysphere, used by William Beebe to explore deep water off Bermuda in the early 1930s. Since that time a diverse group of manned and unmanned vehicles has evolved (Robison, 2000). These research platforms provide new kinds of data and information that could not be acquired through the traditional technologies of nets and acoustics. HOVs (human occupied vehicles) and ROVs (remotely operated vehicles) offer the advantage of direct access to the habitat. This allows in situ observations and surveys of deep-living animals in the context of their natural habitat, as well as the ability to conduct experimental work. This new perspective enables studies of behavior, the interactions between species, in situ physiological measurements, and the gentle capture of specimens for long-term maintenance (NRC, 2003).

For those who built their concepts of midwater ecology on samples and data from net tows and acoustics, the first deep dive with an HOV or ROV can be a startling experience. There are more animals, more particles, more spatial structure, more ecological organization, and more activity than anyone expects (Robison, 1995). By using high-resolution video systems, vehicle-based surveys can be as quantitative as those conducted by nets, and they can resolve spatial distribution patterns at centimeter-scales. For gelatinous animals and other fragile species these platforms are the only means of accurate assessment, because they do not destroy the specimens being measured. A third class of vehicles, AUVs (autonomous underwater vehicles), lack the advantages of real-time control and direct observations but they can be programmed to conduct large-scale surveys, store data, and potentially, to follow individual constituents of the midwater fauna or their aggregations, through their daily ambits.

3. Ecological structure and dynamics

3.1. Comparative studies

Experimentation is fundamental to modern science, yet the scale and scope of most oceanic processes are such that they are not subject to experimental manipulation by researchers. In response, we have learned to seek out places where naturally occurring variations in basic environmental parameters can reveal, through comparison, how these parameters affect the biological processes we wish to study. By working in distant or different waters we can take advantage of natural experiments.

For example, like their counterparts at lower latitudes, Antarctic midwater fishes make extensive diel vertical migrations. However, conditions in these southern waters differ

significantly from those in most other regions. Antarctic species make their vertical migrations in the absence of two of the three selective advantages generally attributed to this behavior. First, because the water column is nearly isothermal, there is no metabolic gain to be derived from moving down into colder water after feeding. Second, because their prey, *Euphausia superba* Dana, do not perform significant vertical migrations themselves, the fish migrations act to diminish rather than enhance their feeding opportunities. For Antarctic midwater fish, the sole advantage of these migrations appears to be the avoidance of visually cued predators in the upper part of the water column. The observation that predation pressure alone can drive these fish away from their food source, even when the nights, and thus their opportunities to feed, are very short, is strong evidence that it may also be the principal factor in the diel migrations of fish at lower latitudes as well (Robison, 2003).

Trophic structure and niche characteristics can be examined by comparing the faunal composition of communities in different water masses. Off the coast of western Mexico and southern California the stomiid fish *Stomias atriventer* Garman extends north to Point Conception. Within this range it has a vertical distribution between 100 and 800 m, where it feeds chiefly on vertically migratory fishes and crustaceans. From central California up to the Gulf of Alaska, another stomiid, *Tactostoma macropus* Bolin occupies the same depth range and feeds on the same type of prey. There is very little overlap of their horizontal ranges and the two species rarely co-occur in net samples. The principal environmental differences between the two zoogeographic regions they inhabit are greater temperatures, lower oxygen concentrations, and higher species diversity within the range of *S. atriventer*. Similar patterns of counterpart replacement by related species are common. They tell us that similar niches exist within many midwater communities and thus that their basic ecological structure is conservative.

In the eastern North Pacific, *Stomias* and *Tactostoma* co-occur with two other abundant, stomiid fishes, *Idiacanthus antrostomus* Gilbert and *Chauliodus macouni* Bean, both of which are unaffected by the apparent zoogeographic boundary near Point Conception. Within their combined ranges these four species define and dominate a mesopelagic feeding guild that includes perhaps a dozen other stomiid species to the north and twice that number to the south. In striking contrast are the highly speciose stomiid assemblages reported from warm-water, oligotrophic regions like the eastern Gulf of Mexico, and the waters around Hawaii (Sutton and Hopkins, 1996). These patterns reflect the general tendencies for species diversity to decrease with increasing latitude and to increase with decreasing productivity.

In much of the eastern North Pacific, appendicularians with large, delicate feeding filters and small, crustacean-eating siphonophores are common components of the pelagic fauna. In deep water around the Galapagos Islands, these animals are rare. In their places are a holopelagic holothurian, *Pelagothuria natatrix* Ludwig, and a yet-to-be described cirrate octopus. Because of nutrients supplied by runoff, the islands create an oasis of pelagic productivity in an otherwise oligotrophic region. However, the islands are swept by strong currents year-round and zooplankton that are weak swimmers are not able to hold station within the plume of productivity that develops in the islands' downstream wake. Apparently, strong swimmers fill the niches in this habitat that can be occupied by poor swimmers in other regions. Here again is evidence that similar niches exist in

different regions but that localized environmental conditions determine the species that fill them.

3.2. Time-series studies

The natural variability of populations of deep pelagic species can be investigated with time-series studies in a single location. In Monterey Bay, seasonal upwelling initiates an annual cycle of phytoplankton productivity. Over several years, a regular series of quantitative video transects made by an ROV showed clear-cut, repeating correlations of siphonophore abundance with ecological factors that accompany upwelling episodes. Three siphonophore species that feed on herbivorous crustaceans, have annual peaks in abundance that occur two to three months after the onset of regional upwelling (Fig. 1). These lag periods in siphonophore population growth are linked to the time that their prey populations need to respond to the increase in upwelling-induced productivity. This seasonal ecological pattern of predator and prey dynamics is significantly correlated with the annual cycle of physical factors (Robison et al., 1998; Silguero and Robison, 2000). Variability associated with non-seasonal events, such as the El Niño Southern Oscillation typically consists of ratio shifts in the relative abundances of resident species, as well as the appearance of species not normally found within a given region (Raskoff, 2001).

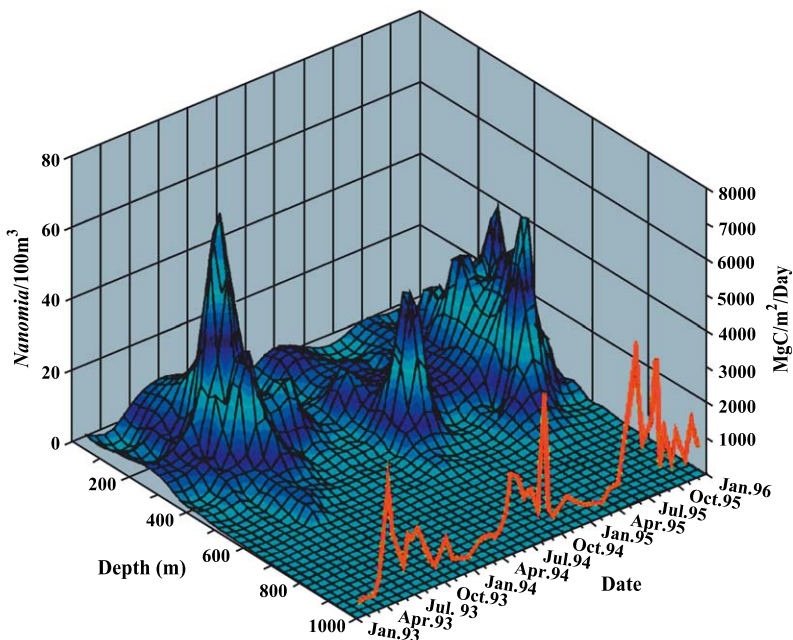


Fig. 1. Abundance and depth distribution of *Nanomia bijuga*, and primary productivity in Monterey Bay from 1993 through 1995 (Robison et al., 1998).

3.3. The jelly web

One of the principal ecological advances enabled by undersea vehicles has been the discovery of a large and complex gelatinous fauna in deep water. As much as a quarter of total pelagic biomass may be incorporated into the bodies of these animals and they can seasonally dominate the second and third trophic levels of midwater communities. This fauna was substantially undersampled by conventional methodologies and with the advent of undersea vehicles a great many new taxa have been described (Madin and Harbison, 1978; Hopcroft and Robison, 1999; Matsumoto et al., 2003).

Gelatinous zooplankton constitute a major infrastructural component within the midwater food web in Monterey Bay, CA. Grazing salps, doliolids, appendicularians (larvaceans), and the aberrant pelagic polychaete *Poeobius meseres* Heath ingest both phytoplankton and marine snow, with the ratio favoring snow as depth increases. Salps and doliolids have wide vertical ranges because their feeding structures are internal and the water they pump through their bodies for feeding can also be used for propulsion. Appendicularians, with external feeding filters, are far less mobile and tend to be stratified in species-specific patterns, partitioning the water column according to its characteristics of particle type and density. *Poeobius* is widely distributed in the vertical plane and uses its tentacles to gather snow particles and material that accumulates on mucus strands.

A distinct advantage of using HOVs and ROVs for trophic studies is that a large percentage of the gelatinous fauna is transparent, making it possible to directly observe what has been ingested, as well as to see what has been captured by tentacles. Gelatinous predators, including siphonophores, ctenophores, and medusae feed on two distinct types of prey: crustacean grazers (e.g. copepods and euphausiids), and other gelatinous animals (both grazers and carnivores), albeit with considerable selectivity. Two general feeding strategies are common to each of these predator groups—active hunters and passive trappers. Among siphonophores the smaller taxa tend to be batch feeders, with active feeding strategies specialized for finding patchily distributed crustacean prey. The largest siphonophores are typically passive predators that rely on the movements of their prey to initiate contact and capture. As a result they feed on a more diverse range of prey types.

Among ctenophores the beroids are active predators that feed principally on other jellies. Cydippid and lobate ctenophores generally have more passive strategies; tentaculate cydippids are specialized to capture crustaceans while the lobates are more likely to be generalists. Medusae also show both active and passive feeding strategies and some species show prey specialization. Size-related trends or patterns operating above the species level are not yet apparent. In contrast to the pattern in siphonophores, active medusae generally have broader diets than do the ambush species. Chaetognaths comprise the fourth major group of gelatinous predators. They are abundant ambush predators that prey chiefly on crustacean zooplankters.

These patterns of interaction and organization reflect a highly complex and dynamic ecological structure that exists within and beyond the boundaries of our conventional understanding of the midwater food web. However, the nature and extent of the gelatinous

portion of the web has been seriously underestimated and our understanding is still incomplete. Data from a 10-year, ROV-based quantitative time series of video observations and transects in Monterey Bay, have begun to shed light on this section of the overall community (Fig. 2). Nutrient energy enters the jelly web through two principal pathways: crustacean and gelatinous grazers. Both groups of grazers are consumed by a variety of gelatinous predators, which are themselves consumed by other gelatinous predators. A significant fraction of pelagic biomass is sequestered in the bodies of these gelatinous animals but its residence time and fate beyond the third and fourth trophic levels of the web are still largely unknown.

One key to the proliferation of gelatinous animals in midwater, particularly the larger forms, is the reduction of shear forces at depths below the mixed layer (Osborn and Barber, 2004). This physical factor allows the production of expansive, yet fragile bodies (Fig. 3) and large feeding structures such as those produced by giant appendicularians (Hamner and Robison, 1992). Large size enhances feeding success by increasing the capture rate of prey and particles. The increase in size is achieved by producing tissue of dilute organic biomass, which offers little appeal as food value for potential predators. The adaptive value of this approach is further enhanced because the advantages of size are achieved without a comparable increase in metabolic demand. Thus the physics of the

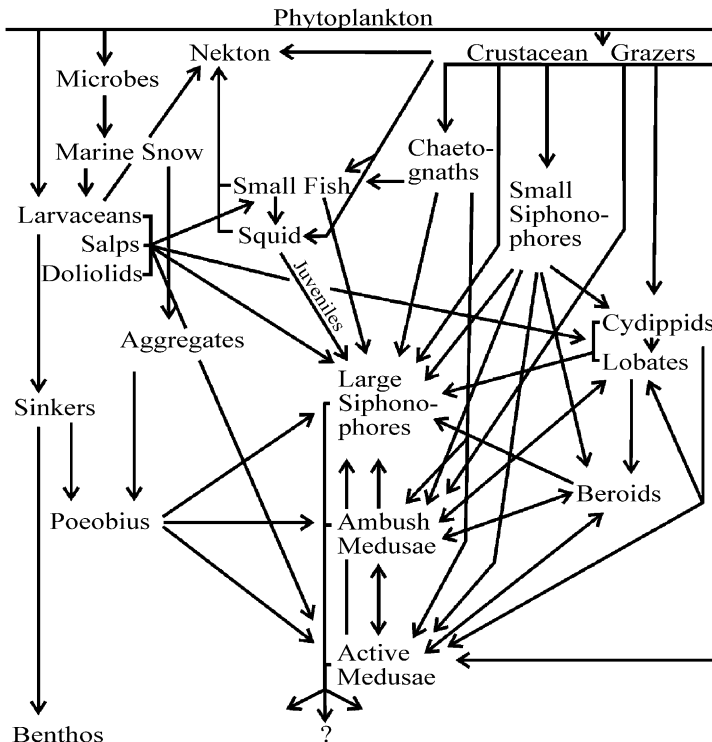


Fig. 2. Diagram of the trophic links of gelatinous animals in the water column of Monterey Bay.

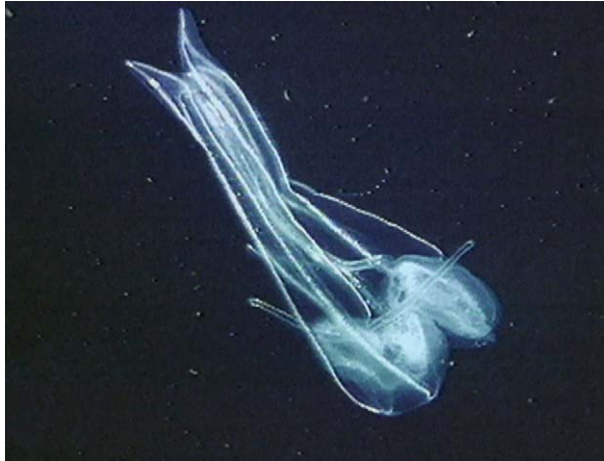


Fig. 3. Video frame grab of *Kiyohimea usagi* Matsumoto and Robison, a large, delicate, lobate ctenophore so fragile that it has never been collected intact.

ocean's deep interior encourages body forms and feeding structures that would be impractical and are thus uncommon at lesser depths.

4. Physiological adaptations

Depth-related morphological differences were readily apparent when the first deep pelagic specimens were hauled up by nets. Compared to their shallow-living counterparts the animals seemed frail, with watery tissues and flimsy bodies. These observations were subsequently confirmed by compositional analyses that showed thinly ossified bones among deep-living fishes and reduced protein and lipid levels among both fishes and crustaceans. When living specimens from increasingly greater depths are compared, measurements of their respiration rates show a much greater decline than could be predicted from Q_{10} temperature relationships alone. The activity levels of enzymes such as citrate synthase (CS) and lactate dehydrogenase (LDH), used as indicators of metabolic rates, also decline significantly with depth. In contrast, gelatinous animals such as medusae, chaetognaths, pteropods, and worms exhibit no significant reduction of metabolism with increasing depth (Childress, 1995; Thuesen and Childress, 1994).

The depth-correlated physiological trends in midwater fishes, crustaceans, and cephalopods have been attributed to lower temperatures, reduced food levels, increased pressure, reduced oxygen content, and decreased light levels at greater depths. Studies designed to investigate the roles of these factors in metabolic declines, compare the covariant environmental factors, in locations or circumstances where they can be separated from depth. Again, using naturally occurring variations in key factors to substitute for experimental manipulation.

For example, in Antarctic waters, where the water column is virtually isothermal, deep-living micronekton still have lower metabolic rates, just like those who live where

temperature decreases significantly with depth. Food availability appears not to be the responsible variable because counterpart species at comparable depths in areas of high and low surface productivity, show no significant differences in metabolic rates. Hydrostatic pressure is not implicated because metabolic rate, measured directly and as indicated by enzyme activity (both CS and LDH), does not change with depth in gelatinous animals. In the case of oxygen, measured metabolic rates are lowest at depths beneath the oxygen minimum layer, not within it (Childress, 1995).

Several lines of evidence suggest that the decrease in metabolic rate with increasing depth is largely due to a reduced need for locomotory capabilities associated with visually cued predator/prey interactions. Near the surface, ambient light levels are adequate for vision at a distance, and predator/prey responses are often based on locomotion triggered by vision. As the light levels decline with increasing depth, alternative strategies emerge and locomotory capacity becomes less valuable. Downwelling light and metabolic rate both decline exponentially with depth through the upper kilometer of the water column. Below that level the light is gone and the decline in metabolism stops (Seibel et al., 2000, 1997; Childress, 1995). Gelatinous animals, the exception to the pattern, rely on transparency rather than locomotion to avoid detection by their sighted predators and prey. Typically, they also lack image-forming eyes.

Most measurements of the metabolism of deep pelagic animals have been made on specimens captured at depth and then brought to the surface for study. In situ measurements eliminate the problems associated with pressure and temperature change during retrieval but are inherently more challenging to conduct remotely. In most cases, measurements made at depth appear to be roughly comparable to those made at the surface (Smith and Laver, 1981; Smith, 1978). However, decompression has been shown to have a substantial effect on gelatinous animals, with in situ respiration rates two to five times higher than those measured at the surface (Bailey et al., 1994).

5. Behavior

Direct observations from undersea vehicles, have greatly improved our ability to study and understand the behavior of deep pelagic animals. In the 1960s Eric Barham (1963, 1971) investigated the behavior of animals that comprised sonic scattering layers and provided the first in situ descriptions of their activity and orientation. As access to the habitat has increased, the range of behavioral observations has expanded, from escape responses and defensive behavior, to predator tactics, aggregation patterns, and reproductive behavior.

In the stillness of the deep habitat, activity levels are generally low between the crepuscular periods of vertical migration. This is probably a result of several factors. Movement usually triggers bioluminescence from particles in the surrounding water and contact with most of the resident fauna also stimulates light production. Energy conservation where food is scarce and the physiological constraints of low oxygen also encourage inactivity. As a consequence many predation strategies rely on ambush. In this mode, the predator lies in wait, motionless or nearly so, either waiting for prey to swim into an array of deployed tentacles, or attracting prey with bioluminescent or

mimetic lures. Other predators use stealth while ranging through the habitat to seek out their prey.

Solmissus is a genus of narcomedusae that is among the most abundant mesopelagic cnidarian taxa in warm and temperate regions worldwide. Their foraging behavior belies the common stereotype of a jellyfish that sits passively with its tentacles hanging below the bell until a prey item makes contact (Mills and Goy, 1988). Instead, *Solmissus* is an active predator, often moving through the water with some or all of its tentacles held foremost (Fig. 4). This behavior serves to decouple hydrodynamic disturbances caused by swimming from the region of prey contact and it is well adapted for capturing large, relatively fast-moving prey (Raskoff, 2002). It is also adaptive for ensuring successful feeding where large prey may be scarce. In situ observations of the stomach contents and of prey capture events reveal that *Solmissus* feeds chiefly on other gelatinous animals: ctenophores, salps, other medusae, siphonophores, and chaetognaths.

The siphonophore *Nanomia bijuga* Chiaje feeds principally on small crustaceans and shows stereotyped behavior during prey capture and handling. It typically positions itself in a J-shaped fishing posture with its tentacles splayed outward and the nectosome angled up. When prey contact and struggle against a tentacle, *Nanomia* begins swimming rapidly, which aligns the body with the tentacle and prey that trail behind it. While swimming, *Nanomia* contracts the tentacle and the prey is drawn toward the body until it can be grasped by other tentacles and palpons, which then maneuver it into a nearby gastrozoid. This behavior explains why the posterior gastrozoids are more likely to contain food than those near the nectosome. After ingestion *Nanomia* settles again into its feeding posture

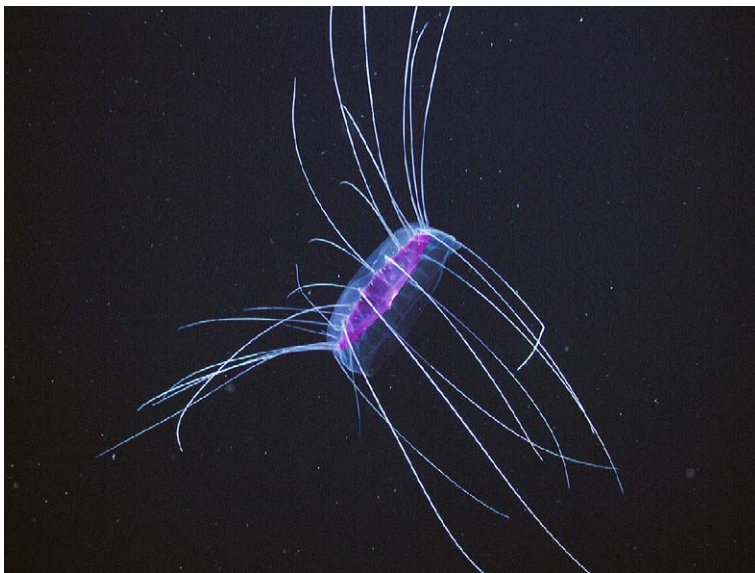


Fig. 4. *Solmissus marshalli* Agassiz and Mayer, with several of its tentacles held forward in the direction of travel; a typical active hunting posture.

and relocates every few minutes. These tactics are well suited for feeding on prey that aggregate in patches.

At depths between about 200 and 800 m a number of species, including fish, worms, and appendicularians, utilize mimicry as a means to deter predation. These animals respond to the presence of predators by curling their elongate bodies into circular shapes. They maintain this posture, hanging motionless in midwater, until the danger passes. The behavior is strongly associated with dim light and occurrences are rare in well-lit shallow depths, or depths beyond the penetration of sunlight, or at night. None of the species that employ this tactic have bioluminescent capabilities for defensive counter-illumination. This behavior is a case of protective mimicry in which the animals change their appearance to resemble medusae as unpalatable models (Robison, 1999).

5.1. Bioluminescence

Bioluminescence appears to be the most widespread form of communication in the deep pelagic habitat, where at least 90% of the inhabitants are capable of producing light in one fashion or another. In most cases the adaptive function of the light produced by the profusion of light organs found in deep-sea animals has been inferred from their structure and location. Opportunities to observe the light, incorporated into the behavior of an animal in its natural habitat, were exceedingly rare. Most bioluminescence is believed to be defensive, but it surely also serves to attract and illuminate prey, and to communicate with others of the same species.

Recent advances in bioluminescence research have provided direct evidence of how the light is used. In many cases this progress has been enabled by undersea vehicles, which allow for in situ observations as well as for the gentle capture of animals, which can then be studied alive and healthy, in the lab. These results have yielded information on new kinds of light-producing organs as well as how they are employed.

Euprymna scolopes Theel, a deep-living benthopelagic holothurian, employs a “burglar alarm” strategy of predator deterrence. After feeding on benthic sediments it lifts off the bottom and spends most of its time up in the water column. Light production is triggered mechanically and is produced by hundreds of granular bodies within the gelatinous integument of the animal. Point stimulation yields a localized response, which spreads gradually to the entire surface of the animal. Broad impact yields a whole-body luminous response. The skin of *E. scolopes* is very fragile and strong physical contact causes the skin to be sloughed off in a glowing cloud. The deciduous skin is also sticky and it readily adheres to most surfaces. Physical contact elicits light production that can “paint” a predator with patches of the glowing skin, thus revealing the presence of the attacker to its own visually cued predators. Lost skin is replaced within 1–5 days (Robison, 1992).

The bathypelagic cephalopod *Vampyroteuthis infernalis* Chun has at least three different means of producing light: two large, bright, circular organs located near the apex of the mantle; light-producing regions at the tips of all eight arms; and a viscous, sticky fluid, secreted by the arm tips that contains numerous glowing particles. It uses these in a complex pattern of defensive behaviors that indicates a high degree of neural control. With strong stimulation *Vampyroteuthis* turns on the paired organs and

the tip-lights while it sweeps its arms and web over the head and mantle to expose the suckers and cirri on the inner surface of its arms (Fig. 5). Luminous fluid released during the sweep envelops the animal in a glowing cloud and illuminates its radically altered appearance (Robison et al., 2003).

Malacosteid dragonfish, like *Aristostomias*, produce red light from photophores on their cheeks that shines along the line of sight of each eye. In the deep sea where nearly all vision is optimized to receive blue light, this bioluminescence will not be seen except by the fish itself, which has a unique visual pigment that reacts to the longer red wavelengths (Widder et al., 1984). Red light reflected from a silvery fish or a red crustacean will be seen by *Aristostomias* without the prey being aware that it has been illuminated. This remarkable adaptation is made possible by pigments in the light-producing organ that absorb short-wavelength light, then re-emit the energy as red light, which passes through a final filter before expression.

In situ observations have also revealed how the mesopelagic squid *Chiroteuthis calyx* Young uses bioluminescence to catch its prey. The fourth arm on each side is larger and more robust with a groove running along its length. The squid's two slender feeding tentacles slide through the grooves, then out and over the supporting arms to hang suspended below (Fig. 6). A series of light organs runs along the length of each tentacle. *Chiroteuthis* moves the long tentacles up and down while flashing the serial photophores. Prey that are attracted to the lights are seized by clustered suckers at the



Fig. 5. *Vampyroteuthis infernalis* in a defensive posture with its arms and web wrapped over the head and mantle. Suckers and cirri are exposed.

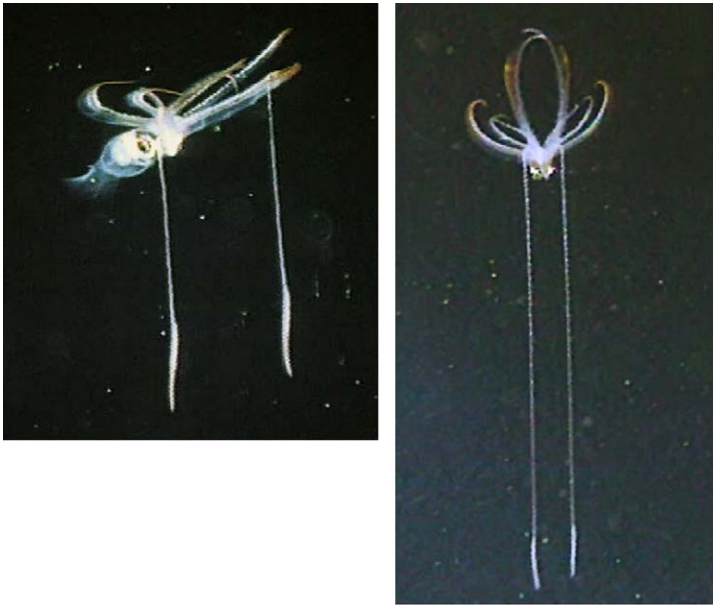


Fig. 6. Video frame grabs of *Chiroteuthis calyx* in its fishing posture, with tentacles deployed over the fourth arms.

end of the tentacle, which is then retracted up the groove where the prey are transferred to the mouth by the remaining three pairs of arms. Then the tentacle is redeployed (Hunt, 1996).

6. Chemical ecology

In the absence of sunlight and with only bioluminescence for visual cues, the deep water column seems a likely habitat for other kinds of sensory communication to have evolved. Among the adaptations to depth in some fishes are enhanced chemosensory capabilities. Compared to their mesopelagic counterparts certain bathypelagic gonostomatid species have expanded nasal rosettes and larger olfactory lobes in their brains (Marshall, 1971), presumably for finding food they cannot see. Likewise, dwarf male ceratioid anglerfish often have enlarged olfactory organs, which they probably use to locate a female by tracking a pheromone gradient she creates. In contrast, the females have regressed olfactory organs, nerves and brain lobes.

The only direct experimental evidence of chemoreception in deep-living pelagic fauna comes from the hydromedusa *Mitrocoma cellularia* Agassiz (Tamburri et al., 2000). In this study specimens were collected by an ROV and transferred to a laboratory ashore, where they responded to substrate- and solution-borne prey extract, just as they responded to the taste and smell of actual prey. Naive experimental animals did not respond to controls that contained no prey extract. To validate the laboratory investigations, the ROV conducted

similar experiments back in the ocean, on specimens of free-swimming *M. cellularia* that were not collected or restrained, yielding the same results.

7. Megafauna

The presence of large animals deep in the water column has long been assumed because of deep-dwelling prey found in the stomachs of cetaceans, strandings at the surface of moribund large animals like giant squid, and occasional captures of large “creatures” by commercial trawl nets. Direct evidence from observations by undersea vehicles and indirect evidence from other sources also suggest that deep megafauna, while elusive, may be much more common than was previously known. Encounters with *Architeuthis*, *Moroteuthis*, *Mesonychoteuthis*, and other large, undescribed bathypelagic squids (Fig. 7) have increased in recent years because of growing public interest and awareness by fishermen, and because of expanding midwater coverage by undersea vehicles (Vecchione et al., 2001). Several lines of evidence indicate that the populations of these animals may be very large.

Deep-diving marine mammals are important constituents of deep pelagic communities, regardless of where they respire. Among pinnipeds, the northern elephant seal spends about 10% of its time at the sea surface, with the rest spent diving to depths of 1500 m or more, where they feed on squid, sharks, and pelagic fishes like hake. Some dives last for more than an hour. Sperm whales feed at depths from 200 to at least 1000 m where their food is chiefly squid, and based on beak sizes these are often very large individuals. Even at its present low level, the global population of sperm whales is estimated to consume more biomass than all of human fishing combined (Whitehead, 2003). Accumulating evidence about the historical sizes of cetacean populations suggests that the abundance of their prey populations must be enormous (Roman and Palumbi, 2003).

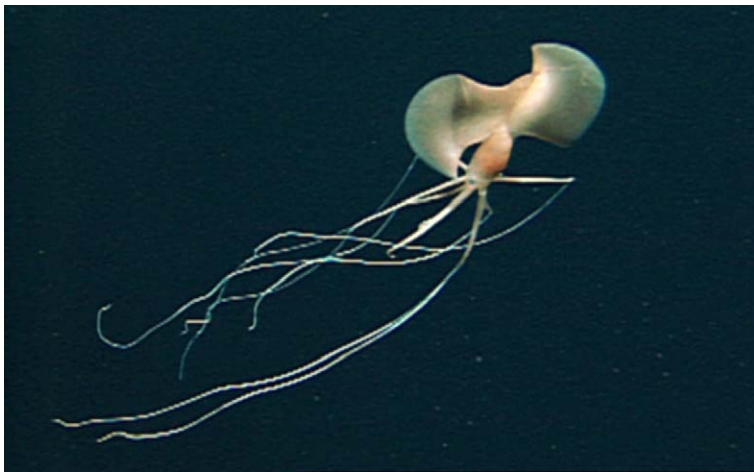


Fig. 7. Video frame grab of an unknown large squid, possibly *Magnapinna*, taken at 3380 m depth off Hawaii.

Observations of large gelatinous animals have increased as more time is spent at mesopelagic depths with HOVs and ROVs. The giant siphonophores *Praya*, and *Apoemia* regularly attain lengths of 30 m and 10 m respectively. *Deepstaria*, a sennaeostome medusa, has extremely pliant bell tissues that can stretch to four or five times its contracted diameter of a meter or more, presumably enabling it to engulf a wide range of prey types. *Stygiomedusa*, another sennaeostome has bell diameters up to 1.5 m and overall lengths of 4 m or more. All of these jellies are large enough to provide ecological substrate for other species. In the case of the siphonophores, juvenile fishes and small amphipods (*Cystisoma*) have been observed sheltering along the lengths of the colonies. Isopods of the genus *Anuropus* are invariably found in association with *Deepstaria* and the fish *Thalassobathia pelagica* Cohen occurs in conjunction with *Stygiomedusa*.

8. Benthopelagic fauna

Benthic submersible vehicles like the HOV Alvin provide glimpses of a mobile fauna in the region above the deep sea floor that is known as the benthic boundary layer (Barnes et al., 1976). This layer is too deep and too close to the bottom to be safely sampled by the lightweight gear suited for collecting pelagic species, and benthic gear is too rugged for many of the relatively delicate animals that inhabit the layer. Camera sleds, acoustic arrays, baited traps, and free-vehicle collecting systems have all indicated the existence of a diverse and surprisingly abundant near-bottom fauna (Smith et al., 1992; Wishner, 1980). The well-known inhabitants of this region include fishes, crustaceans and holothurians, all of which are believed to feed on the bottom but spend the majority of their time swimming or suspended above it. This strategy confers mobility and a degree of protection from benthic predators.

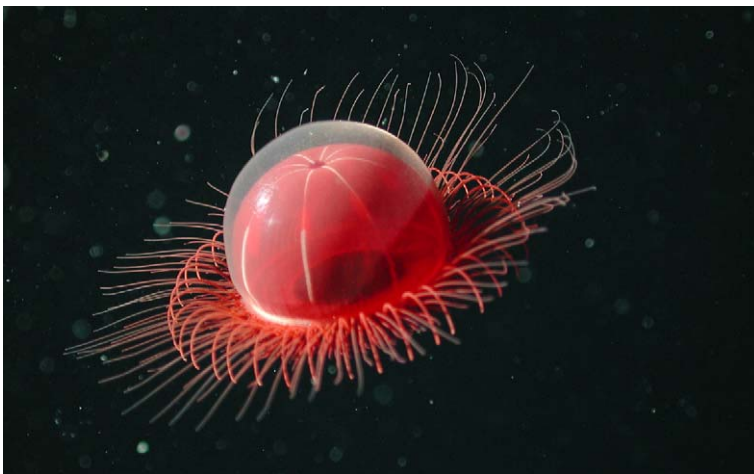


Fig. 8. *Crossota* sp. A benthopelagic hydromedusa found below 3000 m in the eastern North Pacific.

In some areas the boundary layer fauna can also include a surprising number of gelatinous forms. In Monterey Bay, for example, at depths beyond 3000 m an unidentified species of the hydromedusan genus *Crossota* (Fig. 8) has been observed to carpet the bottom in areas covering tens of square meters. After feeding, they lift off the bottom individually and range up to altitudes of 100 m or more above the sea floor. Other forms are too delicate to survive contact and occur only within the layer of re-suspended particles. These include a large lobate ctenophore, probably *Bolinopsis*, and a large, undescribed oikopleurid appendicularian. Links between the benthopelagic fauna and the deep pelagic fauna, if these groups are distinct, are very poorly known.

9. Future research

A dearth of knowledge about the deep pelagic biota and the advent of new technologies to make it accessible, mean that this field is wide open and poised for significant advances. The future rests on the continued development of undersea vehicles, new instrumentation, and their expanded availability to a broader group of users (NRC, 2003). Geographical coverage of the deep pelagic habitat has been very limited and comparative studies of regional community composition, structure and dynamics are fundamentally necessary. As a follow-up to this exploration, time-series studies will be needed to assess the natural patterns of variability. Further advances will arise on several fronts. Some can be achieved with existing technology, while others will come as the tools are developed.

With visual communication limited to bioluminescence in the majority of the habitat, it seems likely that chemoreception must play a large role in biological interactions. Chemical cues are probably in wide use for intraspecific communications concerning reproduction, aggregation and simple recognition. Like their counterparts in shallow water, soft-bodied gelatinous animals may employ aposematic chemical warning signals as well as toxins for defense. Molecular techniques have the potential to address many questions of species identification, the relatedness of known taxa, and population dynamics. Genetic probe technology may allow some of these investigations to be made in situ.

The detection of electromagnetic fields by elasmobranch fishes has been going on for millions of years. Sharks can locate food by detecting the bioelectric fields generated by their prey, and they can use the Earth's magnetic field for navigation (Kalmijn, 1982). At bathypelagic depths, where sunlight does not penetrate, the presence of sense organs similar to the electric field sensors of sharks appear on a wide variety of fishes. This suggests another way of investigating the deep-sea environment, one that is ecologically valid but which represents a sensory "window" that no human has ever looked through. Development of an electric field sensor that can be deployed in deep water might provide a great deal of new information about this habitat and its occupants.

The pelagic equivalent of a benthic time-lapse camera system will be very valuable. Development of AUVs with target acquisition and tracking control software is underway, and once available these systems will tell us a great deal about the daily lives of deep pelagic species by following and recording them through their daily ambits. Large-scale, deep survey requirements, both exploratory and quantitative, can also be met by AUVs. In this case, data from onboard imaging systems will be processed by image recognition and

analysis software that will eliminate the requirement for labor-intensive enumeration by human reviewers. This development will greatly expand the scale and scope of deep pelagic surveys.

Tagging animals is another promising area of research to gather information on their activity, movement, and range. Electronic tags are becoming ever smaller and more powerful, and may soon be suitable for deployment on some of the smaller organisms found in deep water. Acoustic tags provide location data that can be used by an undersea vehicle to track or relocate an animal for recovery or for the downloading of data. They can also be used in conjunction with seafloor observatories or mooring arrays that provide multiple receivers for mapping an animal's movements. Archival tags record data on location or environmental conditions, which is stored until retrieval.

Mobile, midwater research platforms offer great potential for expanding our understanding of the biology and ecology of deep-living pelagic species. However, other technologies are also promising. Larger nets, which expand the capture swath of a midwater trawl to hundreds of square meters, would significantly reduce avoidance problems by larger animals and would provide far more accurate assessments of fishes, squids, and crustaceans. Seafloor observatories, with a continuous power supply, could support a vast array of outward- and upward-looking instrumentation to examine the benthic boundary layer and the water column above. Deep-sea moorings could also provide power to instruments for scanning the water column, as well as sites for in situ experimentation. Deep pelagic biology, which has been rooted in the 19th century for far too long, is finally catching up with technology.

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