Review

Conservation of Deep Pelagic Biodiversity

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Abstract: *The deep ocean is home to the largest ecosystems on our planet. This vast realm contains what may be the greatest number of animal species, the greatest biomass, and the greatest number of individual organisms in the living world. Humans have explored the deep ocean for about 150 years, and most of what is known is based on studies of the deep seafloor. In contrast, the water column above the deep seabed comprises more than 90% of the living space, yet less than 1% of this biome has been explored. The deep pelagic biota is the largest and least-known major faunal group on Earth despite its obvious importance at the global scale. Pelagic species represent an incomparable reservoir of biodiversity. Although we have yet to discover and describe the majority of these species, the threats to their continued existence are numerous and growing. Conserving deep pelagic biodiversity is a problem of global proportions that has never been addressed comprehensively. The potential effects of these threats include the extensive restructuring of entire ecosystems, changes in the geographical ranges of many species, large-scale elimination of taxa, and a decline in biodiversity at all scales. This review provides an initial framework of threat assessment for confronting the challenge of conserving deep pelagic biodiversity; and it outlines the need for baseline surveys and protected areas as preliminary policy goals.*

Keywords: biodiversity, conservation, deep-sea animals, pelagic habitat

Conservación de la Biodiversidad Pelágica Profunda

Resumen: *El mar profundo es uno de los ecositemas más extensos en nuestro planeta. Este vasto dominio contiene lo que pudiera ser el mayor número de especies animales, la mayor biomasa y el mayor número de organismos individuales en el mundo viviente. Los humanos hemos explorado el mar profundo durante casi 150 años, y la mayor parte de lo que se conoce se basa en estudios del lecho marino profundo. En contraste, la columna de agua encima del lecho comprende más de 90% del espacio para vivir, sin embargo se ha explorado menos de 1% de este bioma. La biota pelágica profunda es el grupo faúnico más grande y el menos conocido no obstante su importancia obvia a escala global. Las especies pelágicas representan un reservorio incomparable de biodiversidad. Aunque aun falta que se descubra y describa a la mayoría de estas especies, las amenazas a su existencia son númerosas y están incrementando. La conservación de la biodiversidad profunda es un problema de proporciones globales que nunca ha sido abordado integralmente. Los efectos potenciales de estas amenazas incluyen la reestructuración extensiva de ecosistemas enteros, cambios en la distribución geográfica de muchas especies, eliminación de taxa y una declinación de la biodiversidad en todas las escalas. Esta revisión proporciona un marco de referencia inicial de la evaluación de las amenazas para confrontar el reti de conservar la biodiversidad pelágica profunda; y delínea la necesidad de muestreos básicos y del establecimiento de áreas protegidas como metas preliminares.*

Palabras Clave: animales de aguas profundas, biodiversidad, conservación, hábitat pelágico

Introduction

Deep-sea biologists usually acknowledge the voyage of HMS Challenger (1872–1876) as the genesis of their dis- cipline. Beforehand, debate boiled around whether or not life had penetrated to ocean depths beyond a few hun- dred meters. Most scientists of the day believed that the lack of light, the cold, and the great pressures of depth

precluded the possibility of life in the deep. The Challenger expedition firmly established that abundant life exists on the deep seafloor, and most of what is known today about deep-sea biology stems from these benthic discoveries. Less clear was the picture of life in the water column above the deep seabed. For many additional decades, most naturalists believed that pelagic animals were restricted to two narrow zones—near the surface and near the bottom. What has been learned in the last 60 years has begun to fill in the gap, and it is now clear that the oceanic water column is filled with life.

The largest living space on Earth lies between the ocean's sunlit upper layers and the dark floor of the deep sea, on average some 4000 m below the surface (Fig. 1). Within this vast midwater habitat are the planet's largest animal communities, composed of creatures adapted to a fluid, three-dimensional world without solid boundaries. These animals probably outnumber all others on Earth, but they are so little known that their biodiversity has yet to be even estimated. This is a huge planetary resource, yet far less is known about these species than about the constituents of any other major habitat.

Photosynthesis in the near-surface layers is the primary source of nutrients that flow through the oceanic food chain. Organic matter created in sunlight is transferred downward through a complex, interwoven ecological web, and ultimately to the deep seafloor. Phytoplankton and other organic particles at the base of the web are grazed by small crustaceans and gelatinous filter feeders. These grazers are consumed by micronektonic fishes and squids (Fig. 2) and by four types of abundant gelatinous predators: medusae, siphonophores, ctenophores, and chaetognaths. The next trophic step in the midwater food web is another set of predators, including anglerfishes, dragonfishes, squids, and another suite of gelatinous carnivores (Fig. 3). Although top predators like pinnipeds, whales, tunas, and swordfish feed in midwater as deep as 1000 m or more, the deeper one goes the less is known about midwater ecology and the animals that live there.

To avoid being eaten by visually cued predators near the surface, many midwater animals undertake daily vertical migrations (Childress 1995; Robison 2003). Each morning as the sun rises, they swim downward into the protective darkness of deep water. In the evening they move back into the upper layers, where they graze on organic matter produced there, or feed on grazers. Given the countless individuals involved in these movements, they must be the largest animal migrations on Earth. Animals that live below 1000 m also rely on organic matter generated near the surface, but the vertical distances are too great for efficient migration, so they depend on food that sinks or swims down to their level. Many deep-living pelagic species undertake an ontogenetic vertical migration in their life cycle. Buoyant eggs or larvae rise to the surface layers, where they undergo the first stages of
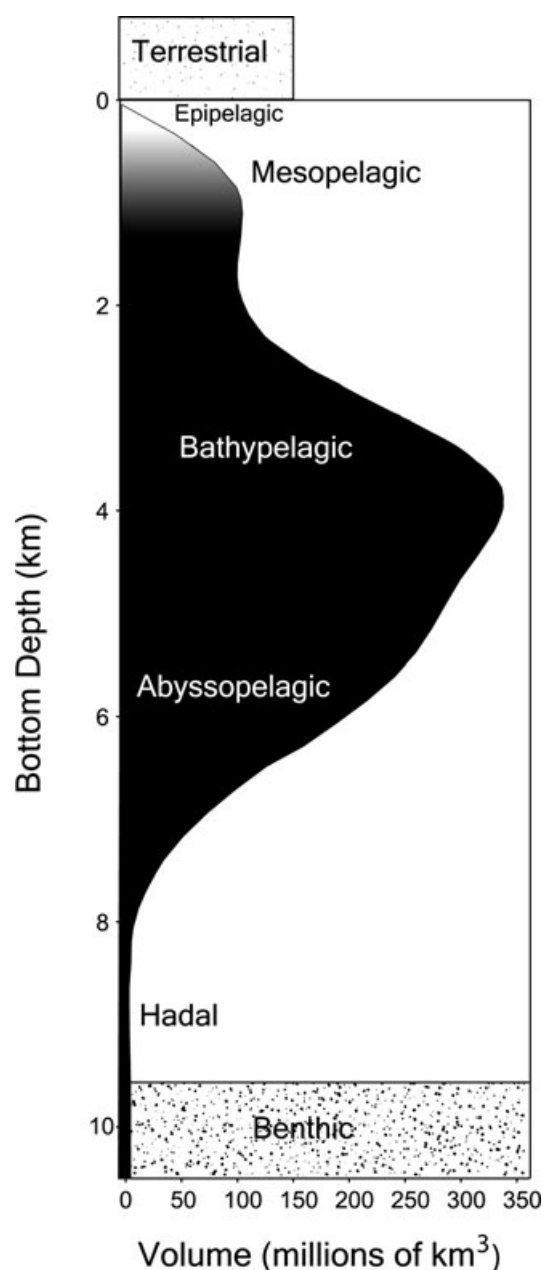

Figure 1. Graphic representation of ocean volume relative to bottom depth. The curve shows the global volume of water above seafloor depths ranging from 0 to 10.9 km (the Mariana Trench). The edge of the continental shelf at roughly 200 m is the traditional boundary of the deep sea, and animals out beyond this margin are said to live in deep water. Ecological depth zones of the oceanic water column: epipelagic, upper 150–200 m; mesopelagic, down to 1000 m; bathypelagic, 1–4 km; abyssopelagic, 4–8 km; hadal, below 8 km. The displayed volumes of terrestrial and benthic environments include the surface areas of the dry land and the seafloor and the air or water above to a height of 1 km. (Data source: UN 2008).
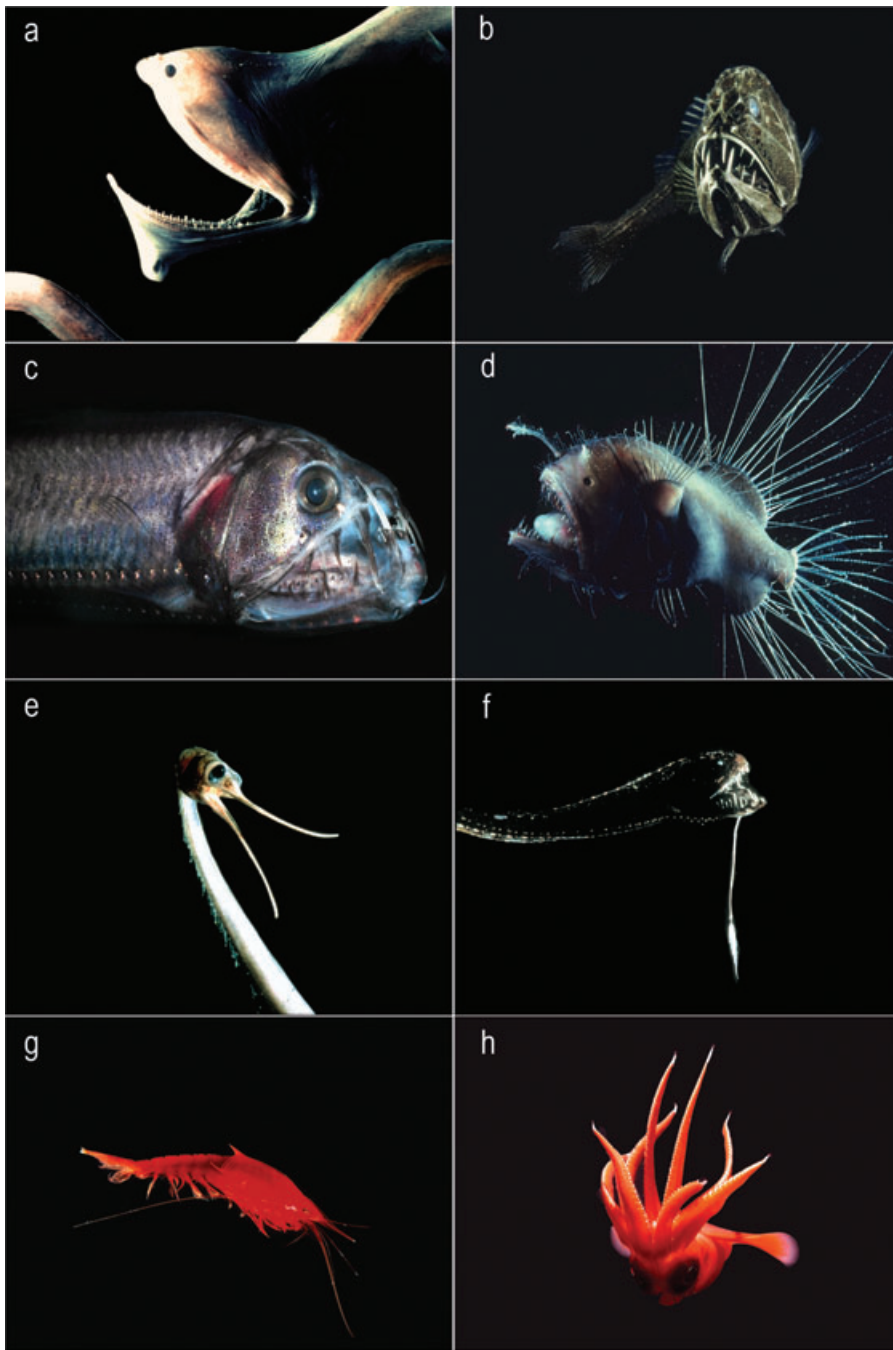
*Figure 2. Firm-bodied deep pelagic animals: (a) gulper eel (*Saccopharynx*); (b) fangtooth (*Anoplogaster*); (c) viperfish (*Chauliodus*); (d) anglerfish (*Caulophryne*); (e) snipe eel (*Nemichthys*); (f) blackdragon (*Idiacanthus*); (g) mysid shrimp (*Gnathophausia*); (h) octosquid (*Octopoteuthis*).*

development; as juveniles, they descend back down to the adult depth range.

Because their prey reside in darkness, predatory midwater fish and squid frequently have highly developed eyes—functional in even the dimmest illumination. Thus, visual trickery is a common practice (Bush & Robison 2007). Many species are camouflaged or cryptically colored, others achieve near invisibility by being transparent, and some use mimicry to fool predators (Robison 1999). Below about 1000 m, the last photons of sunlight disappear and the midwater animals that live very deep are often blind or have primitive eyes that may detect light but do not form images.

In the absence of sunlight, a great many deep pelagic animals produce their own light through the chemical process of bioluminescence. Midwater animals use this light in a variety of ways. Anglerfishes and dragonfishes employ luminous lures to attract prey. Lanternfishes and hatchetfishes have ventral light-producing organs that erase their silhouettes when predators try to spot them from below. Other animals use distinctive light patterns for recognition and finding mates. Many species use light
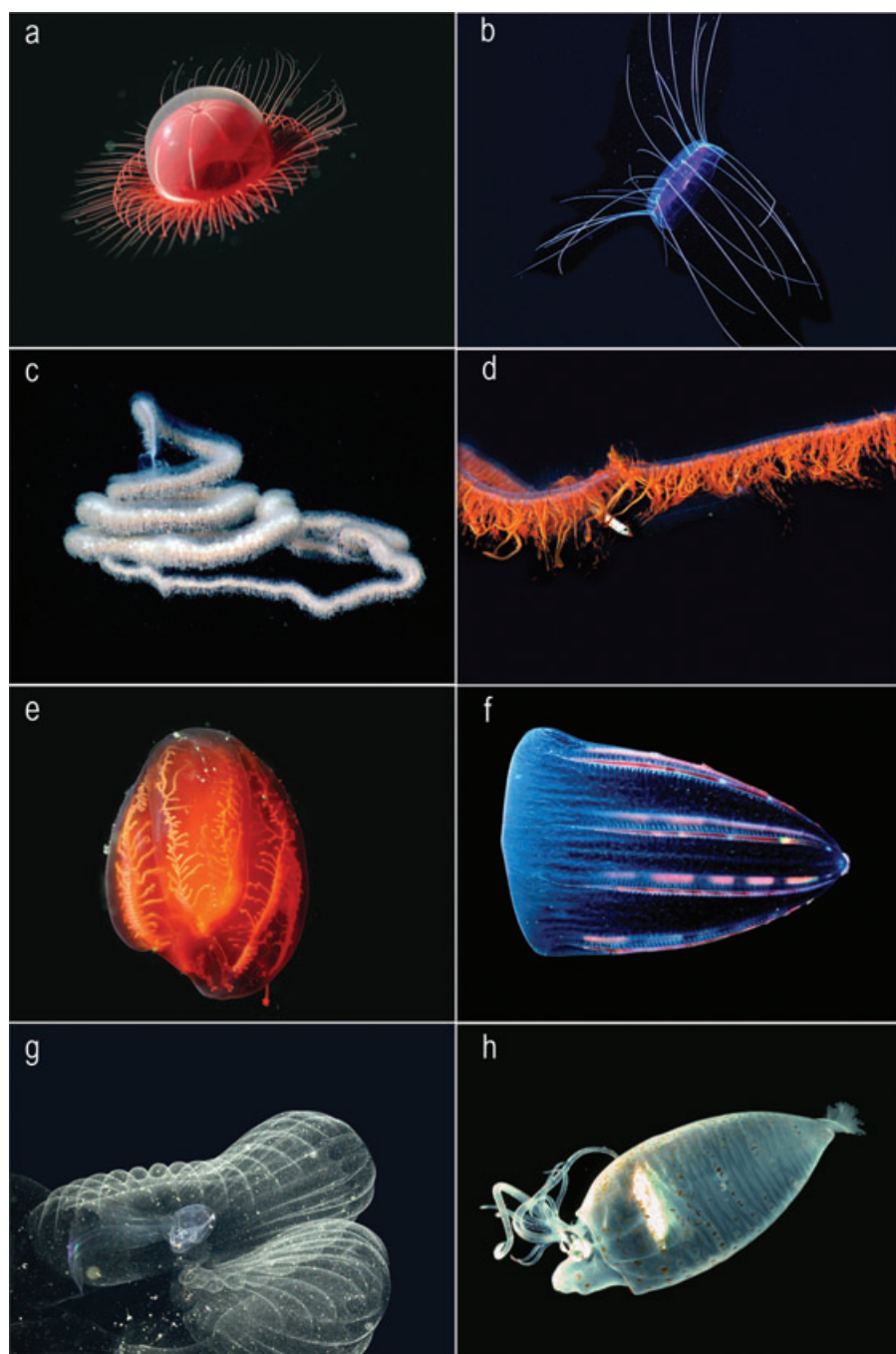
*Figure 3. Gelatinous deep pelagic animals: (a) benthopelagic medusa (*Benthocodon*); (b) holopelagic medusa (*Solmissus*); (c) halyard siphonophore (*Apolemia*); (d) undescribed siphonophore; (e) undescribed cydippid ctenophore; (f) ctenophore (*Beröe*); (g) larvacean (*Bathochordaeus*); (h) transparent squid (*Helicocranchia*).*

to blind or confuse their attackers or to make them vulnerable to their own predators (Robison 1992). Bioluminescence is so widespread that it must be the most common form of communication in the ocean (Widder 2002).

As depth increases the growing weight of the water above creates enormous pressure, which is the primary barrier to scientific operations in the deep sea. Although the animals that live in deep water are well adapted to high pressure and low temperatures, we humans must protect ourselves and our instruments in order to investigate this harsh environment. The deep pelagic habitat

has been a stable, relatively homogeneous environment for millions of years, and its stability has led to a relatively narrow range of physiological tolerances among the species adapted to live there.

One of the most significant discoveries of recent years has been that gelatinous animals comprise a major portion of the deep pelagic fauna (Fig. 3). Prior to the introduction of deep-diving midwater vehicles, these animals were seriously underestimated by conventional sampling methods because nets destroy their fragile bodies (Madin & Harbison 1978). We now know that jellies are the dominant life forms within some broad depth

zones. Technological advances in vehicles, instruments, and imaging systems are rapidly improving our understanding of deep pelagic biology (Robison 2004).

The Importance of Deep Pelagic Animals

Deep pelagic animals comprise critical structural and functional links in oceanic ecosystems. They are a principal food source for most commercially captured pelagic species. Although the majority of midwater species have not yet been described or their ecologies fully characterized, it is clear that the biodiversity of this global fauna plays an essential role in maintaining ecosystem integrity. The deep pelagic fauna comprises what may be the largest reservoir of animal diversity on Earth. Diversity promotes stability (Ives & Carpenter 2007), so protecting the stability of an ecosystem that provides a major portion of the world's food is obviously in our best interests. Deep pelagic animals provide another vital ecosystem service by serving as a huge carbon sink. They capture carbon removed from the atmosphere by phytoplankton, and they keep it at depth.

In addition to their ecological significance, these animals and their genetic libraries offer a global resource of molecular solutions to nature's challenges. They embody the results of countless lines of evolutionary progress over hundreds of millions of years. Marine species have already been the source of many unique chemical compounds with the potential for commercial development as pharmaceuticals, nutritional supplements, industrial enzymes, and for use in biotechnology and agricultural applications. In particular, soft-bodied invertebrates that lack robust physical defenses have provided bioactive compounds based on their chemical defenses (e.g., Munro et al. 1999; Pomponi 2001). The newly discovered diversity of deep-living gelatinous species presents rich potential for antibiotics, antiparasitics, anticancer agents, and other pharmaceutical compounds.

The Conservation Issue

Despite its obvious importance, 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). A million or more undescribed species, with biological adaptations and ecological mechanisms not yet imagined, may live within the vast volume of the deep-sea water column (Robison 2004). Although the deep sea has begun to receive the attention of conservationists, their efforts to date have focused chiefly on the deep seafloor and on pelagic animals that live near the surface (Norse 2005*a*, 2005*b*; Ardron et al. 2008; Halpern et al. 2008). Conservation organizations and the research community have worked successfully to protect deep-sea corals, and they are working to further restrict destructive, deep bottom trawling (Gianni 2004).

This greatest unappised reservoir of animal biodiversity in the ocean, however, has yet to be included in the protective considerations of any conservation, research, or governmental organization. The principal concern here should be the prospect of undetected mass extinctions, which threaten losses in ecosystem function, economic opportunity, and vital ecosystem services (Ehrlich & Wilson 1991; Worm et al. 2006). Conservation of biodiversity is gaining momentum as a global concern, yet the greatest part of the biggest ecosystems on Earth lacks representation in the conservation effort. It is time to address this issue.

Threats

The diversity of deep pelagic animals is threatened by a broad array of influences and circumstances. What follows is a characterization of these threats, surely incomplete, but necessary because to date this issue has been virtually ignored. Some threats are general, others are specific, and the particular ways that these factors might influence the deep pelagic fauna and the types of animals that might be particularly susceptible have yet to be investigated. Although the threats are presented here individually, their effects can be cumulative and multiple threats can be interactive (Zeidberg & Robison 2007; Halpern et al. 2008).

Climate Change

The warming of the ocean's upper layers is producing direct and indirect effects on specific biotic groups throughout the oceanic water column. Of particular concern is the alteration of historical patterns of primary production in the ocean's upper layers, the basic food supply of the animals living below. As the upper layers become warmer, the water column becomes more stratified, which inhibits the vertical mixing needed to replenish basic nutrients required for photosynthesis. On a global scale, it appears that both phytoplankton biomass and growth rates decline as the surface layers get warmer (Behrenfeld et al. 2006). In addition to overall reduction of organic material supplied to the oceanic food web, climate models suggest that continued warming may also result in a geographical shift of production from lower to higher latitudes (Boyd & Doney 2002; Behrenfeld et al. 2006).

Rising temperatures have been implicated in shifting the geographic distribution patterns of plankton and fishes (Batten & Welch 2004; Perry et al. 2005), in the disruption of plankton communities (Richardson & Schoeman 2004; Hays et al. 2005), and in large-scale changes in pelagic biodiversity (Beaugrand et al. 2002). They have also been linked to invasive range expansions by top predators (Zeidberg & Robison 2007). The ocean's upper

layers, because of their high productivity, are where the larvae and juveniles of many deep-living species develop, before returning to the adult depth range. Because these early life-history stages may have narrow physiological tolerances, rising surface temperatures may play a role in altering the abundance and geographical distribution of species that live far below the surface as adults. Likewise, the reproductive cycles of consumer species may be tightly coupled to seasonal pulses of plankton production at the surface. Climate change has begun to disrupt these linkages (Edwards & Richardson 2004), with negative effects at higher trophic levels.

Although most of these effects of climate change have been measured only in coastal waters or in the open ocean's upper layers, it is likely that corresponding changes are occurring in the deeper parts of the food web. In deep water we can also expect that climate change will have large-scale effects by slowing down the ocean's major circulation patterns, reducing the oxygen content at depth, and warming even the deepest layers. The deep pelagic fauna has evolved within a stable physical environment and as a result they may be particularly sensitive to such changes (Koslow 2007).

Carbon Dioxide

The oceans have a great chemical affinity for carbon dioxide, which is readily absorbed from the atmosphere. One result of this affinity is the creation of carbonic acid and a change in the balance of hydrogen ions, so that seawater becomes more acidic when more CO_2 is absorbed. As atmospheric concentrations of CO_2 rise, one can expect to see both direct and indirect effects of ocean acidification on the deep pelagic biota. Increasing acidity will reduce the availability of carbonate ions that are important to coccolithophores and foraminifera at the base of pelagic food webs and to crustaceans, some mollusks, and other organisms with calcified shells or hard structures (Royal Society 2005; Guinotte & Fabry 2008). Increasing CO_2 concentration in seawater can also lead to the same acidic condition in body tissues and fluids (hypercapnia). Internal acidification affects the ability of blood to carry oxygen and imposes other physiological stresses, including negative impacts on reproductive processes (Royal Society 2005).

Direct injection of anthropogenic CO_2 into the ocean has been proposed as a means of reducing its rate of accumulation in the atmosphere (Marchetti 1977). Whether it is released as liquid to form a hydrate-covered lake on the deep seafloor or is dispersed into the water column, CO_2 sequestered in this manner will likely have a profound impact on the deep-sea fauna. Here again, the principal effect will be to lower the pH of seawater and consequently of the animals that live in it. Seibel and Walsh (2001) have examined the potential effects of direct CO_2 injection on the deep-sea biota, and they conclude that these animals

are highly susceptible to the excursions of CO_2 and pH that would accompany sequestration. Among the effects are reduced oxygen uptake capacities. For example, under conditions where its arterial pH drops by just 0.2, the deep-living pelagic shrimp *Gnathophausia ingens* (Fig. 2g) would experience a 50% reduction in the bound oxygen level in its blood (Childress & Seibel 1998). Additional effects include metabolic suppression, a reduction in basic processes such as the protein syntheses necessary for reproduction and growth.

Commercial Fishing

Removing top predators from the oceanic food chain has already had a significant impact on pelagic ecosystems (Frank et al. 2005; Worm et al. 2005, 2006). Although high-seas fisheries are destined to continue because of the growing world demand for protein, the ecological consequences for untargeted, deep-living species have almost never been considered, much less investigated. Trophic cascades that restructure the food web at lower trophic levels appear to be inevitable (Caddy & Rodhouse 1998; Myers et al. 2007). At the present time, the resulting changes to deep pelagic biodiversity are not measurable because too little is known about the trophic webs and because there is insufficient baseline data to reveal changes.

In the open ocean, many top predators feed on species that migrate from deep water to the surface each night, then down again during the day. Thus, the commercial catch of top predators can directly impact deep-living species through the removal of top-down controls. Nevertheless, predicting the effects on the deep-water community is presently beyond our understanding. If a harvested species is pushed to commercial or population extinction, it may not recover when fishing stops. In some cases an affected species may be replaced by others that fill its niche and prevent its resurgence. Species with short generation times and high fecundity, such as gelatinous animals and squids, are particularly suited to the opportunistic replacement of vertebrates with late maturity and fewer young (Lynam et al. 2006; Zeidberg & Robison 2007). Replacement species may not feed on the same mix of prey as those they succeed, producing a differential effect on the deep community, its structure, and its diversity.

Another way commercial fishing pressures may affect deep pelagic biodiversity is by "fishing down the food web" (Pauly et al. 1998). As the numbers of top predators have declined, fishing effort has shifted to species at lower trophic levels. In some cases deep-living species themselves, such as myctophid fishes (Valinassab et al. 2007) and Antarctic krill (Jones & Ramm 2004), have become targets for commercial fisheries. Commercial fishing for krill off the U.S. west coast has been banned in state and federal waters to preclude the expansion of

existing krill fisheries originating in Japan and Canada (PFMC 2006).

High-Seas Fish Farming

The ecological impacts of present-day commercial aquaculture can be small or large, depending on how the facilities are operated. Recently, plans for large-scale, offshore fish farms have been widely discussed (Naylor & Burke 2005; Naylor 2006), and these operations have the potential for significant ecological impact on deep pelagic communities. Although the first steps for this development will be within national exclusive economic zones, initial success may lead to operations in deep international waters.

No assessments have yet been made of how deep pelagic communities might be affected, but the two obvious issues are input and output. If industrial-scale offshore fish farming incorporates natural productivity as its food supply, then the normal food chain may be short-circuited, reducing the natural food supply for the deep pelagic community. If the captive populations are fed with locally harvested wild stock (e.g., krill), then the surrounding natural populations may be depleted. Industrial-scale organic discharge would also have an impact on the deep community outside the enclosures. Requirements for free-flowing water may lead to dispersal beyond the enclosures of parasites and of compounds introduced to enhance growth or reduce disease among the captive fish. Likewise, organic wastes will infiltrate the surrounding waters. Expanding food production will continue to be a major driving force behind the reduction of biodiversity and ecosystem services in the ocean as Earth's population continues to swell (Sarukhan 2006; Worm et al. 2006).

Ballast Water

In addition to the redistribution of pathogens by ballast water discharges, this vector is also a source of invasive colonization by the larvae of exotic pelagic species. Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* is well documented because that species lives near the surface and is readily observed (Kideys 1994). Expanding beyond the Black Sea, *Mnemiopsis* appears to have few natural predators in the region, and it has outcompeted the native ctenophores in some habitats. Because this ctenophore's food consists of zooplankton and the eggs and larvae of fishes, regional anchovy fisheries important to Turkey and Russia were nearly wiped out (Shiganova et al. 2001). If the natural transport of planktonic larvae between regions by currents can be likened to natural levels of genetic mutation, then ballast water can be seen as a mutagen, accelerating the rate of change.

Like *Mnemiopsis*, many deep-living species may be relocated because their larval stages live near the surface,

but this prospect has yet to be considered in threat assessments. Member states adopted a new Ballast Water Convention in 2004 (IMO 2005) that restricts discharges within coastal regions. Nevertheless, the exchange of ballast water on the high seas is not only condoned but is recommended. This practice is undoubtedly causing the redistribution of deep-living species in offshore regions. One alternative, the poisoning of ballast water with toxins, has obvious drawbacks. A promising, nontoxic approach calls for the deoxygenation of ballast water with nitrogen to kill the larvae of potentially invasive species (Tamburri et al. 2002).

Industrial Resuspension of Sediments

Most of the deep seafloor is covered with a thick layer of sediment. This layer is easily resuspended, and once disturbed it hangs in the water column for a very long time. Industrial-scale activity on the deep seafloor will inevitably create persistent clouds of resuspended sediments that reach hundreds of meters up into the water column and spread laterally in currents (Jankowski & Zielke 2001).

Among the most conspicuous inhabitants of the pelagic fauna above the seafloor are filter-feeding larvaceans and carnivorous lobate ctenophores. Larvaceans feed by building intricately structured, mucous filters (Fig. 3g) that select small particles for ingestion, whereas large particles build up externally. When the filters become too clogged for efficient water flow, the animal discards them and builds new ones (Robison et al. 2005). Thick, persistent clouds of resuspended sediment will lead to an acceleration of the discard cycle, which is delicately balanced with nutrient intake, and the extra burden of accumulated particles on the outsides of the filters will defeat the carefully maintained neutral buoyancy these animals must sustain. Likewise, ctenophores will be beset with particle densities that will compromise the ciliary and mucosal motions that trap and help them ingest their prey and will challenge their buoyancy control. Mining of polymetallic sulfide deposits near hydrothermal vents will occur in areas with thinner sediment layers because the seafloor there is relatively new. Nevertheless, perturbations in the form of toxic compounds and the pumping of ore from deep to shallow water will occur (Halfar & Fujita 2007).

Expansion of Oxygen Minimum Layers

Oxygen minimum layers are depth zones in the water column where the dissolved oxygen content is very low, diminished by microbial oxidation of organic matter. Because of stratification, vertical mixing does not replenish the oxygen. Many fewer animals and many fewer species inhabit these layers than occur at depths above and below. Another consequence of climate change and increasing CO_2 input may be the expansion of oxygen minimum

layers in many parts of the ocean and their creation in places where they do not already exist (Keeling & Garcia 2002; Chan et al. 2008). The effects of such changes, in general, will be to enhance ecological stratification in the water column. Expanding the vertical extent of existing layers will further separate many deep pelagic species from their food sources in the upper layers and may reduce the amount of food that sinks through. The creation of new oxygen minimum layers in geographic regions where they do not presently exist is equivalent to desertification in terrestrial ecosystems.

Bioprospecting and Oil Extraction

At present, threat levels to deep pelagic animals from bioprospecting seem vanishingly small, although the potential for profitable discovery is high (Pomponi 2001). The principal problems will arise after a promising biocompound is discovered. Ideally, laboratory synthesis should provide adequate supplies for subsequent commercial testing and development. Nevertheless, many marine bioactive compounds are highly complex and difficult to synthesize in the quantities necessary for industrial-scale processing (Faulkner 2000). Thus, harvesting from the natural habitat may be necessary. For screening purposes the material requirements are small, but for development stages, many tons may be necessary, bringing about the threat. Selective harvesting of a deep pelagic species in large quantities will be very challenging and will likely require indiscriminate, large-volume collecting. Problems of bycatch and consequent damage to hundreds of other species or to entire communities may ensue.

As offshore drilling technology evolves, rigs and platforms are moving ever deeper. In the Gulf of Mexico drilling rigs are working in water depths over 2000 m, and an exploratory well has been drilled in water 3000 m deep. A consequence of offshore drilling is the discharge of drilling fluids and cuttings. Drilling fluids are often recycled, but they are also released intermittently throughout the drilling process. Their constituents include barite and bentonite to increase density and viscosity. Toxicity studies, bioaccumulation studies, and field monitoring have indicated relatively little negative impact from short-term exposure to water-based drilling fluids (e.g., Neff et al. 1989), but only benthic animals have been studied. Non-aqueous drilling fluids have substantially higher negative impact (Melton et al. 2000). Another type of discharge, generated in high volumes from working offshore wells, is "produced water" or water that has been trapped, long-term, with oil and gas below the seafloor. Unlike drilling fluids, which are associated only with drilling, produced water is generated as long as the well is active. Produced water may be treated to remove some contaminants before being discharged or recycled through the well, depending on local regulations and compliance, but polycyclic aromatic hydrocarbons remain as a particular

concern for negative environmental impact, especially for pelagic species (Durell et al. 2006). The effects of these discharges on deep pelagic animals are unknown.

Iron Fertilization and Waste Disposal

The debate continues over whether it is useful or appropriate to artificially fertilize the ocean with iron to draw down atmospheric levels of CO_2 (Chisholm et al. 2001; Buesseler & Boyd 2003). The effects of large-scale fertilization on the deep pelagic fauna might include a reduction in the oxygen content of the midwaters due to the oxidation of sinking phytoplankton masses by microbes, and a restructuring of planktonic communities near the surface due to species shifts among the targeted phytoplankton (Koslow 2007). Either effect could have a substantial impact on the deep-living biota.

In a progression of agreements from 1972 to 1996, the London Convention and Protocol has led to international bans on the dumping of radioactive and other industrial wastes at sea (IMO 2003). Nevertheless, the deep seabed has long been attractive as a site for depositing humankind's worst waste products, based on the principle of out of sight, out of mind. This alternative still has advocates. The principal problem with all such dumping is that once these materials are on the deep seabed, they are nearly impossible to extract if later it is determined to be not such a good idea after all. For example, before it was known how ephemeral polar ice sheets can be, they were seriously considered as burial sites for long-term radioactive waste disposal (OTA 1985). The very remoteness and inaccessibility of the deep ocean, factors that make it so appealing as a dumping ground, are also what make it so dangerous to consider. Once in place the transfer of pollutants to the deep pelagic food web is most likely to occur through contaminated sediments resuspended by activity or currents and ingested by filter-feeding pelagic animals, and through trophic transfer by benthopelagic animals.

Policy Recommendations

Establish a Baseline

The oceans are in transition: rising temperatures, overfishing, acidification, and pollution are growing threats that individually and interactively will have profound effects on deep oceanic biology. As the ocean's stewards, we must answer the following questions: How can the effects of these changes be recognized, measured, and evaluated? How can predictive capability be gained so that policies can be developed that will positively affect the deep oceans?

Biodiversity is a fundamental measure of ecosystems that is widely used as a diagnostic indicator of environmental status. Sufficient data are lacking to determine

the rates and directions of ongoing changes in the biodiversity of deep pelagic systems or to identify and quantify the ecosystem services they provide. With no baseline, the problem cannot be assessed. To develop such a baseline, the following fundamental questions must be addressed: What practical definitions of biodiversity can be applied to this fauna? What are the ecologically valid spatial scales that should be measured? What are the appropriate temporal scales to investigate? What synoptic environmental measurements must also be made? What are the technological limitations and potential solutions?

The task of establishing a biodiversity baseline for the deep pelagic biota is daunting if only because of the sheer size of the habitat. Angel (1993) points out that "[t]he scales of oceanic ecosystems are so large that the methodologies developed for terrestrial conservation and resource management are inapplicable." Nevertheless, this challenge can be met, and it is long past time we started. As for locations, the large-scale patterns of pelagic biodiversity are apparent from biogeographic investigations over the last century. Locality, exclusive of neritic regions, is far less important than in terrestrial ecology (Angel 1997), although local productivity levels affect diversity, biomass, and abundance and isolated populations may be more common than expected (Miya & Nishida 1997).

The initial content of a baseline data set would be a list of species and their relative abundances. Alternatives to complete biodiversity baselines include the assessment of functional ecological groupings at each trophic level, such as guilds of predatory fishes or large, omnivorous siphonophores. Another approach is to measure the diversity of taxonomic proxy groups (Solow 1995), such as copepods or ctenophores.

Protected Areas

Efforts to conserve deep-sea biodiversity have focused chiefly on seamounts, deep-sea corals, and damage by indiscriminate bottom trawling (Watling & Norse 1998; Thrush & Dayton 2002; Gianni 2004). Considerations of pelagic protection have been directed at the conservation of wide-ranging, epipelagic megafauna (Norse 2005*b*), and because these animals are often migratory, the concept of a fixed area may be inappropriate. But for deep pelagic animals, which are far less mobile, a geographically static protected area makes sense. The general concept of an open-ocean international reserve that included the full water column and the deep seafloor was proposed by Mills and Carlton (1998). They envisioned restrictions on shipping, fishing, mining, dumping, weapons, and floating cities. They also argued that such refuges should be established soon, without holding out for more data on the best location or optimal size.

Although this latter point might seem controversial, the issue of moving quickly to begin protecting some representative component of deep pelagic biodiversity is not unreasonable. The question then becomes how to select the areas to protect. The basic ocean-scale patterns of pelagic biogeography are well established (Angel 1997), and the identification of regions for conservation that are typical of the major oceanic provinces would be straightforward (Lourie & Vincent 2004). Likewise, the spatial and temporal dynamics of basic ocean processes that affect these provinces are well known. Biodiversity hotspots (Myers et al. 2000) within the principal oceanic provinces could define the location of suitable reserves. Linking the protection of deep pelagic biodiversity to deep benthic communities would be the most effective approach to policy and management because the two faunas are ecologically coupled.

Discussion

How is it that the greatest assemblage of animal species on the planet has been largely overlooked in plans for conserving marine biodiversity? The simple truth is that they live in an immense and inaccessible habitat that is difficult to sample and even harder to visualize. The account of threats presented here is incomplete, but it reflects the scope of the challenges to deep pelagic biodiversity. Although some threats stem from resource extraction and industrial use, climate change and acidification have an irreversible momentum that will build in the short term, regardless of human efforts at mitigation. These two forces will directly and indirectly affect the deep pelagic biota through the physiological effects of temperature change and hypercapnia and through alterations in the food web that supplies their nutrition. The underlying issue, regardless of the specific threat, is that this enormous reservoir of animal diversity must be included when the implications of these developments are discussed.

Removing vertebrate top predators has had a profound effect on biodiversity in coastal ecosystems. Historical reconstruction of ecosystems before their transformation by human or natural influences is a valuable tool for conservation and restoration (Jackson 2001; Willis & Birks 2006), but in deep water the raw materials for attaining historical perspectives may not be available. Although we can apply lessons learned from coastal and terrestrial ecosystems to the high seas, specific knowledge of what was natural is elusive. In addition, there is the similar problem of "shifting baseline syndrome" in fisheries science (Pauly 1995). Given the changes occurring in the upper layers of the ocean, there can be little doubt that substantive changes must be taking place in deeper waters as well. Yet because there is no baseline of species composition and relative abundance for the deep pelagic biota, we cannot quantify or evaluate those deep changes. The longer we wait, the farther we will be from knowing what constitutes a pristine natural system.

Baseline studies could begin immediately because there are no technological limitations or international constraints, and the resource requirements for such an effort are relatively small. The Census of Marine Life's MAR-ECO project reflects the broad scope of international expertise that can be successfully brought to bear on this issue (Bergstad et al. 2008). Protected areas will take more time to initiate and will require a greater effort, if only for the requirements of international agreements. But as Mills and Carlton (1988) argue, we should not wait to get started.

The phrase *protecting marine biodiversity on the high seas* is common language in most international agreements regarding deep marine protected areas. But the existing agreements focus almost exclusively on the seabed (Ardron et al. 2008). An important policy development will be to change the substance of these agreements to include protection of the full water column above the seafloor as well. Recently, the scope of biodiversity protection language has begun to expand in international agreements about protection of the high seas (e.g., IUCN 2008).

Another necessary policy initiative is to elevate the level of public awareness about the existence of deep pelagic animals and their significance in Earth's biosphere. This immense resource is our common heritage, and yet the high seas are still a frontier, and their exploitation takes place without regard for our common good. Common sense tells us that the oceans should be protected and that protection should include the conservation of deep pelagic biodiversity.

The single most important point of this review is the salient fact that despite the global significance of the deep pelagic fauna and the obvious benefits of protecting its biodiversity, the basic information necessary to do so is still lacking. There is no baseline. Even so, we must begin the process of protecting deep pelagic biodiversity without waiting for that job to be finished.

Acknowledgments

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