16 Human Impact, Biodiversity and Ecosystem Processes in the Open Ocean

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16.1 INTRODUCTION

Only recently have efforts begun to focus the attention of the scientific community on issues of the status of global marine biodiversity and the potential ramifications on basic ecosystem processes. Two of the current initiatives are Norse's (1993) coordination of the development of a global marine biodiversity strategy and BIOMAR (Butman and Carlton 1993; NRC 1995), a US effort to establish and fund a research agenda. While both initiatives consider oceanic and coastal ecosystems, neither focussed specifically on open-ocean biodiversity. Our purpose here is to spur discourse specifically on open-ocean biodiversity, and focus attention on the possible links between changes to biodiversity and response at the ecosystem level. This is in contrast to the usual treatment, in which the impacts of ecosystem alteration on biodiversity are the relevant issue.

The open-ocean biome consists of all marine environments beyond the continental shelf, which extends seawards from all land masses to a depth of 200 m (Figure 16.1). Pelagic and deep-sea (below 200 m) environments exist here. It is the world's largest biome, covering over 70% of the world's surface area and an even greater percentage of its inhabitable volume. It is also the biome about which we know the least. New families and phyla have recently been described, and newly discovered life forms exist in the open ocean that rely on novel energy pathways in ecosystems significantly different from those on land (Edmond and Von Damm 1983; Cavanaugh 1985; Tunnicliffe 1991). In contrast to many terrestrial systems, and some marine environments which have a characteristic biogenic structure and endogenous properties, oceanic systems are thought to be structured primarily through physical processes (Steele 1985; Holling 1992; Holling *et*

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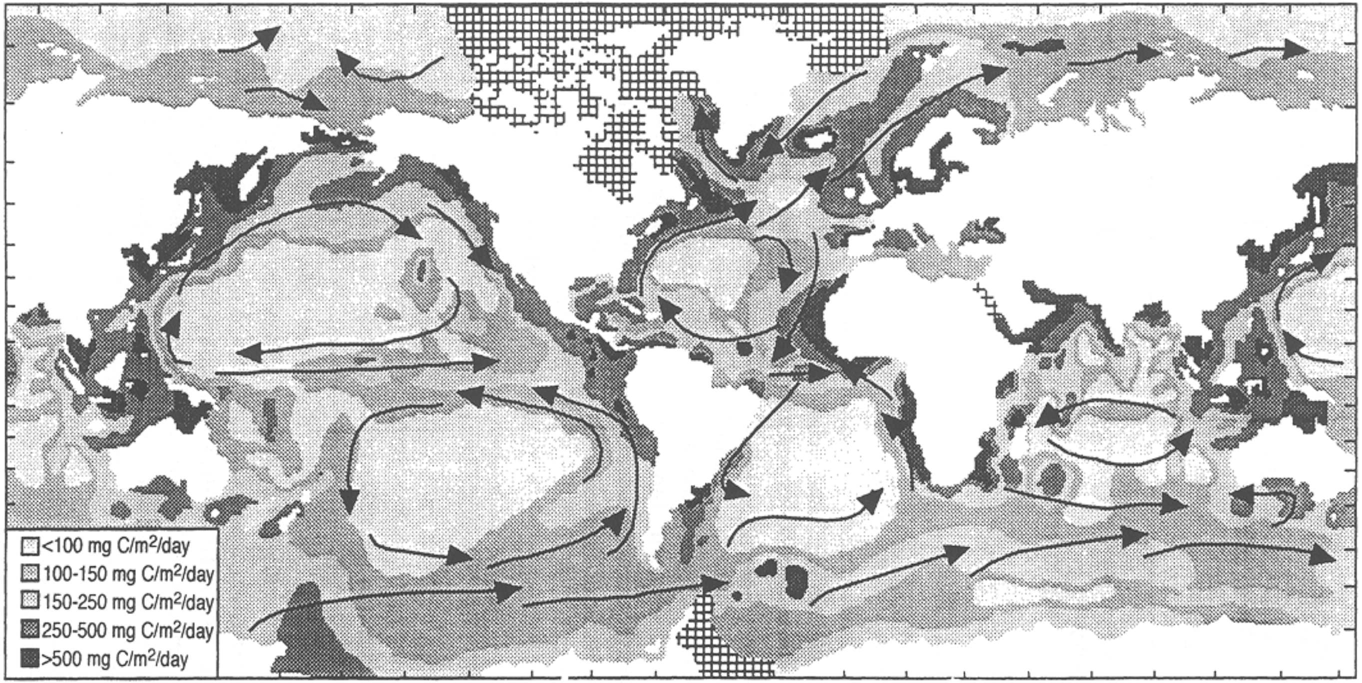

Figure 16.1 A representation of the world's oceans, showing levels of primary productivity in mg C fixed per square metre per day (after map 1.1 in *Atlas of the Living Resources of the Seas*, FAO, Rome, 1972), and the major currents that structure the ocean's basins. The open ocean covers all marine environments away from land and is usually defined by the continental shelf, which extends from land to a depth of about 200 m, or about 200 km from the shore. The actual boundary between coastal and ocean biomes depends on the prevailing currents, and is thus highly dynamic

al. 1994). We begin by describing the principal physical forces that structure open-ocean ecosystems, and follow with a brief introduction to the patterns of oceanic biodiversity that map onto this physical template. We then provide a summary of the ways that humans impact open-ocean diversity. A simple theoretical framework is then given that couples ocean biodiversity and ecosystem processes.

We propose that seven general ecosystem processes operate in the open ocean, and then examine where the important functional groups reside. We then list where the strongest evidence exists for a relationship between diversity and processes. Although we know little about the functional role of many of the species that reside in this biome, the extent of potential impacts is clearly great.

16.2 PATTERNS OF OPEN-OCEAN DIVERSITY

16.2.1 Structure of the waterscape

Open-ocean environments are principally differentiated by their physical and chemical differences. All ocean ecosystems are closely inter-linked by a dynamic medium (water), which is mixed by currents that operate at all scales and link latitudinal extremes with each other and connect the deep ocean with pelagic environments. Because of the over-all connectedness of oceanic environments, delimiting major biogeographic regions is not a trivial task (Rex 1983), We present here a hierarchical classification system of the fundamental ecosystems found in open oceans which reflect key processes that structure these ecosystems. These processes are the source of energy for primary producers, the physical heterogeneity of the environment, depth and latitude (Figure 16.2).

Most organic compounds in the marine environment are derived from photosynthesis in the upper layers of pelagic environment. This is not the sole source of energy for ocean life. Organisms which do not depend upon photosynthetic energy were first discovered around geysers, but the most flourishing of these communities occur around hydrothermal vents and cold seeps in the open ocean and marginal seas (Edmond and Von Damm 1983; Tunnicliffe 1991). The primary source of energy for these communities is chemosynthesis, generated by free-living bacteria (thermophilous at 100°C) using as electron donors Fe, Mn, SO_4 and CH_4 among others (Huber *et al.* 1989). These novel communities were discovered less than 20 years ago, and more than 190 new species have been described from them (Grassle 1989; Van Dover 1990). Symbiosis with bacteria is a common characteristic of many of the metazoan species found in hydrothermal vents and cold seeps (Roberts *et al.* 1991; Cavanaugh 1994).

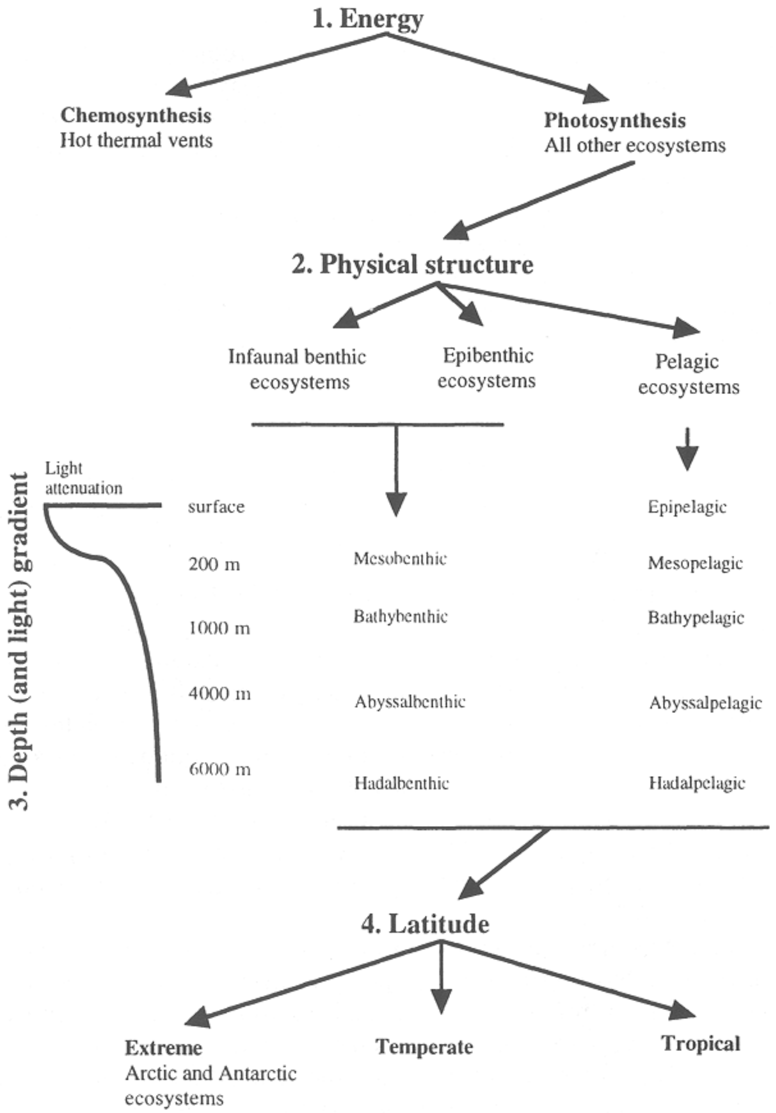

Figure 16.2 A heuristic view of the mechanisms that structure open-ocean basins (after Chandler *et al.* 1996)

Most terrestrial and coastal communities are delimited by some dominant form of life (usually but not exclusively an angiosperm: for example, temperate deciduous, boreal coniferous and tropical forests, grasslands, kelp beds and coral reefs). The separation of open-ocean communities is usually by physical or chemical parameters. A subtle boundary separates the epipelagic from the mesopelagic ecosystem, defined by a combination of light penetration depth (photic zone), thermocline and wind-driven mixing depth. Usually all of these processes are manifested between 100 and 200 m depth. The epipelagic ecosystem often extends over the edge of the continental shelf, and the lateral distinction between epipelagic and coastal surface waters is highly dynamic. This boundary is sometimes sharpened by the meeting of different water masses (oceanic fronts), for example, at the inner edge of the Gulf Stream off the eastern United States. It may also be greatly blurred, both by periodic littoral incursions of large, highly-mobile pelagic species such as tuna (*Thunnus*) and leatherback turtles (*Eretmochelys*), and by warm-core gyres containing translocated epipelagic assemblages in a coastal sea.

In some coastal areas, a narrow continental shelf drops precipitously to extremely deep water, bringing the open-ocean water column into unusually close proximity to the shore and terrigenous influences. This we refer to as the coastal open-ocean ecosystem. The distinction is more than semantic: it is here that land-based impacts are likely to have the most direct and immediate effect on pelagic assemblages. It is also where alterations in pelagic biodiversity and food-web structure have the most immediate effect upon human society. Cold, nutrient-rich waters are upwelled in coastal areas, stimulating primary production that cascades through the mesopelagic and down to the benthic communities. The mesopelagic and abyssal benthic ecosystems are commonly referred to as the "deep sea". The largest inhabited volume on earth is the mesopelagic realm. Here organisms exist at 1°C, in darkness, at extremely low organic carbon levels and organism densities.

The effect of latitude on the duration and intensity of seasons also plays a major role in structuring oceanic communities. In most tropical oceans, the build-up of a permanent thermocline inhibits the redistribution of nutrient-rich waters from the deep, up into the nutrient-depleted photic layer. In contrast, temperate epipelagic waters are more productive, but also more variable. Seasonal changes in productivity alter the temporal distribution of nutrients to the benthic community, impacting reproduction, and thus affecting recruitment in the deep sea. The ocean currents which provide boundaries for many of the ocean's regions are to a large degree determined by winds, which themselves are determined by latitude and gravitational forces (Coriolis). These currents play a large role in the shaping of the ecological communities in the open oceans (Figure 16.1).

Although the pelagic realm dominates the inhabitable volume of the open ocean, the greatest diversity of marine life inhabits the physically structured benthos. Here, often fast-moving, cold currents descend from the poles and move towards the equator, occasionally creating powerful underwater storms which carry vast amounts of sediment across the ocean bottom, disrupting much of the epibenthic life (reviewed by Hollister *et al.* 1983). Colonization of benthic communities following medium- to large-scale disturbances has been found to be generally slow for macro-, meio- and micro-fauna in one experiment (Desbruyeres *et al.* 1985), and dependent on opportunistic colonization events (Grassle and Morse-Porteous 1987; Grassle 1989).

Open-ocean systems are heterogeneous at all scales (Figure 16.3a; Steele 1985; Colebrook 1991; Kawasaki 1991); hydrodynamic structure predominates and is provided to oceanic systems principally by currents and waves from small-scale eddies, through warm-core rings of water moving across ocean basins, to transoceanic currents (Figure 16.3a,b). Some ocean basins are biologically more self-contained; large-scale circulating masses of water, or gyres, dominate the North Pacific and North Atlantic Oceans. Other basins are more dynamic or open (e.g. currents: the Atlantic–Pacific conveyor belt, the Gulf Stream). Mesoscale structure in the pelagic is provided by floating rafts of weed (e.g. Sargasso Sea) and/or flotsam, sea-ice, storms and large mats of diatoms (Kemp and Baldauf 1993). In the benthos, there are abyssal plains (structured by turbidity currents), rifts and occasional deadfall (wood or animal carcasses). Temporal variation also occurs at all levels, from diurnal fluctuations in light, to tidal cycles and annual cycles, up to the Milankovitch cycles. Although the dynamics are poorly understood, long-term variability in the abundance of fish and plankton has suggested important concordance between climate and ecosystem processes (Cushing 1982; Colebrook 1991; Kawasaki 1991).

16.2.2 Phyletic diversity

Knowledge about species diversity in the open ocean is inadequate (NRC 1995). Many of the latest scientific publications on open oceans are devoted to describing new species; familiar species, thought to be robust, are revealing a much more complex nature when analyzed using molecular tools. The biomonitoring workhorse, *Mytilus edulis*, is in fact at least three different species and not one (McDonald *et al.* 1992), and the polychaete *Capitella capitata*, once thought to be a single cosmopolitan species, is in fact a complex of at least 15 different taxa (Grassle 1980). Approximately 15% of currently described species are marine, and a rough calculation suggests that about 2% are found in the open ocean (Groombridge 1992). Recent sampling of deep-sea benthic communities has revealed a much higher number of undiscovered taxa than anticipated (Sanders 1968, 1977; Sanders and Hessler 1969; Grassle *et al.* 1991; Poore and Wilson 1993; Poore *et al.* 1994), pushing up estimates of marine biodiversity substantially (Grassle *et al.* 1991; Angel 1993). If these estimates are correct, the deep-sea benthos will be one of the most diverse ecosystems in the world (but see Briggs 1994).

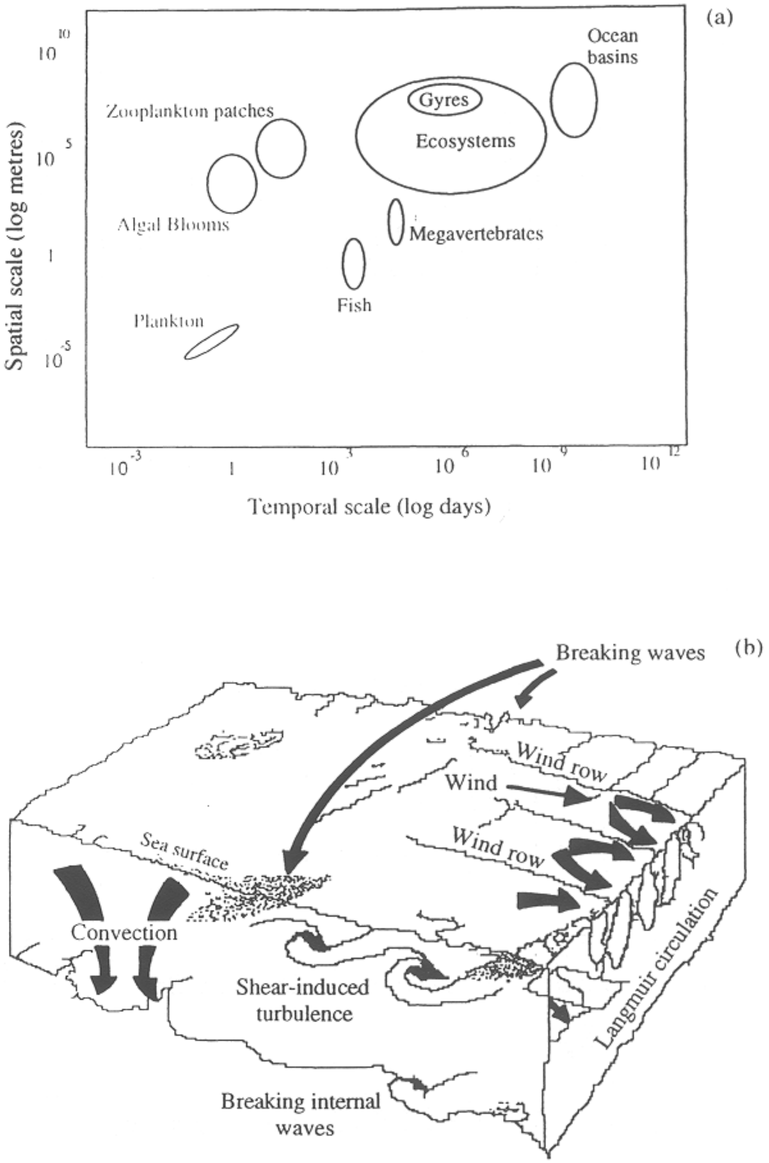

Figure 16.3 (a) The temporal and spatial scaling of processes that structure the open oceans, and (b) the scaling of the principal mixing processes in the epipelagic ecosystem (after E.T. Degens, *Perspectives on Biogeochemistry* Springer, 1989). Each "wave" operates at a different scale, creating a continuum of physical disturbances. Larger oceanic currents such as the Gulf Stream or the Humboldt Current would be superimposed on top of these smaller-scale "waves"

Table 16.1 A complete list of phyletic biodiversity of eukaryotic organims. The phylogeny is taken from Margulis and Schwartz (1988). Information about a phylum's biome, lifestyle, the marine biome and habitat is provided. If a category was only occasionally found in a phyla then it was included in parentheses. Working estimate of species diversity were derived from the most recent literature avialable. The number of species described was similarly derived

Phylum	Biome[1]	Lifestyle[2]	Marine biome	Marine habitat	Working estimate	Described species	Source
Animalia							
Acanthocephala	Fw/Ma/Te	P	Coastal		1150	700	Rupert and Barnes (1994)
Annelida	Ma(Fw, Te)	C/D (P)	Coastal/oceanic	Benthic	8700	8700	Barnes (1989)
Arthropoda	Fw/Ma/Te	C/D	Coastal/oceanic	Benthic/pelagic	9 000 000	1 000 000	Groombridge (1992)
Brachipoda	Ma	C	Coastal/oceanic	Benthic	325	325	Barnes (1989)
Chaetognatha	Ma	C	Coastal/oceanic	Pelagic	100	100	Brusca and Brusca (1990)
Chordata	Fw/Ma/Te	C	Coastal/oceanic	Benthic/pelagic	49 933	49 933	Barnes (1989)
Cnidaria	Ma(Fw)	C	Coastal (oceanic)	Benthic/pelagic	9000	9000	Barnes (1989)
Ctenophora	Ma	C	Coastal/oceanic	Pelagic (benthic)	50	50	Barnes (1989)
Echinodermata	Ma	C	Coastal (oceanic)	Benthic	6000	6000	Barnes (1989)
Echiura	Ma	D	Coastal (oceanic)	Benthic	140	140	Barnes (1989)
Ectoprocta (Bryozoa)	Ma(Fw)	C	Coastal	Benthic	5000	4000	Rupert and Barnes (1994)
Entoprocta	Ma(Fw)	C	Coastal	Benthic	150	150	Barnes (1989)
Gastrotricha	Ma(Fw)	c/d	Coastal/oceanic	Benthic	460	460	Barnes (1989)
Gnathostomulida	Ma	C	Coastal/oceanic	Benthic	100	80	Barnes (1989)
Hemichordata	Ma	C/D	Coastal/oceanic	Benthic	85	85	Barnes (1989)
Kinorhyncha	Ma	C	Coastal/oceanic	Benthic	150	150	Rupert and Barnes (1994)
Loricifera	Ma	C	Coastal/oceanic	Benthic	9		
Pogonophora	Ma	C	Coastal/oceanic	Benthic	80	80	Barnes (1989)
Porifera	Ma (Fw)	C	Coastal (oceanic)	Benthic	10 000	5000	Barnes (1989)
Priapula	Ma	Ca	Coastal/oceanic	Benthic	13	13	Barnes (1989)
Rotifera	Fw (Ma, Te)	C	Coastal	Benthic	2000	1500	Rupert and Barnes (1994)
Sipuncula	Ma	C	Coastal	Benthic	320	320	Barnes (1989)
Tardigrada	Te (Fw, Ma)	C/D	Coastal/oceanic	Benthic	600	600	Rupert and Barnes (1994)
Fungi							
Ascomycota	Te (Fw, Ma)	C/D/P			30 000	30 000	Raven *et al.* (1981)
Basidiomycota	Te	C/D/P			25 000	25 000	Raven *et al.* (1981)
Deuteromycota	Te	D/P			25 000	25 000	Raven *et al.* (1981)
Zygomycota	Te	D (P)			600	600	Margulis and Schwartz (1988)
Mycophycophta	Te	C/D/PP			18 500	17 000	Groombridge (1992)

Plantae							
Angiospermophyta	Te (Fw, Ma)	PP	Coastal	Benthic	300 000	250 000	Groombridge (1992)
Bryophyta	Te (Fw)	PP		Benthic	14 000	14 000	Groombridge (1992)
Conferophyta	Te	PP			596	596	Groombridge (1992)
Cycadophyta	Te	PP			101	101	Groombridge (1992)
Filicinophyta	Te	PP			12 000	12 000	Groombridge (1992)
Ginkgophyta	Te	PP			1	1	Groombridge (1992)
Gnetophyta	Te	PP			71	71	Groombridge (1992)
Lycopodophyta	Te	PP			1390	1390	Groombridge (1992)
Psilophyta	Te	PP			7	6	Groombridge (1992)
Sphenophyta	Te	PP			22	22	Groombridge (1992)
Protoctista							
Acrasiomycota	Te	C/D			26	26	Curtis (1975)
Actinopoda	Ma (Fw)	C	Coastal/oceanic	Pelagic (benthic)	6000	6000	Vickerman (1992)
Apicomplexa	Te	P			5000	5000	Vickerman (1992)
Bacillariophyta	Fw/Ma	PP	Coastal/oceanic	Pelagic	100 000	12 000	Andersen (1992)
Caryoblastea	Fw	C/D			1	1	Margulis and Schwartz (1988)
Chlorophyta	Ma (Fw)	PP	Coastal (oceanic)	Benthic (pelagic)	10 000	2600	Andersen (1992)
Chrysophyta	Fw (Ma)	PP	Coastal/oceanic		2400	1200	Andersen (1992)
Chytridiomcota	Fw/Te	P/D			750	750	Raven *et al.* (1981)
Ciliphora	Fw/Te/Ma	C			8000	8000	Margulis and Schwartz (1988)
Cnidiosporidia	Ma	P	Coastal/oceanic		800	800	Vickerman (1992)
Cryptophyta	Fw (Ma)	C/(P)			1200	200	Andersen (1992)
Dinoflagellata	Ma (Fw)	PP/C	Coastal/oceanic	Pelagic	7250	3250	Andersen (1992)
Euglinophyta	Fw (Ma)	PP			2000	900	Andersen (1992)
Eustigmatophyta	Fw	C		Pelagic	5500	12	Anderson (1992)
Foraminifera	Ma	C/(PP)	Coastal/oceanic	Benthic (pelagic)	10 000	7000	Vickerman (1992)[3]
Gamophyta	Fw	PP			20 000	12 000	Andersen (1992)
Haptophyta	Ma (Fw)	PP	Coastal/oceanic	Pelagic	500	500	Vickerman (1992)
Hyphocytridiomycota	Fw	P/D			15	15	Margulis and Schwartz (1988)
Labyrinthulomycota	Ma (Fw)	P	Coastal/oceanic	Benthic	36	36	Vickerman (1992)
Myxomycota	Te	D			500	450	Raven *et al.* (1981)
Oomycota	Fw (Te)	P			500	475	Margulis and Schwartz (1988)
Phaeophyta	Ma	PP	Coastal (oceanic)	Benthic (pelagic)	2000	1500	Andersen (1992)
Plasmodiophoromycota	Te	P			35	35	Margulis and Schwartz (1988)
Rhizopoda	Fw/Te (Ma)	C (P)			2500	2500	Vickerman (1992)
Rhodophyta	Ma (Fw)	PP	Coastal (oceanic)	Benthic (pelagic)	12 750	5000	Andersen (1992)
Xanthophyta	Fw	C			2000	600	Andersen (1992)
Zoomastigina	Fw/Te	P/C			1200[4]		Vickerman (1992)

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[1] Biome: Ma, marine; Te, terrestrial; Fw, freshwater: [2] Lifestyle: PP, primary producers; P, parasitic; F, free-living; C, consumers; D, detritivores. [3] Barnes (1989) contributed the number of species described. [4] The species estimate for Zoomastigina was from Vickerman (1992) and Rupert and Barnes (1994).

Differences at higher phyletic levels Differences in biodiversity between marine and terrestrial systems are perhaps most pronounced at higher taxonomic levels (Table 16.1; May 1988, 1992; Ray and Grassle 1991; Angel 1993). Over half of the phyletic diversity of animals are unique to the open ocean, most probably because life has existed there for longer than elsewhere. In contrast, almost all fungal and plant phyla are terrestrial. Overall, there are more marine phyla than terrestrial phyla, and marine phyla are more evenly distributed with respect to extant species richness, a measure of present-day radiation (Figure 16.4). The most successful terrestrial phyla have more species than their marine counterparts; the most successful phyla are those which have adapted well to existence on land and in the water. The functional diversity of marine organisms, reflected in some part by this phyletic diversity, is even more profound. Indeed, the evolution of functional diversity on earth began as life's first prokaryotes attempted to use fundamentally different biochemical pathways in an ocean of primary compounds. Life on earth faced a harsh environment without an atmosphere to stabilize the climate, and thus a variety of extreme habitats existed. Under such circumstances, there emerged a plethora of respiratory and metabolic pathways, leading to very different ways of living (Fenchel and Finlay 1994; Trüper 1992). Many of the original functional groups still exist on earth, but not on land, and so are hidden from human perspective. These organisms dwell in environments extreme to our view, i.e. deep down in the earth's core, geysers, hot thermal vents or anoxic sediments (Bolliger *et al.* 1991;

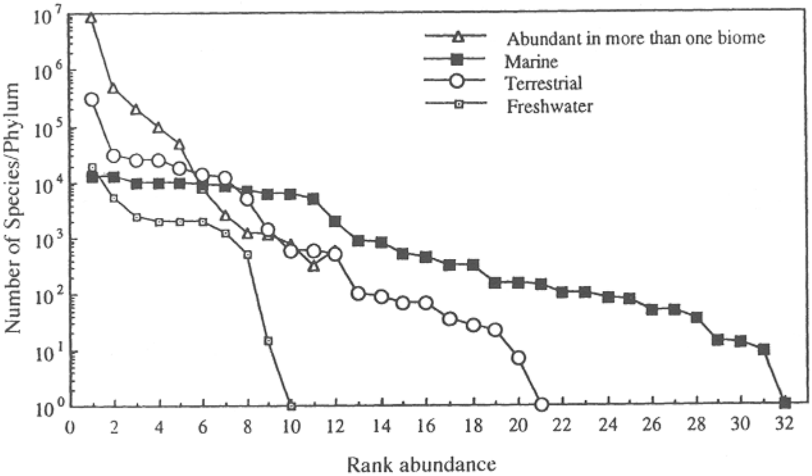

Figure 16.4 The rank abundance of species abundance per phyla for all four eukaryotic kingdoms. The data were drawn from Table 16.1. Phyla were grouped into a single biome if all or almost all (>80% species) occurred in only one biome (see Table 16.1)

Gold 1992). The fact that we frequently overlook these life forms, or that they fail to comply with a narrow species concept distilled chiefly from data on tetrapods, does not diminish their importance to ecosystem processes. These organisms could become even more important in the near future, as hostile environments increase because of anthropogenically caused environmental degradation. The microbial world of both the pelagic and the benthic open are poorly understood, in part because suitable culture techniques have yet to be developed. Recent molecular techniques should increase our knowledge about this group of organisms (Bergh *et al.* 1989; Giovannoni *et al.* 1990; Bolliger *et al.* 1991; Fuhrman *et al.* 1992, 1993).

Are open-ocean communities cosmopolitan? Ocean basins are the pelagic equivalent of continents: each has a distinctive biota, and the pelagic species are widely distributed within a basin (Angel 1993; McGowan and Walker 1993). This impression is reinforced by the distribution of conspicuous elements such as *Physalia* the Portuguese man-of-war, across the globe's oceans. The degree of endemism within ocean basins is generally unknown, and sampling is too sparse to rule out its potential importance. Planktonic diversity, especially the smallest plankton, may be an order of magnitude higher than the number of described species would suggest, given the current rate that taxa are being discovered (Waterbury *et al.* 1979; Li *et al.* 1983; Platt and Li 1986; Chrisholm *et al.* 1988; Fuhrman *et al.* 1992). The supposedly cosmopolitan nature of the plankton is quite possibly a taxonomic artifact (a result of inadequate data and lumping), or the pattern may be real, but anthropogenic, as a result of species introductions (Carlton 1989; Carlton and Geller 1993). Although most deep-sea benthic organisms have planktonic larvae that inhabit the pelagic realm, many benthic organisms have direct development (e.g. species of gastropod) or brood their young (isopods), and are thus capable of extreme regional differentiation. Vinogradova (1979a,b) estimated that 85% of deep-sea fauna was endemic to one ocean. Dispersal in time through the production of dormant spores exists as a strategy among some oceanic species. The significance of such a mode of dispersal is unclear.

16.3 HUMAN IMPACTS ON BIODIVERSITY OF THE OPEN OCEAN

Biodiversity and ecosystem processes are intertwined in a tangled web with complex feedback loops. Changes in one aspect of biodiversity, loss of a top predator for example, will affect some aspect of the food web, which can then lead to changes in other biodiversity and ecosystem processes. Figure 16.5 summarizes the idea that human impacts *interact* to change biodiversity in

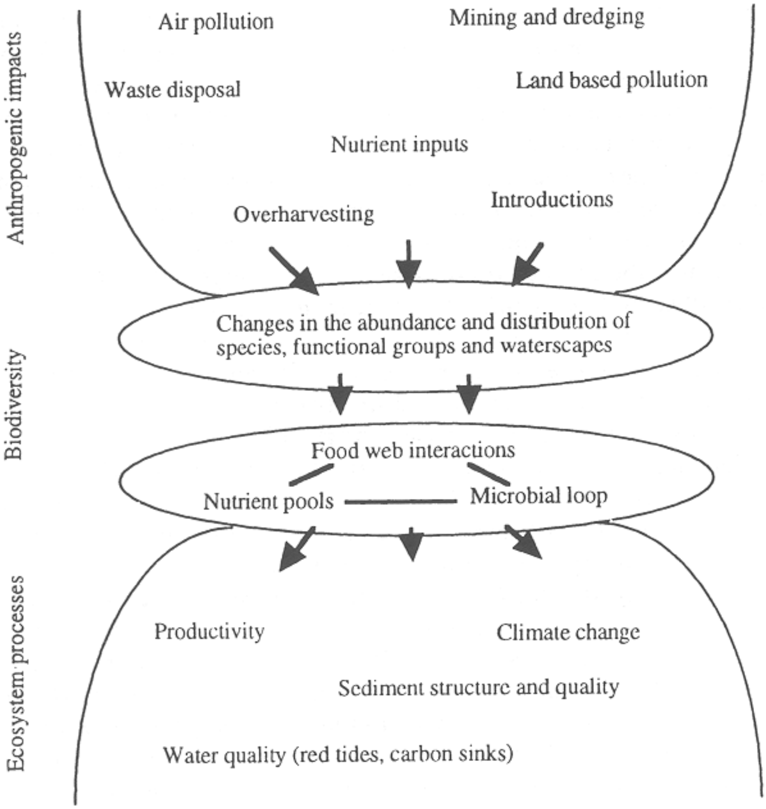

Figure 16.5 A conceptual relationship between anthropogenic impact on biodiversity and subsequent effect on ecosystem processes. Perturbations to ecosystem processes would feed back onto the components of biodiversity, which would lead to further changes to ecosystem processes

many ways. Changes in the distribution and abundance of taxa alter the food web, at least temporarily disturbing it from its previous state. These alterations in the food web can have repercussions on the microbial loop and nutrient pools in the open ocean, which ultimately result in changes to ecosystem processes. This is not meant as a substitute for a careful analysis of the specific effects of impact A on ecosystem process B, but rather a reminder that the impacts are likely to be many-fold, diffuse and not always predictable.

Human impacts on open-ocean biodiversity are as diverse in nature and scale as any on land (Table 16.2). Recent reviews include those by GESAMP (1990) and Norse (1993). Despite the large distances that connect most human activities to the open ocean, much of our impact is land-based (GESAMP 1990).

Table 16.2 A list of potential anthropogenic impacts on coastal and oceanic ecosystems. Coastal systems are limited to the continental shelf; epipelagic systems occur above a depth of 200 m, and the mesopelagic below 200 m. Ranking of impact: ***, expected serious impact; **, expected moderate impact; *, expected mild impact. Indirect effects result from cascading impacts from other ocean systems

	Coastal benthic and pelagic	Open ocean		
		Epipelagic[1]	Mesopelagic	Benthic
Land based activities				
Air pollution				
Change in atmospheric gases (e.g. CO_2, acid rain)	***	***(3,4,7)	Indirect	Indirect
Increased UV radiation	***	***(8,13)	Indirect	Indirect
Global warming	***	***(10)	Indirect	Indirect
Land pollution				
Siltation	***	*(10)	Indirect	**
"Accidental" waste disposal (e.g. flotsam)	***	**(21,22)		*
Waste disposal	***	**(10)		**
Ocean-based activities				
Additions				
Introductions	***	***(5,6)	?	
"Accidental" waste disposal (e.g. oil spills)	***	***(1,11,15–18,20,21)***		
Waste disposal	***	**(11,15–18)		***
Subtractions				
Resource extraction (harvesting and mining)	***	***(2,9,12,14,19)	*****	

[1] Addison 1989; 2, Beddington and May 1982; 3, Broecker 1987; 4, Broeker and Denton 1989; 5, Carlton 1989; 6, Carlton and Geller 1993; 7, Charlson *et al.* 1987; 8, Häder *et al.* 1991; 9, Manire and Gruber 1990; 10, Norse 1993; 11, NRC 1985; 12, Anon. 1994; 13, Smith *et al.* 1992; 14, Thiel 1992; 15, Tanabe *et al.* 1984; 16, Young *et al.* 1985; 17, Tanabe 1988; 18, Cox 1993; 19, Watling and Langton 1994; 20, Suchanek 1994; 21, GESAMP 1990; 22, Suchanek 1993.

16.3.1 Addition and subtraction of species

Direct take in fisheries has had an immense impact on open-ocean food webs, virtually clearing many parts of the ocean of large predators and marine mammals. Of about 200 fisheries tracked by the FAO, fully one-third are severely depleted, and many are on the verge of collapsing, or have already collapsed, commercially. Many fisheries which were thought to be successfully managed for "sustained yield" prove to have experienced a series of sequential collapses of different target species close enough together in time to create the illusion of sustained yield for several years; once the last target species is exhausted, the fishery disintegrates. Exploitation is not limited to adult fishes or mammals. Humans take everything from top carnivores to copepods. The methods employed in pelagic fisheries are particularly non-selective and thus ecologically destructive. Large numbers of sharks, marine mammals, and other non-target species are part of an incidental catch that may equal or exceed the commercial take.

Another important human impact comes from the transport and introduction of many marine species into novel environments via tanker bilge water, etc. (Carlton 1989; Carlton and Geller 1993; see section on productivity).It is often assumed that open-ocean taxa are more cosmopolitan in distribution and that open-ocean systems should be less prone to the introduction of novel organisms, but this has yet to be tested. Introduction of new organisms into an environment may result in the exposure of endemic taxa to novel diseases or predators (Carlton 1989; Carlton and Geller 1993), potentially altering the food web.

16.3.2 Addition and redistribution of chemical substances

The most recent review of ocean pollution concluded that most coastal areas are contaminated, some extensively, but that the open ocean is relatively unimpacted (GESAMP 1990). Despite apparent freedom from human impact, even distant oceanic ecosystems have traces of human activities (Flegal *et al.* 1993); no oceanic system is free from human influence. Pollution has impacted open-ocean systems through chemical discharges, toxic inputs (oil spills, ocean dumping of PCBs, heavy metals, pseudohormones), and alteration of nutrient regimes (Tanabe *et al.* 1984; Young *et al.* 1985; Tanabe 1988; Cox 1993; Suchanek 1993, 1994). Atmospheric pollution has been detected on the deep-sea floor (La Flamme and Hites 1978; Takada *et al.* 1994). Plastic products and monofilament "ghost" drift nets are among the more persistent forms of human-caused hazards that kill substantial amounts of oceanic life (Shomura and Godfrey 1990). Oil input into marine systems may be as high as 8.8×10^6 metric tons per year (NRC 1985). This sort of pollution is currently thought to be a coastal phenomenon, but this idea is almost certainly a product of ignorance. Our knowledge of the "natural" levels of open-ocean water quality is so patchy that almost any change in water quality from anthropogenic causes would go unnoticed. The pervasive nature of chemical pollution suggests that open-ocean organisms and ecosystems are likely to experience the same kinds of disruption as coastal systems, although on a longer time scale, with the exception of acute local impacts from leakage of oil or other contaminants at depth. The biomagnification of toxins up through the food web could lead to significant changes in community structure if the larger apex organisms are negatively affected (Tanabe *et al.* 1984; Tanabe 1988; Addison 1989). These changes in community structure could have ramifications through changes to the food web, microbial loops, nutrient pools and feedback to the atmosphere.

16.3.3 Indirect alteration of ecological processes

Not all human impacts are simple or direct. The occurrence of toxic blooms of dinoflagellates (e.g. red tides) appears to have increased substantially over the past couple of decades (Smayda 1989; World Resources Institute 1992; Hallegraeff 1993; Anderson 1994). The toxins impact shellfish and humans, potentially causing extensive mortality. The increase in frequency of red tides has been tied to increased nutrient inputs to coastal systems. The blooms may be primarily coastal in nature, but this may be an artifact of observation. Limited monitoring of dynamic events in the open ocean leaves the question of impact of toxic algal blooms very much as open one.

A decrease in the earth's ozone protection will allow more biologically damaging UV–B radiation to reach sea-level. Atmospheric UV–B radiation can penetrate through tens of meters of water in most marine environments (Smith *et al.* 1992). UV–B radiation at levels found today in some oceans is known to be detrimental to many forms of life in marine ecosystems at all levels (Hunter *et al.* 1981; Hardy and Gucinski 1989; Häder *et al.* 1989; Karentz *et al.* 1991; Behrenfeld *et al.* 1993a, 1993 b; Herndl *et al.* 1993; Bothwell *et al.* 1994). Historic alterations to the atmosphere point to planktonic species being the most sensitive species (McKinney 1987), suggesting that they would suffer first from current changes to the atmosphere.

Climate change will have a significant, but largely unpredictable, impact on the open ocean. Changes in sea-surface temperature can alter wind patterns and thus oceanic currents. Because hydrodynamics affects the ecological and evolutionary spatial and temporal scale of so much of oceanic life, any change to ocean currents will percolate throughout the pelagic food-web and down to the benthos. Past climatic changes are thought to have been the principal driving forces behind shifts in the abundance of the dominant fishes in many different systems (Alheit and Bernal 1993; Bas 1993; Kuznetsov *et al.* 1993; Tang 1993). Oscillations in the relationship between oceanic and atmospheric conditions in the Southern Ocean periodically produce meteorological events known as the El Niño phenomenon. Off the Pacific coast of South America, El Niño years result in significant shifts in water masses of different temperature, with accompanying shifts in productivity and diversity. Coastal-based seabirds and marine mammals may die by the tens to hundreds of thousands during particularly strong El Niño years. Although initially thought to be a localized phenomenon, the El Niño Southern Oscillation is now known to have global effects with largely unpredictable results. It is likely that anthropogenic alterations to the world's atmosphere or oceans will modify El Niño events, and thus the distribution of productivity and biodiversity, although the direction and magnitude of this change in uncertain.

Open-ocean biomes are generally not dominated by biogenic structure, such as angiosperms, that humans can alter. Reports at the close of the 19th century talk of "seas of weeds" in the centers of many of the major ocean basins, but there has not been a single report of this phenomenon in recent years (J.T. Carlton, personal communication 1994). The reasons why this pelagic biogenic superstructure has disappeared are unclear. In the Sargasso Sea, very large rafts of floating seaweeds support a complex community complete with pelagic morphotypes of *Ascophyllum* and *Fucus*, and an endemic isopod, *Idotea metallica*. The disappearance of the seaweeds will have an impact on forms of life that depend on it.

Physical structure is important to the functioning of the deep benthos, primarily because of the tunneling and mixing of the sediments by specific biota, which alter biogeochemical cycling of nutrients and oxygen availability. Much of the benthic environment is very distant from most human activities, although mining and the collection of benthic organisms by dragging sleds or nets may impact significant members of the benthic community (Watling and Langton 1994). Because of the importance of bioturbation in modulating the quality of the sediments, a reduction in the diversity of these taxa will have a significant impact on the rest of the community that can be supported in the benthos.

Removal of manganese nodules by mining can eliminate one important type of surface structure exploited by a distinct assemblage of epifauna (Thiel 1992). Several decades may be required for the re-establishment of these communities. Whether this activity has altered in any manner the biodiversity living in these environments is unknown, but the possibility for impact exists through alteration of physical structure, chemical or radiological contamination, and alteration of nutrient inputs from surface waters.

16.4 BIODIVERSITY AND ECOSYSTEM PROCESSES: GENERAL THOUGHTS

Whether species are important to the "functioning" of ecosystems processes has often been phrased as choosing between the species as "rivets" hypothesis (Ehrlich and Ehrlich 1981), and the species as "passengers" hypothesis (Walker 1992). In the latter case, one, or a very few, species are key to the operation of the ecosystem process; the other species are accessories that play no additional role in the system, in effect, passengers on a bus driven by a few key species. Under the rivet hypothesis, each species has a small yet important role in the dynamics of the system, and although the removal of one species may not lead to any perceptible loss in the functioning of the ecosystem, loss of several species will lead to a gradual reduction in the ability of the ecosystem to "sustain" itself. A continuum exists between these two hypotheses; at one extreme, variance in the contribution of each species to ecosystem processes is high, and at the other extreme, all species are equal contributors and variance is minimized.

One must consider at least one other factor when assessing the role of diversity in ecosystem processes. Ecosystems are dynamic entities, structured by processes that operate at multiple scales, and the dynamics of any one patch is generally unpredictable in either time or space (Williamson 1988; Bell 1992; Holling 1992; Bell *et al.* 1993). Some processes occur in a more or less predictable cycle, especially when there is some endogenous biological feature to the process (e.g. fire, spruce budworm outbreaks, hare–lynx population cycles). Other processes are less predictable (i.e. rare colonization events, volcanic eruptions), and are independent of the organisms that form part of the ecosystem. With respect to identifying the relative importance of species to ecosystem processes, an understanding of the predictable dynamics that occur in ecosystems can help identify the species important in the succession of communities that maintain sustainability or system resilience over scales that matter to the functioning of whole ecosystems. What about the less predictable dynamics that occur, such as the "accidental" introduction of alien species (chestnut blight, rabbits, cattle egrets), or other dramatic changes to the landscape? In these cases, ecosystems are less likely to be pre-adapted to these specific perturbations, and stability may depend on unforeseen properties of the species assembly. When stochastic effects play a large role in ecosystem dynamics, our ability to predict the importance of specific biodiversity in ecosystem processes decreases as temporal and spatial scales increase.

It would be difficult to come up with a list of the most indispensable species for even the best-studied ecosystem, let alone one such as the open ocean, about which so little is known. The four areas of ecosystem dynamics that we know least well, and for which ranking species for importance is most difficult, are:

- identifying the alternate states of each stage of succession, and the paths between successional stages;
- identifying the facilitator or mediator species that help direct the rate and direction of succession;
- identifying the species that buffer the ecosystem process against the less predictable disturbances;
- identifying the biotic interactions that create threshold effects within the system.

We will proceed by briefly examining the nature of structuring processes in open-ocean systems and the stability of ocean ecosystems. We then discuss the general nature of functional groups in pelagic and benthic ecosystems.

16.4.1 Structure and stability of open-ocean ecosystems

Holling alluded to the overwhelming importance of the size-scaling of biogenic habitats, referring to levels of habitable volume (as defined by pine needles, canopies, and so on up to the landscape scale) as "nuggets" or "lumps" in terrestrial ecosystems (Holling 1992). There is no evidence as yet for such a structure in open-ocean communities (Steele 1985; Holling *et al.* 1994). Consequently, there is also little reason to expect the existence of discrete, alternate, stable configurations linked by disturbance or successional processes, such as exist in terrestrial and coastal marine benthic communities (Sutherland 1974; Margalef 1978; Holling 1992; Holling *et al.* 1994). Holling *et al.* (1994) stated that "terrestrial systems are functionally more localized than marine systems". The potential consequences of these differences are intriguing. Are pelagic communities devoid of ecosystem resilience (in the classical sense of Holling 1973), i.e. does the community shift frequently and without much resistance from one "stable" state to another? At what state are biotic interactions important? Is there no inter-annual succession in pelagic assemblages? Are cyclical shifts in species dominance entirely stochastic?

In the open ocean, the dynamics of epipelagic life vary greatly over even short time periods (Steele 1991). The populations themselves may be susceptible to short-term perturbations (i.e. over-harvesting, physical fluxes, nutrient pulses), but the community is flexible and adaptable to these new conditions and shows resilience over short time-scales. This is because pelagic species have planktonic larvae, and because of the physical mixing that dominates oceanic ecosystems. At moderate time-scales, changes in the ocean's physical characters, or over-harvesting, can lead to a breakdown of community resilience and a change of state. Empirical evidence for this comes from the frequent "flips" in the dominant pelagic fish (e.g. anchovy to sardine, these changes appear to be a natural switch between two different "stable" states (Soutar and Isaacs 1974; Alheit and Bernal 1993). Such changes to alternate states in community structure appear regularly (Sherman and Alexander 1986, 1989; Bas 1993; Blindheim and Skojdal 1993; Kuznetsov *et al.* 1993; Tang 1993). Many of these changes have been driven by over-fishing, and not all previously abundant fish populations have rebounded from depressed populations. These changes may be truly permanent, or they be oscillating in a cycle with a a longer period than we have been monitoring.

Steele (1991) compared the response of large oceanic fish to the response of trees in terrestrial systems and concluded that terrestrial organisms are less able to respond/adapt to short-term disturbances. This trend needs to be confirmed in a more rigorous manner, but the pattern is interesting. Primary producers in the open oceans (i.e. plankton) do respond more quickly to environmental disturbances than their terrestrial counterparts, the trees. In general, pelagic organisms may disperse more rapidly in space and not very much in time, whereas terrestrial organisms and benthic marine taxa disperse in both, but in neither very quickly. With the demise of the ocean's large apex consumers as a caveat, it may not be unreasonable to assume that species which live in the pelagic open ocean are more resilient to small-scale perturbations (Steele 1991) because of their dynamic metapopulation structure and the physical mixing of oceanic systems.

16.4.2 Niche breadth

The epipelagic world is more variable over small spatial and temporal scales, containing generalists with broad diets which are widely distributed in their biogeographic region (low among-region diversity; Angel 1993; McGowan and Walker). Broad niche structure among pelagic species does not imply that the niches are overlapping, i.e. that there is high species redundancy. For some marine groups, e.g. cetaceans, the lack of functional redundancy is fairly obvious: each species is highly distinct, and there is even significant (and perhaps reiterative) differentiation within species, in the bottlenose dolphin, *Tursiops*, for example. It is no accident that we have no trouble in recognizing functional differences among whales, but tend, erroneously, to lump the microbes, together. McGowan and Walker (1992) presented evidence that species of zooplankton do not to shift in rank abundance over time. Some shifts do occur, but rare forms tend not to displace abundant ones, and abundant species do not become rare. If the ranking of species dominance in pelagic systems is indeed robust, functional redundancy would appear to be low among abundance classes. In contrast, the benthic communities may be more specialized, with species having restricted dispersal, and communities with high among-region diversity (Grassle 1989; Grassle and Maciolek 1992). Pelagic ecosystems may be more fine-grained than benthic ecosystems.

Each group of organisms tends to be adapted to its particular environment and the scaling of natural disturbances that occur in that ecosystem. Novel perturbations caused by humans, such as exploitation, mining or pollution, will affect the system in ways that it is not used to adjusting to. In the advent of such novel disturbances, generalists with high dispersal will tend to increase the stability of the system by being able to respond more quickly to the changes in the environment (resilience in the sense of Pimm 1991). Moreover, the mixing of the epipelagic biome by oceanic currents will "quickly" restore perturbed systems to all but very large-scale disturbances (McGowan and Walker 1993). The fate of benthic taxa may depend more on their own dispersal capabilities. Buzas and Culver (1991) recently compared the distribution of present-day benthic foraminiferans that exist in the fossil record with the distribution of those that do not occur in the fossil record. Taxa that are ubiquitously distributed throughout the biogeographic regions are more likely to be found in the fossil record, suggesting that well-dispersed taxa are more likely to persist through time.

16.5 BIODIVERSITY AND ECOLOGICAL PROCESSES: EMPIRICAL EVIDENCE

It cannot be emphasized enough that knowledge about the relationship between biodiversity and ecosystem processes is very primitive. Despite the lack of concrete evidence, some people feel very strongly that changes in the structure of food webs, through changes in the abundance of biodiversity, will have significant impacts on both the state and the rates of ecosystem processes in open oceans. It is tempting to make such generalizations because of the ocean's unique characteristics, and because any change in the configuration of the open ocean *could* have a very large impact on any or all of the ecosystem processes and, through climate change, on terrestrial ecosystems as well. Because of the lack of knowledge about specific biodiversity impacts on many of the ocean's processes, discussion about certainties is limited. We have attempted to expose the most likely impacts of changes in biodiversity on ecosystem processes. The following list of open-ocean processes is not exhaustive, but should provide a basic list of the important processes operating in this biome (Figure 16.6).

16.5.1 Nutrient regeneration in the pelagic zone (microbial loop)

The pelagic microbial loop allows organic detritus to enter a detritivore food chain while still suspended in the water column, leading to local regeneration

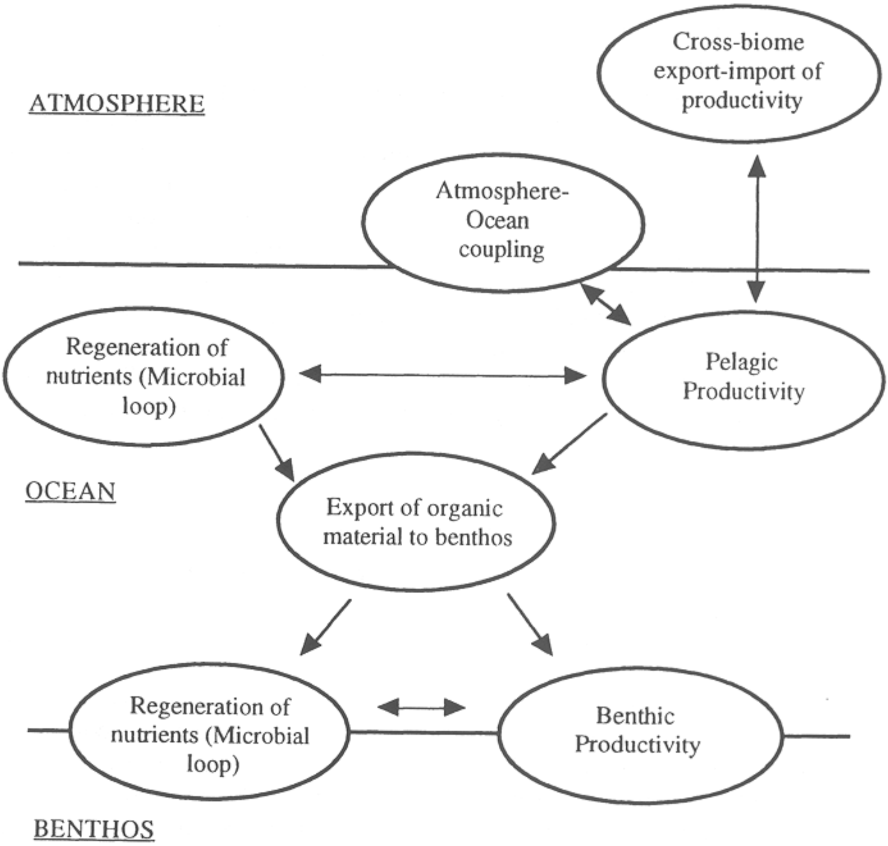

Figure 16.6 Seven ecosystem processes in the open ocean that depend on biodiversity rather than physical processes. Arrows indicate levels of interactions between processes. Nutrients are returned from the benthos to the epipelagic ecosystem by upwelling currents (i.e. physical processes)

of inorganic nutrients (Lenz 1992). The heterotrophic microbial loop in some ocean systems may account for over 70% of the total carbon and nitrogen in the euphotic zone (Fuhrman and Capone 1991). It may be appropriate to regard trophic relationships among macroscopic organisms (Lenz's "classical food web") as a phenomenon that flourishes only under exceptional circumstances, as dictated by local surfeits in food, or the concentrating effects of wind and current. The microbial loop is thought to be limited by grazing (Ducklow 1992). It is important to note that in pelagic systems, viral predation is an important component of grazing on the microbial biota. Host – parasite dynamics between bacteria and viruses is a new research field. Because of the large numbers of parasitic viruses found in open oceans (Bergh *et al.* 1989; Proctor and Fuhrman 1990), diversity of bacterial lineages may be important in stabilizing the microbial loop.

Ducklow (1992) has argued that functional variation *among ocean habitats* may be related to both bottom-up (i.e. differences in availability of organic carbon, under the influence of a host of environmental factors) and top-down (predation and grazing pressure) effects. However variation at smaller scales, i.e. within habitats, will almost invariably be due to top-down effects.

Chemical pollution could have a serious effect on microbial diversity by differentially impacting specific species. Circumstantial evidence suggests that microbial processes such as degradation and the use of specific nutrients are most efficiently performed by specific microbes. Although the specific mechanics are not known, changes in the abundance of these organisms could alter the microbial loop.

16.5.2 Pelagic Biomass Production

Primary and secondary production, as generally conceived, correspond to Lenz's "classical food web" (Lenz 1992). In fact, the food web in the open ocean can hardly be called "classical" from the standpoint of a terrestrial ecologist. Primary producers in oceanic food webs for the most part cannot root themselves into physical structure, and thus have not evolved into the massive and long-lived primary producers found in terrestrial ecosystems (angiosperms) and shallow marine environments (kelp and coral). Instead, primary production in the open ocean is dominated by microscopic algae and bacteria (Figures 16.7 and 16.8). Because differences in body size are accompanied by differences in longevity, turnover rate, buffering capacity, etc. (Peters 1983), the ecological scaling effects of dominance by microproducers are substantial. The difference in body size of the primary producers in terrestrial and marine environments has been suggested to be one key area where terrestrial and marine ecosystems operate differently (Steele 1991). In the open ocean, primary producers exhibit a higher turnover rate than their terrestrial counterparts. They are grazed more heavily, and are found at lower densities than is usual for other ecosystems (Cyr and Pace 1993). Remarkably, the standing crop of primary producers in planktonic communities is often lower than that of primary consumers. Upwelling systems tend to be species-poor and dominated by relatively short food chains and a larger standing crop of primary producers, whereas tropical gyres are species-rich, have longer food chains and have a lower primary producer to herbivore biomass ratio (Valiela 1984). Over large spatial and temporal distances, there is relatively high temporal resource predictability (i.e. at the metacommunity level), although the lack of small-scale predictability limits the ability of organisms to specialize. These generalists with highly

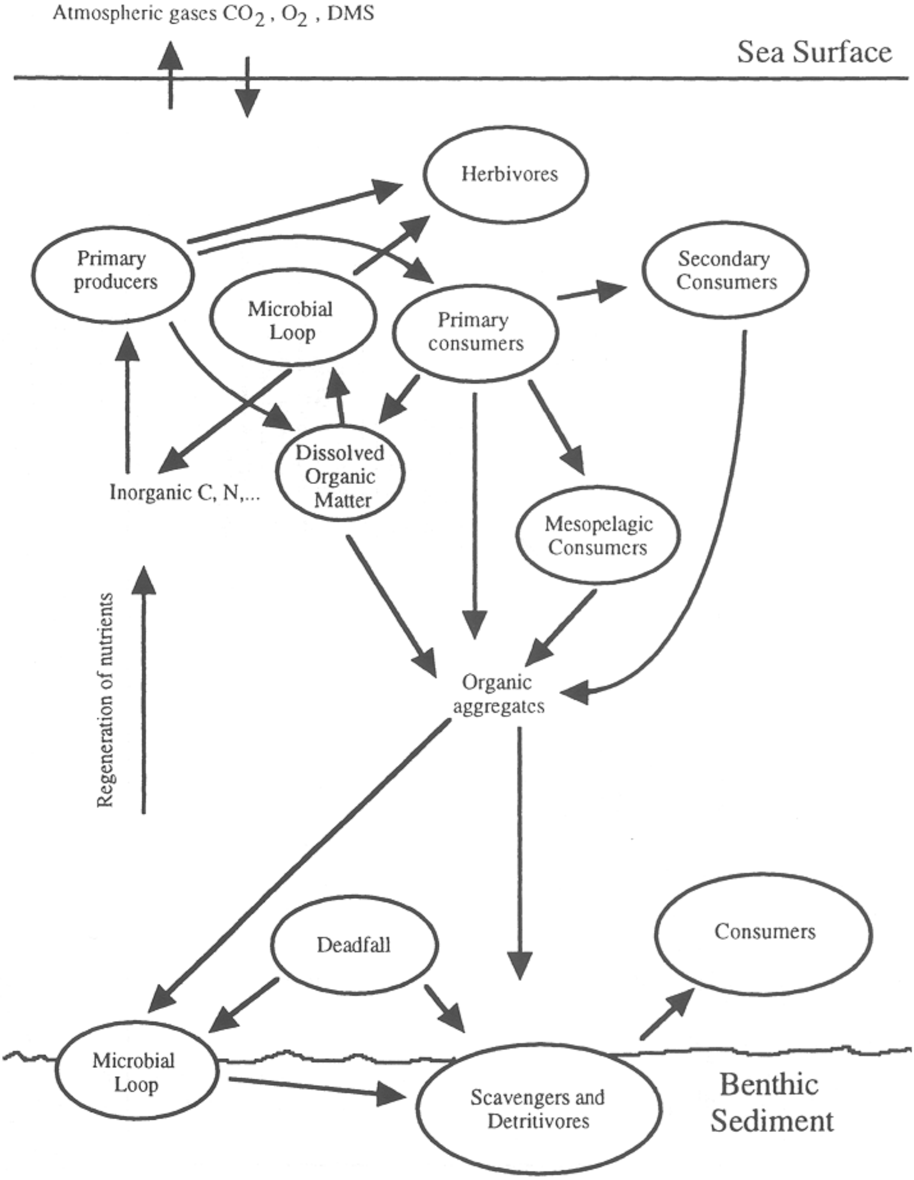

Figure 16.7 A simplified food web of the open ocean. "Real" oceanic food webs derive complexity from the broad diets of many species, often profound ontogenetic and seasonal shifts in diet, and the inherent cyclicity of the system. For example, the eggs or larvae of many fish become food for zooplankton, which themselves become food for the adult fish, and cannibalism by the higher trophic links (e.g. cod) on their young is not uncommon

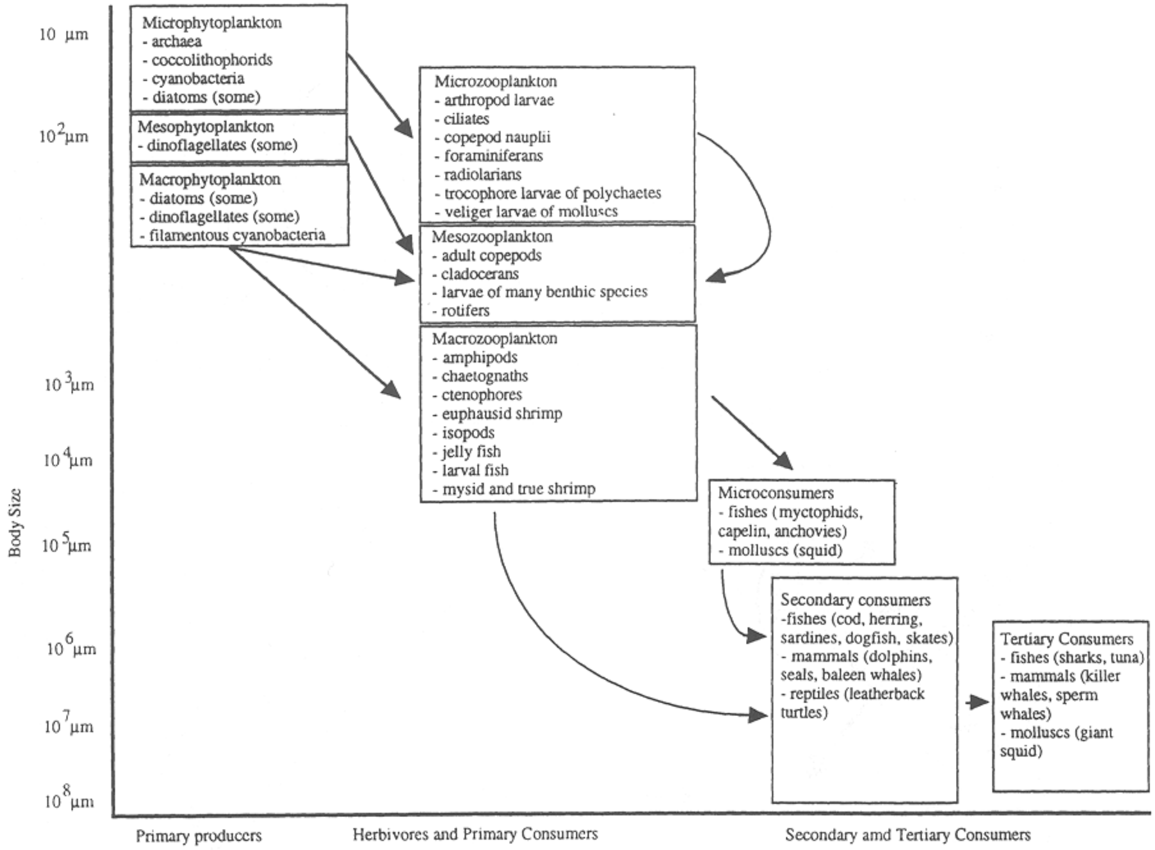

Figure 16.8 The size structure of an epipelagic food web. The information was adapted from Kennish (1989). Three more size classes of even smaller phytoplankton have been proposed. i.e, picoplankton (0.2–2μm), femtoplankton (0.02–0.2 μm) and nanoplankton (2–20 μm), which have been subsumed into the microplankton in this figure for the sake of simplicity

dispersed, planktotrophic larvae yield an ecosystem with high overall stability at large scales.

Another area of contrast between pelagic and terrestrial ecological processes is in the relationship between biodiversity and food-web structure. In general, the food-web structure of open oceans is similar to that found in terrestrial systems. There are important differences, however, particularly in mean chain length and species density across trophic levels. Schoener (1989) found a median of five trophic links in pelagic food webs, as compared with four in terrestrial, sea bottom, lake and upper estuarine webs, and only three links in marine estuaries and rivers. The proportion of primary producer and top carnivore species is low in the pelagic realm, and that of intermediate species is comparatively high. On a broad scale, biomass production is influenced principally by factors related to latitude and depth (Mann and Lazier 1991). Local variation in productivity is driven by (a) spatial dynamics of wind and current creating an underlying template for patch structure and (b) succession within patches due to tracking of primary producers by consumers on temporal scales of weeks and seasons (Valiela 1984).

One aspect of primary production that does appear to be very important is the size threshold at which phytoplankton can be more efficiently consumed by the primary consumers. Nutrient-rich environments, such as upwelling areas, tend to have a greater proportion of larger phytoplankton, and thus move energy up the food chain more efficiently (Valiela 1984, 1991). The phytoplankton communities of nutrient-poor areas, such as the tropical seas, tend to be dominated by many small nanoplankton. These phytoplankton are too small to be consumed by most zooplankton, and a succession of zooplankton is needed as the energy is channeled to larger consumers. Alternatively micropredators or parasites may recycle the energy back into primary nutrients and the microbial loop.

Anthropogenically derived changes to biodiversity can have significant impacts on food web configuration and the size distribution of organisms within the food web at small to moderate scales. For example, there have been major intra- and inter-specific shifts in life-history profiles of the dominant marine taxa due to overextraction in fisheries (Nelson and Soule 1987; Rijnsdorp 1993; Stokes *et al.* 1993). Whether these impacts result in the overall productivity of the open ocean changing at moderate to large scales is unclear. At the interspecific level, human fisheries have systematically reduced (in some cases to extinction) all species of large organisms from the epipelagic zone. Because body size limits the range of prey available and turnover time, changes in the frequency distribution of size classes will alter pelagic food webs, as well as the size distribution of organic deadfall to deep-sea communities (see below).

Recently, a entirely new group of primary producers have been discovered that could substantially alter our estimates of primary productivity in some regions of the ocean (Chrisholm *et al.* 1988, 1992; Olson *et al.* 1990). These discoveries of major new contributors to the oceanic food web makes predicting human impacts on food chain dynamics speculative at best. Resolving the issue of functional similarity will have to wait until we understand the taxonomic breadth of these new groups.

Undoubtedly, the greatest direct impact that humans are having an open-ocean biodiversity is the overexploitation of major vertebrate stocks, causing the current collapse of most of these stocks worldwide (Manire and Gruber 1990; Groombridge 1992; Anonymous 1994). Many of the organisms exploited by humans play pivotal roles in the food web, and because many of the top-level species are simultaneously being exploited, substantial changes in the composition of oceanic communities can be expected (Laws 1985; Weber 1986; Katona and Whitehead 1988; Manire and Gruber 1990). The shift from a bony-fish to a cartilagenous-fish dominated community in the north-western Atlantic is one good example of the reconfiguration of an ocean community (Figure 16.9). Examples of major shifts in fish populations (ecosystem flips) are known from the Norwegian – Barents Sea system (Blindheim and Skojdal 1993; Hamre 1994), the Baltic–North Sea system (Hammer 1993), the Yellow Sea in China (Tang 1993), the Okhotsk Sea in Russia (Kuznetsov *et al.* 1993), and the Humboldt and California Current systems (Soutar and Isaacs 1974; Alheit and Bernal 1993). Many of these "flips" are driven by density-independent shifts in physical oceanic conditions, but several were apparently influenced by human predation (Sherman 1989; Hammer 1993; Kuznetsov *et al.* 1993; Tang 1993). The shifts in abundance of non-cetacean planktivores in Antarctic waters is probably a consequence of the over-exploitation of cetaceans there (Beddington and May 1982; Valiela 1984). Although principally driven by physical factors, these ecosystem shifts may be exacerbated by human fishing effort. In the Okhotsk Sea system, near Russia, human predation produced an initial increase in walleye pollock production by decreasing cannibalism and thus "rejuvenating" the population. However, the narrowed range of size and age classes ultimately decreased the overall stability of the population, and rendered it more vulnerable to environmental perturbations (Kuznetsov *et al.* 1993).

The attributes of ocean systems may make apex predators especially vulnerable to ecosystem effects pursuant to biodiversity impacts (Manire and Gruber 1990). The first is *pelagic recruitment*. The larvae are subject to highly stochastic determinants, and when disrupted sufficiently the outcome is highly unpredictable on small scales. Large-scale ecosystem resilience is predicted from the prevalence of pelagic larval dispersal and a broad diet found among many pelagic organisms that includes the young of even their

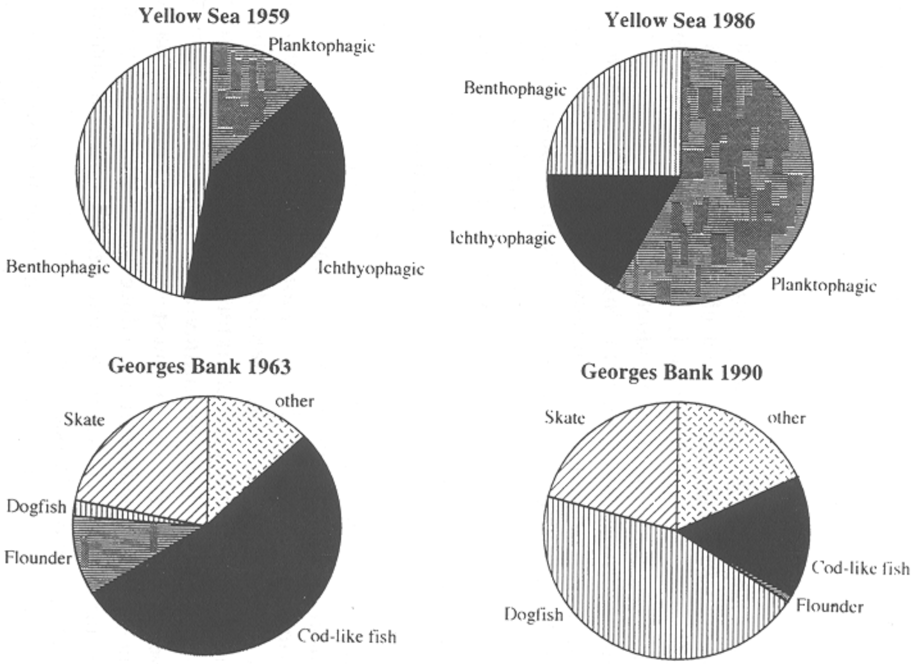

Figure 16.9 The change in fish community composition in the Yellow Sea, China (after Tang 1993), and the Georges Bank system. northwest Atlantic (after World Resources Institute 1994). Initial fisheries were concentrated on the most desirable species (e.g. cod and flounder off the Georges Bank), but now "less desirable" fish species dominate.

own species. The effects of removal of large epipelagic species should cascade through the rest of the water column, as these are principal agents of nutrient transport, both as living individuals undergoing frequent vertical migration, and as deadfall (Smith *et al.* 1989; Pfannkuche and Lochte 1993). These systems are ordinarily very resilient, so that the complete elimination of a dominant species may make system reconfiguration extremely difficult to reverse.

Recent simulations of oceanic systems suggest the effects of altering species composition are very difficult to predict, may be highly counter-intuitive, and are dependent on the time frame and spatial scale involved (Yodzis 1988).

Eutrophication and introductions Ocean productivity may be further altered by two other human impacts, the indirect effects of increasing the nutrient inputs to oceanic systems, and the introduction of novel organisms to the system. Human impacts on the total productive capacity in the open ocean will be principally primary i.e. nutrient loading within coastal regions, rather than impact on open-ocean biodiversity (Young *et al.* 1985; Suchanek 1994). Recent evidence suggests that humans have helped contribute to the eutrophication of such large basins as the Mediterranean and Black Seas (Caddy 1993). Nutrient enrichment has been postulated to increase the frequency of red tides (Smayda 1989; Anderson 1994). The production of toxins by dinoflagellates in so-called red tides, is one example of a localized disturbance by one or a few taxa that often has direct links to human activity (Smayda 1989; World Resources Institute 1992; Hallegraeff 1993; Anderson 1994). These toxins percolate their way through the food web, altering the ecosystem through mortality of many other species, including humans. In addition to the "red tide" dinoflagellates, other toxins are produced by a wide variety of plankton taxa. The factors that trigger the ephemeral blooms of these organisms and the subsequent impact on marine ecosystems are unknown. In most of the oceans, the large-scale mixing of water masses is sufficient to reduce the impact of any one taxa upon overall water quality. However, as one moves down in spatial scale, significant impacts probably do occur.

The open ocean is thought to be more immune to introductions than coastal systems because global currents have already created a cosmopolitan distribution of species. However, some introductions can have dramatic effects! The invasion of the comb jelly, *Mnemiopsis leidyi* into the Black Sea, most probably from ballast water, is one example of an introduction with dramatic effects (Vinogradov *et al.* 1989; Shushkina and Musayeva 1990). Up to a 10-fold decrease in zooplankton biomass, a 90% decrease in the jelly fish *Aurelia* biomass, and a 90% decrease in the pelagic fishery could be attributed to the introduction of this novel predator.

16.5.3 Pelagic–benthic coupling (export of benthic material to the benthos)

Since photosynthetic primary production in the open ocean occurs only in the epipelagic zone, the mesopelagic and abyssal zones are almost totally dependent upon down-transport of nutrients, with the limited exception of hydrothermal vent environments (Honjo 1980; Deuser *et al.* 1981; Lampitt 1985). Benthic biomass decreases with depth and distance from the coastal areas (Menzies *et al.* 1973; Wolff 1977). There are three major processes by which nutrients are transported into abyssal waters. To some extent, nutrients entrained in surface waters can be down-drafted in currents and aquatic storms of all scales. Gravitational transport of organic matter is probably most important. This comes in two forms: the steady rain of small particles consisting of faecal pellets, dead and dying cells, etc. called pelagic "snow" (Silver *et al.* (1994), and the occasional phytoplankton blooms (Pfannkuche 1993) and sinking carcasses of large marine organisms, such as whales, large fishes (and unfortunate sailors). Overall biomass in the deep ocean is probably a direct function of the absolute quantity of nutrient transported from above. Biodiversity, however, will be influenced by the spatial and temporal distribution of nutrients, which appear as small-scale disturbances to the system (Grassle and Morse-Porteous 1987; Grassle 1989).

The reconfiguration of the pelagic food webs through species shifts, and perhaps more importantly shifts in size distribution of organisms, may come about through the loss of specific key epipelagic taxa which will result in a concomitant change in the organic material reaching the benthos (Peinert *et al.* 1989). The reduction in pelagic megafauna has compromised deadfall to the deep. This deadfall serves both as a source of nutrients for benthic species (mentioned above), and as an important stepping stone for dispersal of species associated with hydrothermal vents. Dead whale carcasses have been found with communities more typically found on hydrothermal vents (Smith *et al.* 1989), potentially linking vent communities hundreds of miles apart. The role of some organisms in the rate of movement of nutrients through the open ocean is now coming under investigation. The death and subsequent sinking of large organisms from the epipelagic systems is one effective link between the deep-sea benthic communities and the productive surface waters (Smith *et al.* 1989; Bennett *et al.* 1994). Altering the number and distribution of these (primarily) vertebrates will have profound effects on the dynamics of benthic and infaunal communities.

A recent study found that salps (Urochordata) also couple epipelagic productivity to the abyss by converting small nanoplankton (e.g. cyanobacteria) into larger concentrated packages of nutrients (i.e. fecal pellets) which make it to the bottom more quickly. Changes in the proportion of salp-like organisms will undoubtedly affect ecosystem processes in the deep-sea benthic communities. Not only would the patchiness of nutrients be altered, but the quantity of nutrients actually arriving at the bottom would be altered, i.e. the smallest plankton may not penetrate through the thermocline, and thus remain in the pelagic realm. It has also been suggested that Rhizosolenid diatoms may also play a similar role in affecting the flux of nutrients from the epipelagic regions to the deep-sea benthos (Villareal *et al.* 1993; Hayward 1994). Interestingly, mass sinking of such large diatoms may bring moderate to large-scale nutrient flux to the benthic systems.

16.5.4 Productivity and nutrient regeneration in the benthos

Limited in scope, chemosynthesis-driven hydrothermal vents are one benthic system which is rich in life. Alternative sources of energy provide the grist for flourishing communities of bacteria worms and molluscs. Hydrothermal vents are deserving of much greater attention than can be devoted here.

Most other open-ocean benthic communities are food- rather than space-limited, unlike so many shallow water marine systems. The full functional significance of this difference has yet to be appreciated. In contrast to the pelagic ecosystems, the benthos is dominated by deposit feeders and scavengers which depend upon the down-fall of organic material from the epipelagic zone (see previous section), and consequently, overall productivity is considerably lower. Much of the variability in the deep sea is driven directly from changes in the epipelagic zone (Lampitt 1987; Smith 1987). Through their activities, deposit feeders modify the physical and chemical characteristics of the sediment, and could be considered "ecosystem engineers" or "habitat fabric interactors" (*sensu* Jones *et al.* 1994). Some deep-sea species may be important in the creation of biogenic structures in the benthos which provide microhabitats for many other species which inhabit this realm (Jumars 1975; Thistle 1979; Gooday 1984; Levin *et al.* 1986).

The possibility of losing specific taxa or strains from the benthic microbial loop as a result of direct human alteration of sections of sea bottom should be taken seriously. The diversity of microbial activity in the deep benthos is not only a key attribute of the system, but also of enormous potential value to humanity. The infauna (that life below the living in the sediments) lives in an environment where basic life conditions are directly determined by the dynamic flow of life-sustaining molecules (oxygen, sulfur, nitrogen). The point at which the environment becomes toxic to an organism strongly depends upon bioturbation, i.e. the physical mixing of sediments caused by animal movement. Life quickly becomes limited to groups of specialists who can tolerate these extreme habitats. Some species appear to play a key role in modulating this environment (Thistle 1979; Gooday 1984; Levin *et al.* 1986; Grassle 1989; Levinton 1994), presumably altering the microbial loop and the productivity/food-web structure of deep benthic environments. Whether many of the macrofauna species perform the same role, and could be compensated for if eliminated, is not clear, at least for coastal benthic communities (Giblin *et al.* 1994; Levinton 1994). The high species diversity found in deep-sea environments is thought to be the result of small-scale nutrient pulses from the pelagic zone, which act as small disturbances to the system (Grassle 1989). If this is true, then much of the deep-sea benthic diversity may be composed of rare species with greatly overlapping fundamental niches, and the elimination of much of this diversity will have little impact on either the regeneration of nutrients or benthic productivity. This result ignores any potential effect of species-specific biotic interactions which could percolate through the food web; however, we are unaware of evidence for such specific interactions. To recapitulate, it is possible that many of the deep sea species may act like "passengers" rather than "rivets" in deep-sea processes, although there is only scant evidence to support this idea at the moment. Taxa which alter the physical structure of the sediments are most likely to be key functional species, taxa which impact the microbial loop taxa are another key group in the benthos.

16.5.5 Ocean–atmosphere coupling

The physical structure of the ocean is of obvious importance to all pelagic organisms. Less visible, but no less important in the long run, are feedback relationship between living organisms and atmospheric processes. In a controversial but provocative calculation, Takahashi (1989) proposed that the oceans account for more than twice the amount of CO_2 removed from the atmosphere than terrestrial systems. In fact, there are serious problems with many recent estimates of carbon flux, although most overlap in suggesting that the ocean is far more important in this equation than previously allowed (Siegenthaler and Sarmiento 1993; Toggweiler 1993). The ocean is also a much greater reservoir for carbon than either the land or the atmosphere, with a total of about 4.0×10^{19} g of carbon versus 0.2×10^{19} g carbon for terrestrial organisms (Valiela 1984). Considering the fact that the oceans comprise more than 70% of the earth's surface, this should not be surprising. There is a strong bias among terrestrial biologists toward discounting the oceans as a carbon sink, however, due to the absence of large trees and other conspicuous concentrations of organic carbon.

Human impact on the diversity of life which influences atmospheric processes is difficult to ascertain because the relative contribution of different biogenic products on climate change, ozone depletion and CO_2 increase is still unknown. Dimethyl sulfide, carbonyl sulfate and bromoform are gases which can have an important impact on cloud formation or the greenhouse effect. Marine organisms, mainly non-calcifying coccolithophorids and diatoms, are known to produce all three gases (Charlson *et al.* 1987; Turner *et al.* 1988; Iverson *et al.* 1989; Kiene and Bates 1990). The relative abundance of these species and their distributions are poorly known, although anthropogenic activities will most likely alter their current status because different taxa respond differently to eutrophication, chemical pollution, UV–B radiation and species introduction. Possibly, only a narrow range of taxa play a disproportionately large role in controlling flux rates of these gases, such that even small changes in their relative abundances may lead to significant alteration of atmospheric processes. It has been predicted that changes in regional climate will occur to the extent that the relative abundances of carbonyl sulfate and dimethyl sulfide producing plankton are impacted by human activities in the open ocean (Fuhrman and Capone 1991). Atmosphere–ocean coupling may be one of the systems most susceptible to anthropogenic impacts on taxonomic diversity. A better understanding of the relative role of all these organisms in producing these gases is clearly an important area for future research.

The ocean is an important carbon sink, and changes to the phytoplankton species composition may greatly affect globally increasing levels of carbon dioxide. These effects may be played out because of species-specific differences in carbon-fixing rates, or by changes to the size distribution of phytoplankton. Gradual changes in greenhouse gases may cross thresholds or "switches" in the ocean–atmosphere feedback system, causing rapid shifts to other stable states (Broecker 1987). These transitions could be accompanied by changes in ocean currents, and lead to a major reorganization of ocean biomes (Broecker and Denton 1989). This is a largely unexplored yet important field, with possibly wide-ranging ramifications given the potential impact on global weather predicted by small changes to climate models. The possibility that biology can drive the physical dynamics of the open ocean is an important hypothesis that needs further testing. For example, sea-surface heating through light absorption and heat release by the phytoplankton could play a significant role in regulating global climate.

16.5.6 Open-ocean continental-shelf coupling

The most commonly cited functional link between the open ocean and coastal systems is probably the upwelling of nutrients along precipitous coastlines. These nutrients are brought the rest of the way to the surface by prevailing winds, and then entrained in surface waters, resulting in high primary productivity. As an adjunct, highly local process, the upwelling of hypoxic waters can generate organic carbon highs in benthic communities as a result of anoxic kills. Many of these processes are driven by physical factors; however, the benthic biota control the breakdown and remineralization of nutrients (making them available to other ecosystems), and reduce oxygen availability. To this extent, this is an important ecosystem process with repercussions that extend beyond the open-ocean biome.

In addition, the open ocean and coastal biomes are interwoven functionally through the complex life histories of the organisms that live there. Anadromous fishes, born in the headwaters of the world's river systems, acquire the bulk of their mass during a period of several years spent at sea as part of the open-ocean food web. When they return to the rivers to spawn, the greater part of this mass is deposited, and utilized, within the watershed. For some catadromous species, net transport could be in the opposite direction. Newly metamorphosed young of species such as the Atlantic menhaden and American eel ascend rivers and estuaries to feed and grow for from one to five years, after which they return to sea. To the best of our knowledge, the energetic balance sheet for these biomass shifts has not been worked out.

Another crucial linkage lies in the reliance of both coastal and pelagic organisms on open-ocean currents for the early nurturing and dispersal of their young. The majority of marine organisms produce pelagic gametes or larvae which drift, usually within the portion of the water column occupied by the adults, over vast horizontal distances.

16.6 CONCLUSIONS

Our effort was to explore the system-level consequences of human-caused changes in open-ocean biodiversity. Of the 15 biomes examined in the course of the SCOPE project, the open ocean is the most underdescribed. It is in many ways premature to describe ecosystem function when we have not become familiar with all of the components. Due to the taxonomic structure of marine assemblages, when an open-ocean creature is newly discovered there is a reasonable likelihood that an entire family, class or even phylum has been overlooked: the recent description of a new phylum, the Loricifera, is but one example. Few of the new groups turn out to be especially rare, and some are astonishingly abundant, albeit unfamiliar. The novelty of new taxa from the open ocean is much higher than that for new rain forest species, heightening an already extreme imbalance of attention and resources between rain forest and pelagic systematics. A true understanding of the significance of diversity to open-ocean processes will only come after careful experimental manipulations. Unfortunately, we are simultaneously altering so many of the ocean's species, primarily through resource extraction, that we may never have a baseline against which to understand how humans are actually impacting this biome.

The picture of marine functional diversity that emerges is one of a rich mélange not only of species, but also of basic body plans and metabolic capabilities. The biota may be highly adaptable, but functional equivalency is not necessarily very high, with the possible exception of the species-rich deep-sea benthos. In general, the dynamics of marine systems, and in particular pelagic systems, are likely to change considerably if species are eliminated, even a relatively few species. Extinction probabilities may be much lower for pelagic than for terrestrial organisms, but functional similarity is probably also lower. Any one marine extinction, once it occurs, is expected to have a more profound impact on the system than the loss of a terrestrial species. Buddemeir (cited in Culotta 1994) warned that "You don't want to get trapped into a linear comparison of terrestrial and marine ecosystems. . . The marine system is less extinction-prone, but if you do start getting extinctions, it means you've got a problem on a much larger scale. The rules *are* different in the sea". Even at the subspecific level, functional diversity exists among marine organisms, even among cetaceans, where we would least expect it because of their enhanced buffering capacity (large size, endothermy, high vagility) (Perrin 1991). This suggests that different functional roles are strongly selected for in the open ocean, and that the loss of even one species of cetacean could result in a significant change to that ecosystem. A similar argument could be constructed for sharks. Populations of cetaceans and sharks are depressed around the world today, and the current pelagic assemblage may already reflect this loss.

Recent consensus holds that marine systems are organized, and function, in fundamentally different ways than terrestrial systems (Steele 1985, 1991; Ray and Grassle 1991; Holling 1992; Holling *et al.* 1994). Direct services to humans include the production of food and oxygen, and a dumping ground for toxic and non-toxic wastes, although indirect services, such as climate regulation, may be more important over the long term.

Certain organisms play key roles in the open ocean, and their disappearance would have particularly strong ramifications. The likely key organisms include those that transport nutrients from epipelagic systems to deeper ecosystems (e.g. salps, large vertebrates, rhizsolenid diatoms), and organisms that modulate extreme environments (chiefly microorganisms) such as sulfate reducers, methanogens and fermenters, and organisms that modify the physical structure of the deep-sea benthos. The impact of global reduction in apex consumers will be possibly the single greatest impact that humans will have over the short term on the productivity of pelagic ecosystems. Over the long term, changes in ocean–atmosphere coupling through the selective elimination of specific phytoplankton (for example through UV–B radiation, climate change) may be of even greater importance. As for impacts arising from the loss of deep-ocean, soft-sediment species, nothing can be surmised at this time.

In many parts of the world, particularly around the Pacific Rim, the continental shelf is reduced to a few kilometers. Under these circumstances, the open ocean virtually abuts the land. This is the oceanic biome in which the lag between coastal signal and oceanic impact is the shortest, and functional links the strongest (e.g. the guano–anchovy link in South America). It is misleading to treat these systems as strictly coastal. Indeed, these situations may offer the ideal monitoring outposts for both signs of change in pelagic biodiversity, and the impacts of such change on ecological processes and human affairs.

The productivity of pelagic fisheries is one key ecosystem process that oceans provide to humans. Changes in the species composition of landings have been much greater than fluctuations in the overall catch rate of all fishes. Whether one regards these species shifts as changes in ecosystem process depends on the scale examined. In several regions managed as one system, such as the Grand Banks or the Yellow Sea, there have been significant changes in species composition over a short period of time. However, there probably has not been much change in total fish productivity . With respect to processes provided to humans, this is not a trivial matter. There is strong cultural and economic value associated with each specific fishery. In the North Atlantic, the cod fishery cannot be replaced easily with a dogfish or skate fishery. A tourist industry based on whale watching is another example of a human service that depends on a *stable* pelagic community of specific species. The benefits derived from ecosystems, especially those linked to human culture, usually depend on processes that operate at much smaller scales than those typically associated with ecosystems.

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