American Museum of Natural History
Center for Biodiversity and Conservation
Network of Conservation Educators & Practitioners

Introduction to Marine Conservation Biology

Author(s): Tundi Agardy

Source: *Lessons in Conservation*, Vol. 1, pp. 5-43

Published by: Network of Conservation Educators and Practitioners, Center for Biodiversity and Conservation, American Museum of Natural History

Stable URL: ncep.amnh.org/linc/

Introduction to Marine Conservation Biology

Tundi Agardy[*]

[*]Sound Seas, Bethesda, MD, USA, email tundiagardy@earthlink.net

D. Brumbaugh

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This document is specifically about those aspects of marine biology that are used in marine conservation. It is not intended to be a complete primer on marine conservation, which incorporates other sciences (most notably the social sciences) as well as traditional knowledge. To learn more about other aspects of marine conservation, please refer to the following marine modules: *Marine Conservation Policy, Marine Protected Areas and MPA Networks*, and *International Treaties for Marine Conservation and Management*, all of which complement this module.

Introduction

Marine and Coastal Systems

Almost three-quarters of the Earth's surface (exactly 70.8% of the total surface area or 362 million km^2), is covered by oceans and major seas. Within these marine areas are ecosystems that are fundamental to life on earth and are among the world's most productive, yet threatened, natural systems. *Continental shelves* and associated Large Marine Ecosystems (LMEs) provide many key ecosystem services: shelves account for at least 25% of global primary productivity, 90-95% of the world's marine fish catch, 80% of global carbonate production, 50% of global denitrification, and 90% of global sedimentary mineralization (UNEP, 1992).

Marine systems are highly dynamic and tightly connected through a network of surface and deep currents. In marine systems, the properties of the watery medium generate density layers, *thermoclines*, and gradients of light penetration. These phenomena give the systems vertical structure, which results in vertically variable productivity. Tides, currents, and *upwellings* break this *stratification* and, by forcing the mixing of water layers, enhance production (MA, 2005c). Coastal systems also exhibit a wide variety of habitats that in turn contribute significantly to global biological diversity.

Marine and coastal systems play significant roles in the ecological processes that support life on earth and contribute to human well-being. These include climate regulation, the freshwater cycle, food provisioning, biodiversity maintenance, and energy and cultural services including recreation and tourism. They are also an important source of economic growth. Capture fisheries alone were worth approximately 81 billion USD in 2000 (FAO, 2002), while aquaculture netted 57 billion USD in 2000 (FAO, 2002). In 1995, offshore gas and oil was worth 132 billion USD, while marine tourism brought in 161 billion USD, and trade and shipping were worth 155 billion USD (McGinn, 1999). There are currently approximately 15 million fishers employed aboard fishing vessels in the marine capture fisheries sector, the vast majority on small boats (90% of fishers work on vessels less than 24 m in length) (MA, 2005c).

Key Concepts in Marine Conservation Biology

Marine ecosystems are complex and exhibit diversity at various hierarchical levels. Of 32 common phyla on the earth, only one living phylum is strictly terrestrial; all others have marine representatives (Norse, 1993). Interestingly, all of these phyla had differentiated by the dawn of the Cambrian, almost 600 million years ago, and all evolved in the sea. Since that time the sea has been frozen, experienced extensive anaerobic conditions, been blasted by meteorites, and undergone substantial sea level variation. The sea has thus been fragmented and *coalesced*, resulting in a vast array of habitats (MA, 2005a).

Marine species are poorly known relative to those on land. The actual species diversity in the ocean is not known, and fewer than 300,000 of the estimated 10 million species have been described (MA, 2005a). One of the rare efforts to sample all of the *mollusk* species at a tropical site found 2,738 species of marine mollusks in a limited area near New Caledonia (Bouchet et al., 2002).

Natural systems in the sea, as on land, exhibit non-linear dynamics. Thresholds for responses to perturbation occur in some systems, though few have actually been identified. Significant alteration in ecosystem structure and function can occur when certain triggers result in changes in the dominant species. *Regime shifts* are common in *pelagic* fisheries, where thresholds are surmised to be related to temperatures (IPCC, 2003). Most well known is the example of the anchovy/sardine regime shift, which is expressed as a periodic oscillation between dominant species, not an irreversible change. Irreversible shifts occur when a system fails to return to its former state in time scales of multiple human generations, after driving forces leading to change are reduced or removed (IPCC, 2003).


Pillar coral, *Dendrogyra cylindrus*, and juvenile bluehead wrasse off of the coast of Andros Island (Source: D. Brumbaugh)

Some phase shifts are essentially irreversible, such as the coral reef ecosystems that undergo rather sudden shifts from coral-dominated to algal-dominated reefs (Birkeland, 2004). The trigger for such changes is usually multi-faceted, and includes increased nutrient input. This leads to eutrophied conditions and removal of the herbivorous fishes that maintain the balance between corals and algae. Once the thresholds for the two ecological processes of nutrient loading and herbivory (one upper and one lower) are passed, the phase shift occurs suddenly (within months). The resulting ecosystem, though stable, is less productive and less diverse. Human well being is affected not only by reductions in food supply and decreased income from reef-related industries (e.g., diving and snorkeling, aquarium fish collecting, etc.), but also by increased costs accruing from the decreased ability of reefs to protect shorelines. Algal reefs, for example, are more prone to being broken up in storm events, leading to shoreline erosion and seawater breaches of land. Such phase shifts have been documented in Jamaica, elsewhere in the Caribbean, and in Indo-Pacific reefs (MA, 2005b).

Introduced alien species (or invasive species) can also act as a trigger for dramatic changes in ecosystem structure, function, and delivery of services. In the marine environment, species are commonly brought into new areas through *ballast water* discharges, and can quickly gain a foothold as they outcompete native species for food and space. A prime example of a sudden, and irreversible, change in an ecosystem occurred in the Black Sea. Introduction of the carnivorous *ctenophore Mnemiopsis leidyi* caused the loss of 26 major fisheries species, and has been implicated (along with other factors) in subsequent growth of the *anoxic* "dead zone" (Zaitsev and Mamaev, 1997). Introduced species arrive via other vectors as well, such as through the disposal of packing materials for marine resources, and are not always accidental.

Changes in biodiversity and other environmental changes influence each other, in marine systems as well as in terrestrial. Biodiversity loss can reduce an ecosystem's resilience to environmental perturbation. This can be brought about by, for example, climate change (warming), ozone depletion (increased radiation), and pollution (*eutrophication*, toxics). All of these impacts can also reduce biodiversity. Diverse marine systems in which neither species, population, nor genetic diversity has been severely constricted, are better able to adapt to changing environmental conditions (Norse, 1993). Unaltered coral reefs, for instance, are less likely to experience disease-related mortality when ocean temperatures increase (Birkeland, 2004). However, all environmental change has the potential to cause biodiversity loss, especially at the level of genes and populations. The greater the magnitude and the more rapid the rate of change, the more likely biodiversity will be affected, and the greater the probability that subsequent environmental change will lead to greater ecosystem degradation (MA, 2005a).

Comparisons Between Marine and Terrestrial Systems

Marine and terrestrial systems exhibit differences in scale and process (Steele, 1985). The obvious distinction is that on land, air is the primary medium for food transmission, and in marine systems, water is the primary medium. Although both terrestrial and marine systems exist in three-dimensional space, land-based ecosystems are predominantly two-dimensional, with most ecological communities "rooted" to the earth's surface. The seas present a different picture, with the bulk of life moving about in a non-homogeneous space, and few processes linking the water column with the *benthos*. The water medium has freed organisms from the constraints on body type posed by gravity, thus the array of life, as expressed by *phyletic diversity*, is much wider in the sea (Kenchington and Agardy, 1990; Norse, 1993). In the sea and its coastal interface, the transport of nutrients occurs over vast distances, and both passive movement and active migrations contribute to its highly dynamic nature. Marine species must also meet the challenges posed to reproduction in an aqueous environment: gametes released into the water column are quickly dispersed, and most species are highly *fecund* and time their *spawning* to release gametes en masse (Kenchington and Agardy, 1990). Perhaps most importantly, physical features of the marine ecosystem dictate its character, more so than on land (Agardy, 1999).

In the marine environment, all habitats are ultimately connected – and water is the great connector. Some habitats are more intimately and crucially linked, however. Coral reefs provide a good example of this interconnectedness. For years, diverse and biologically rich coral reefs were thought of as self-contained entities: very productive ecosystems with nutrients essentially locked up in the complex biological community of the reef itself. However, many of the most crucial nursery habitats for reef organisms are actually not on the coral reef itself, but rather in seagrass beds, *mangrove forests*, and sea mounts sometimes far removed from the reef (Hatcher et al., 1989). Currents and the mobile organisms themselves provide the linkages among the reefs, nursery habitats, and places where organisms move to feed or breed (Mann and Lazier, 1991; Dayton et al., 1995). Thus, managing marine systems like coral reefs requires addressing threats to these essential linked habitats as well.

The ocean and coastal habitats are not only connected to each other, they are also inextricably linked to land (Agardy, 1999). Although the terrestrial systems are also linked to the sea, this converse relationship is neither as strong nor as influential as is the sea to land link. Freshwater is the great mediator here. Rivers and streams bring nutrients as well as pollutants to the ocean, and the ocean gives some of these materials back to land via the atmosphere, tides, and *seiches*. Other pathways include the deposition of *anadromous* fish (Deegan, 1993). Many coastal habitats, such as estuaries, are tied closely to land, and are greatly affected by land use and terrestrial habitat alteration (MA, 2005b).

In coastal and marine systems, habitats include freshwater and brackish water wetlands, mangrove forests, estuaries, *marshes*, *lagoons* and salt ponds, rocky or muddy *intertidal* areas, beaches and dunes, coral reef systems, seagrass meadows, kelp forests, nearshore islands, semi-enclosed seas, and nearshore coastal waters of the continental shelves. Many of these coastal systems are highly productive and rival the productivity of even the most productive terrestrial systems (MA, 2005b). Table 1 illustrates the relative productivity of some of these coastal ecosystems in comparison to select terrestrial ecosystems.

Table 1: Relative productivity estimates for select coastal and terrestrial ecosystems

Ecosystem type	Mean net primary productivity ($g.m.^{-2}$ $year^{-1}$)	Mean biomass per unit area (kg/m^2)
Swamp and march	2000	15
Continental shelf	360	0.01
Coral reefs and kelp	2500	2
Estuaries	1500	1
Tropical rain forest	2200	45

Source: Modified from Table 3-4 in Odum and Barnett, 2004

Marine Organisms and Environments

Marine Biodiversity

Habitat diversity

Biodiversity is defined as the variety of life in all of its forms. Although we usually think of diversity in terms of species numbers, an equally important metric is the amount of variability of habitat within a unit area, or the spatial autocorrelation of species within an area (MA, 2005a). This is broadly known as beta-diversity (see the *What is Biodiversity* module). The oceans and coastal areas exhibit a vast array of habitat types, and many ecosystems are highly diverse at this level of organization.

Phyletic and species diversity

Phyletic diversity in the sea is much greater than on land. Major marine phyla include microbes, such as *protists*, fungi, bacteria, archaea; plants such as algae and flowering plants like sea grasses; invertebrates such as *sponges*, *cnidarians*, *echinoderms*, mollusks, *crustaceans*; and vertebrates, including the bony and cartilaginous fishes, reptiles (sea turtles, sea snakes, marine iguanas), mammals (sea otters, manatees and dugongs, seals, whales and dolphins) and birds (seabirds, shorebirds, etc.).

Species richness is valued as the common currency of the diversity of life - the "face" of biodiversity. The problem with this emphasis is the potential masking of important trends and properties, beyond taxonomy (MA, 2005a). Given the complexity of biodiversity, species- or other taxon-based measures-rarely reflect the real attributes that provide insight into roles and functions. There are several limitations associated with the emphasis on species. First, what constitutes a species is often not well defined (MA, 2005a). For example, it is not necessarily easy to know when one is measuring population or species diversity. Indeed, the dynamic nature of marine systems confounds the species/population dichotomy, since members of the same marine species are often isolated by populations so discrete that intermixing is functionally impossible (see discussion of genetic diversity, below).

Second, species richness and ecosystem function may not correlate well. Productive ecosystems, such as estuaries or wetlands, are often species poor. Third, although species are taxonomically equivalent, they are rarely ecologically equivalent. For example, taxa that are *ecosystem engineers*, like beavers or marine worms, and *keystone species*, whose presence maintains a diverse array of species in a community, often make greater contributions to ecosystem functions than others. Fourth, species vary extraordinarily in abundance, often exhibiting a pattern in which only a few are dominant, while many are rare (MA, 2005a). Thus, to simply count taxa does not take into consideration how variable each might be in its contribution to ecosystem properties.

Genetic diversity

The fundamental differences in marine and terrestrial ecosystems are in degree, not in kind (Steele, 1995). But there are semantic problems that arise from the different ways we label marine systems and those on land. Understanding species diversity and genetic diversity in the sea is a case in point. Most marine species are widespread in distribution, being cosmopolitan or even circumglobal. However, marine populations are structured into distinct demes, such that the genetic make-up of a population or stock can be profoundly different from that of a neighboring stock or population, even though we refer to them as being of the same species.

Physical Oceanography

Physical Environment at Various Scales

The physical environment of the oceans drives their biological make-up to a greater degree than in terrestrial systems. The oceanographic phenomena that underlie how the oceans are structured and how they function occur at three scales. The first is the macro-scale, on which large-scale hydrographic processes and patterns manifest themselves in oceanographic circulation and major currents. On the *meso-scale*, temperature and salinity create *thermohaline* regimes. On the micro-scale, tidal exchange, upwelling, and *longshore currents* frame the physical environment of different marine habitats in different coastal and continental shelf areas.

Macro scale oceanography

Although the ocean waters appear homogeneous, there are both stratification into horizontal layers and vertical mixing between layers that take place below the visible surface. The surface layer, with uniform hydrographic properties, is an essential element of heat and freshwater transfer between the atmosphere and the ocean. It usually occupies the uppermost 50 - 150 m, but can reach much deeper. Winter cooling at the sea surface produces convective overturning of water, releasing heat stored in the ocean to the atmosphere. During spring and summer, the mixed layer absorbs heat, moderating the earth's seasonal temperature extremes by storing heat until the following autumn and winter. Mixing is achieved by the action of wind waves, which cannot reach much deeper than a few tens of meters, and tidal action. Below the layer of active mixing is a zone of rapid transition, where (in most situations) temperature decreases rapidly with depth. This transition layer, called the seasonal thermocline, is shallow in spring and summer, deep in autumn, and disappears in winter. In the tropics, winter cooling is not strong enough to destroy the seasonal thermocline, and a shallow feature, sometimes called the tropical thermocline, is maintained throughout the year (Tomczak, 2000).

The depth range from below the seasonal thermocline to about 1000 m is known as the permanent or oceanic thermocline. It is the transition zone from the warm waters of the surface layer to the cold waters of great oceanic depth. The temperature at the upper limit of the permanent thermocline depends on latitude, reaching from well above 20°C in the tropics to just above 15°C in temperate regions. At the lower limit, temperatures are rather uniform around 4 - 6°C, depending on the particular ocean (Tomczak, 2000).

Meso scale oceanography

Ocean and atmosphere form a coupled system. The coupling occurs through exchange processes at the sea surface interface (Tomczak, 2000). These determine the energy and mass budgets of the ocean. In the North Atlantic, for example, solar heating and excess evaporation over precipitation and runoff creates an upper layer of relatively warm, saline water in the tropics. Some of this water flows north, through the passages between Iceland and Britain. On the way it gives up heat to the atmosphere, particularly in winter. Since winds at these latitudes are generally from the west, the heat is carried over Europe, producing the mild winters that are so characteristic of that region, relative to others at similar latitudes. So much heat is withdrawn that the surface temperature drops close to the freezing point. This water, now in the Greenland Sea, remains relatively saline, and the combination of low temperature and high salinity makes the water denser than deeper water below it. Convection sets in and the water sinks - occasionally and locally right to the bottom. There it slides under and mixes with other water already close to the bottom, spreading out and flowing southward, deep. This thermohaline circulation (warm surface water flowing north, cooling, sinking and then flowing south) provides an enormous northward heat flux (Stewart, 1991).

Circulation at the surface of the oceans is wind-driven. It is generally referred to as zonal or meridian flow, depending on whether it is predominantly across latitudes or longitudes (IPCC, 2003). Under about 1 kilometer of depth, however, water flows are not driven by wind but rather by temperature (thermal) and salinity (haline) effects. This is known collectively as thermohaline circulation. The driving force for thermohaline circulation is water mass formation. Water masses with well-defined temperature and salinity are created by surface processes in specific locations. They then sink and mix slowly with other water masses as they move along. The two main processes of water mass formation are deep convection and subduction, which are linked to the dynamics of the mixed layer at the surface of the ocean (Tomczak, 2000).

The thermohaline circulation described above has become known as the 'Great Ocean Conveyor Belt' (Tomczak, 2000). The water that sinks in the North Atlantic Ocean (North Atlantic Deep Water) enters the Antarctic Circumpolar Current and from there, all ocean basins, where it rises slowly into the upper kilometer and returns to the North Atlantic in the permanent thermocline. Although this is only one of the circulation paths of North Atlantic Deep Water, it is the most important from the point of ocean/atmosphere coupling, since it acts as a major sink for atmospheric greenhouse gases. The only other region of similar importance is the Southern Ocean, where Antarctic Bottom Water sinks.

Micro scale oceanography

Tides, longshore currents, and upwellings also affect the ecology of marine areas. Tides are long waves caused by the force of gravity from the moon. The dominant period of tidal cycles usually is 12 hours 25 minutes, which is half a lunar day (Tomczak, 2000). Tides are generated by the gravitational potential of the moon and the sun, and their propagation and amplitude are influenced by friction, the rotation of the earth, known as *Coriolis force*, and resonances determined by the shapes and depths of the ocean basins and marginal seas. The most obvious expression of tides is the rise and fall in sea level. Equally important is a regular change in current speed and direction; tidal currents are among the strongest in the ocean. If the tidal forcing is in resonance with a seiche period for the sea or bay, the tidal range is amplified and can be enormous, such as occurs in the Bay of Fundy on the Canadian east coast, which with 14 meter tides has the largest tidal range in the world (Tomczak, 2000).

Longshore currents result from coastal topography, and are highly influenced by coastal constructions such as breakwaters, jetties, seawalls, etc. Perhaps even more than tidal regimes, longshore currents influence the distribution and abundance of coastal marine organisms. Even offshore marine biodiversity is affected by longshore currents, since some pelagic species have some life stages in nearshore waters (MA, 2005b).
Upwellings are vertical currents that deliver cold, nutrient-rich bottom waters to the surface (Tomczak, 2000). The most productive areas of the ocean are upwellings, including the Benguela upwelling off southwest Africa, and the Humboldt upwelling off Peru. These major upwellings are the product of the movement of cold bottom water hitting the edge of the continents and flowing upwards as a result; however, there are many minor upwellings that occur in places where the bottom topography influences deepwater currents. Upwelling areas may not be particularly diverse in species per unit area, but they support geographically massive food webs that include many marine organisms and seabirds. The extent to which upwellings provide a foundation for extensive food webs is highlighted by what happens during El Nino Southern Oscillation events in which upwelling flows diminish and large numbers of organisms, especially seabirds, starve.

Links Between Physical Oceanography and Biota

There is a strong correspondence between physical features in the ocean environment and biodiversity, irregardless of whether those features have to do with bottom topography or ocean circulation. In general, the more complex and heterogeneous the physical environment, the more productive and diverse are the food webs supported by it. Marine food webs are based largely on primary production by microscopic algae, the *phytoplankton*. This occurs in the lighted, upper layers of the ocean, especially the *coastal zone*. Production is intensified by processes that lift nutrient-laden water from deeper layers. Most of this production is then either grazed by herbivorous *zooplankton* (mainly *copepods*), or falls to the sea bottom in the form of detritus aggregates known as *marine snow*. It is attacked by bacteria on the way down, and consumed by benthic organisms upon reaching the sea bottom. Little marine snow reaches the bottom of tropical seas due to, among other things, the higher metabolic rates of bacteria in warm waters. Hence, there is less benthos, and fewer ground fish to catch in the deeper reaches of tropical seas, than in otherwise comparable temperate or polar seas. This creates a limit for the expansion of deep-sea bottom fisheries in tropical areas (MA, 2005c).

The higher the trophic level, the lower the biological production. In other words, the farther organisms are from phytoplankton and other primary producers, the smaller the population size and biomass. In fishes, the greatest production occurs at a trophic level of 3 (small fishes such as sardines and herrings that feed on herbivorous zooplankton), and near trophic level 4 (fish such as cods and tunas that prey on zooplanktivorous fishes). Many fish, however, have intermediate trophic levels, as they tend to feed on a wide range of food items, often feeding on zooplankton as juveniles and feeding on other fish as adults (Pauly et al., 1998). Biomass energy is transferred up the food web with transfer efficiencies between trophic levels ranging in marine ecosystems from about 5% to 20%, with 10% a widely accepted mean (MA, 2005c). This implies that the productivity of large, higher trophic level fish that have traditionally been targeted in the most lucrative fisheries is lower than that of less desirable, lower trophic level fishes. However, historical fishing has followed a path now known as "fishing down the food web" (Pauly et al., 1998), in which the natural proportion of predators and producers has been grossly altered, skewed towards the lowest trophic levels. This process is occurring as a result of the susceptibility to fishing pressure of large, slow-growing high trophic level fishes, which are gradually being replaced, in global landings, by smaller, shorter-lived fishes at lower trophic levels. Globally, both the landings and their mean trophic levels are currently going down under the pressure of fisheries (MA, 2005c).

Major Marine Ecosystems

Nearshore Ecosystems

Kelp forests and hard bottoms

Kelp forests are distinctive for the structure provided by the very large, anchored macroalgae that give this temperate habitat type its name; they occur in many different canopy types. The productivity of kelp ecosystems rivals that of the most productive land systems, and they are remarkably resilient to natural disturbances. They are highly diverse systems organized around large brown algae, and the complex biological structure supports a high variety of species and interactions (Dayton, 2003). They support fisheries of various invertebrates and finfish, and the kelps themselves are harvested. Kelp communities have many herbivores, but the most important are sea urchins, capable of consuming nearly all fleshy algae in most kelp systems. Unfortunately, predators which help keep urchins in check within kelp forests have been destabilized by fishing to such an extent that the kelp forests retain only a fraction of their former diversity (Dayton et al., 1998; Tegner and Dayton, 2000).

The temperate kelp forest is one of the best-understood marine communities in the world in terms of local processes at work at a particular time and location (Dayton, 2003). It is a system dominated by patch dynamics based on frequent disturbance, effective dispersal, and both inhibitory and facultative succession. Strong and weak interactions are well studied at the small scales (Paine, 2002). However, discerning the differences between direct human impacts from natural changes or changes related to regional or global change has proven difficult.

The paradigm of fishing impacts on coastal habitats cascading down to much simplified sea urchin-dominated barren grounds has proven very general (Sala et al., 1998; Steneck, 1998). The actual mechanisms, however, vary across systems. No kelp forest is pristine, and humans have vastly reduced expectations of how the systems should exist. For example, in the Atlantic large fish such as halibut, wolfish, and cod are the key predators of sea urchins. These predators largely have been removed from the system, and, as a result, sea urchin populations have exploded (Witman and Sebens, 1992; Steneck, 1998). Then, directed exploitation and disease have led to a collapse of the urchin populations leaving a once healthy and productive ecosystem degraded by waves of exotic species (Harris and Tyrell, 2001).

Non-kelp forested hard bottom communities are also highly productive, and important for fisheries. Below the *photic zone* these tend to be dominated by sponges, corals, bryozoans, and compound ascidia (Dayton, 2003). The architectural complexity provided by these colonies of organisms is important to supporting other living beings. They provide refuge from predators, and generally play an important role in maintaining the biodiversity and biocomplexity of the seafloor (Levin et al., 2001). In the more stable habitats, the species present are usually clones and long-lived individuals, and the associations are stable over decades and perhaps centuries. The populations are marked by very low dispersal, often with larvae that crawl only centimeters during their larval lifespan, and they are characterized by extreme resistance to competition, invasion, or predation (reviewed in Dayton, 1994).

Encrusting communities often appear to have several examples of alternative stable states that are self-perpetuating in the face of normal disturbances (Sebens, 1986). The mechanisms involve powerful, often chemical, defenses from predation and *biofouling*, asexual reproduction or non-dispersing larvae, and the ability to protect juveniles from predation (Dayton, 2003). Witman and Sebens (1992) demonstrated that overfishing along the coastal zone greatly reduced the top predators and caused population explosions in their prey. This in turn has changed much of the community structure. Aronson (1991) argues that this overfishing has virtually eliminated many evolutionarily "new" predators and released a "rebirth" of the Mesozoic communities dominated by echinoderms. While robust to natural disturbances from predation, competition, and biofouling, the fact that the species in these systems tend to have extremely limited larval dispersal means the recolonization and recovery following perturbation can be very slow (Dayton, 2003). Lissner et al. (1991) consider many types of disturbances and the subsequent succession and recovery to the original association. Large disturbances, such as widespread damage from fishing gear, almost never allow recovery to the pre-existing condition (Dayton, 2003).

Estuaries and tidal wetlands such as mangroves

Estuaries—areas where the freshwater of rivers meets the saltwater of the oceans—are highly productive, dynamic, ecologically critical to other marine systems, and valuable to people. Worldwide, some 1200 major estuaries have been identified and mapped, yielding a total digitized area of approximately 500,000 square kilometers (MA, 2005b). Estuaries and associated marshes and lagoons play a key role in maintaining hydrological balance, filtering water of pollutants, and providing habitat for birds, fish, mollusks, crustaceans, and other kinds of ecologically and commercially important organisms (Beck et al., 2001; Levin et al., 2001). The 1200 largest estuaries, including lagoons and *fiords*, account for approximately 80% of the world's freshwater discharge (Alder, 2003; Figure 1 shows the largest of the world's estuaries). Of all coastal subtypes, estuaries and marshes support the widest range of services, and may be the most important areas for ecosystems services. One of the key processes is the mixing of nutrients from upstream as well as from tidal sources, making estuaries one of the most fertile coastal environments (Simenstad et al., 2000). There are many more estuarine-dependent than resident species, and estuaries provide a range of habitats to sustain diverse flora and fauna (Dayton, 2003). Estuaries are particularly important as nursery areas for fisheries and other species, and form one of the strongest linkages between coastal, marine, and freshwater systems and the ecosystem services they provide (Beck et al., 2001).

Estuaries and coastal wetlands are critical transition zones linking the land and sea (see review by Levin et al., 2001). Important nutrient cycling and fluxes, primary and secondary productivity, nursery areas, and critical habitats of many birds and mammals are examples of essential services provided by this once ubiquitous habitat. Most of these functions are mediated via sediment-associated *biota* including macrophytes (mangroves, salt marsh plants, and sea grass beds as well as macro algae), heterotrophic bacteria and fungi, and many invertebrate taxa. Functional groups (organisms with similar roles) include roles such as decomposition and nutrient recycling, resuspension, filter feeding, and bioturbation.

Plants regulate many aspects of the nutrient, particle, and organism dynamics both below and above ground. Further, they often provide critical habitats for endangered vertebrates. Importantly, a wide variety of animals move in and out of this habitat for many reasons, including the completion of life cycles, feeding, use of larval nurseries, and migration. The bioturbation (or movement of sediment by burrowers) is itself an important structuring mechanism, providing mounds and depressions that serve as habitats to hundreds of small invertebrate species (Dayton, 2003).

Mangroves are trees and shrubs found in intertidal zones and estuarine margins that have adapted to living in saline water, either continually or during high tides (Duke, 1992). Mangrove forests are found in both tropical and subtropical areas, and global mangrove forest cover currently is estimated between 16 and 18 million hectares (Spalding et al., 1997; Valiela et al., 2001). The majority of mangroves are found in Asia. Mangroves grow under a wide amplitude of salinities, from almost freshwater to 2.5 times seawater strength. They may be classified into three major zones (Ewel et al., 1998) based on dominant physical processes and geomorphological characters: a) tide-dominated fringing mangroves, b) river-dominated riverine mangroves, and c) interior basin mangroves. The importance and quality of the goods and services provided by mangroves varies among these zones in terms of habitat for animals, organic matter export function, reducing soil erosion, protection from typhoons, etc. (Ewel et al., 1998).

Soft sediments and sea mounts

About 70% of the earth's seafloor is composed of soft sediment (Dayton, 2003). Although soft-sediment habitats do not always appear as highly structured as some terrestrial or marine reef habitats, they are characterized by extremely high species diversity. There is now strong evidence of fishing effects on seafloor communities that have important ramifications for ecosystem function and resilience (Rogers et al., 1998; Steneck, 1998; Dayton, 2003). Given the magnitude of disturbance by *trawling* and *dredging* and the extension of fishing effort into more vulnerable benthic communities,

Figure 1: **Distribution of major estuaries around the world**

Modified from: MA, 2005b

this type of human disturbance is one of the most significant threats to marine biodiversity (Dayton, 2003). Sponge gardens in soft substrates face particular threat from bottom trawling, since the soft substrate is easily raked by heavy trawling gear (MA, 2005).

Apart from their extremely high species diversity, soft-sediment marine organisms have crucial functional roles in many biogeochemical processes that sustain the biosphere (Dayton, 2003). Within the sediments, microbial communities drive nutrient recycling. In addition, the movement, burrowing, and feeding of organisms such as worms, crabs, shrimps, and sea cucumbers, markedly increase the surface area of sediment exposed to the water column. This affects nutrient recycling back into the water column, where it can again fuel primary production. Organic debris produced on the continental shelf finds its way to the shelf edge, where it accumulates in canyons that act as sinks to the deep ocean. There, it supports extremely high densities of small crustaceans that in turn serve as prey for both juvenile and mature fish (Vetter and Dayton, 1998).

The ocean floor's soft sediment is interrupted by highly structured seamounts with highly diverse communities of organisms (Dayton, 1994). These underwater mountains or volcanoes are usually found far offshore and are thought to be crucial for many pelagic fish species. They are sites for breeding and spawning, as well as safe havens for juvenile fishes seeking refuge from open ocean predators (Johannes et al., 1999). Because their high species diversity is concentrated into a relatively small, localized area, and because of their occasionally high endemism, sea mounts are extremely vulnerable to fishing impacts.

Coral reefs

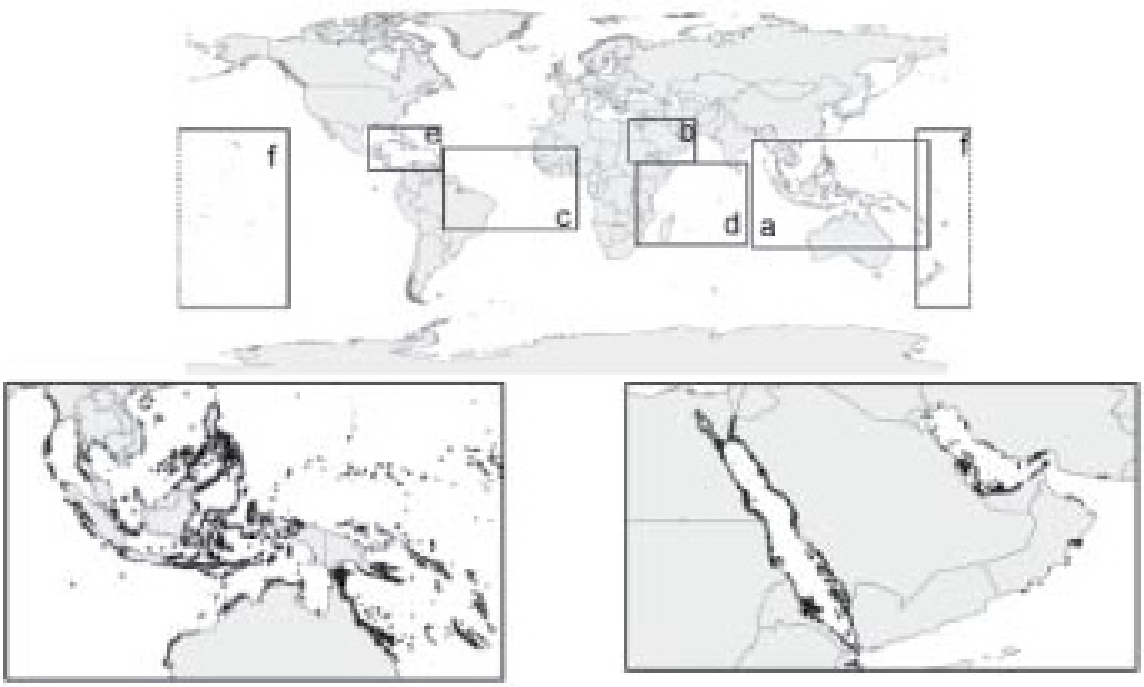
Coral reefs exhibit high species diversity and endemism and are valued for their provisioning, regulating, and cultural services (McKinney, 1998). Reef-building corals occur in tropical coastal areas with suitable light conditions and high salinity, and are particularly abundant where sediment loading and freshwater input is minimal. The distribution of the world's major coral reef ecosystems is shown in Figure 2. Reef formations occur as barrier reefs, atolls, fringing reefs, or patch reefs, and many islands in the Pacific Ocean, Indian Ocean and Caribbean Sea have extensive reef systems occurring in a combination of these types. Coral reefs occur mainly in relatively nutrient-poor waters of the tropics, yet because nutrient cycling is very efficient on reefs, and complex predator-prey interactions maintain diversity, productivity is high. However, with a high number of trophic levels, the amount of primary productivity converted to higher levels is relatively low, and reef organisms are prone to overexploitation.

The fine-tuned, complex nature of reefs makes them highly vulnerable to negative impacts from over-use and habitat degradation. When particular elements of this interconnected ecosystem are removed, negative feedbacks and cascading effects occur (Nystrom et al., 2000). Birkeland (2004) describes ecological ratcheting effects through which coral reefs are transformed from productive, diverse biological communities into depauperate ones, and similar cascading effects caused by technological, economic, and cultural phenomena. Coral reefs are one of the few marine ecosystems displaying disturbance-induced phase shifts. This phenomenon causes diverse reef ecosystems dominated by stony corals to dramatically turn into biologically impoverished wastelands overgrown with algae (Bellwood et al., 2004). Reefs are highly vulnerable to being negatively affected by global warming; rising sea temperatures cause coral bleaching, and often subsequent mortality.

Seagrass beds

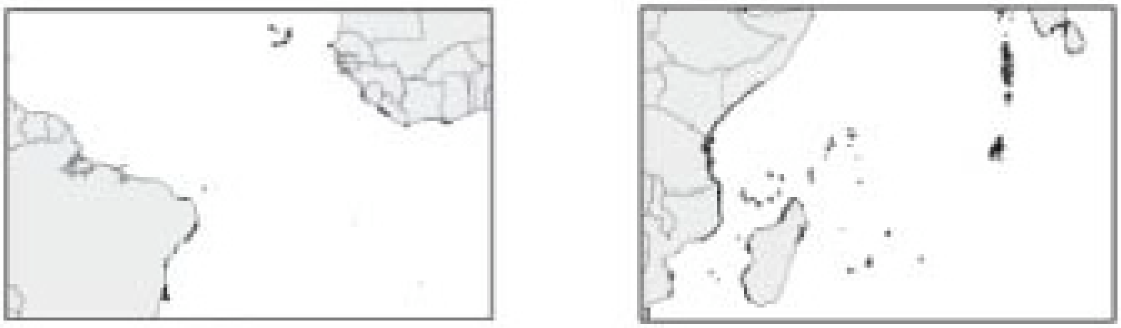
Seagrass is a generic term for the flowering plants that usually colonize soft-bottomed areas of the oceans from the tropics to the temperate zones (some seagrass can be found on hard-bottomed areas but the areas occupied are usually small). In estuarine and other nearshore areas of the higher latitudes, eelgrass (e.g. *Zostera spp.*) forms dense meadows (Deegan and Buchsbaum, 2001). Further towards the tropics, manatee and turtle grass (e.g. *Thalassia testudinum* and *Syringodium filiforme*) cover wide areas. These popular names are due to the important role seagrass plays as the main food source of these

Figure 2: Global distribution of major coral reefs



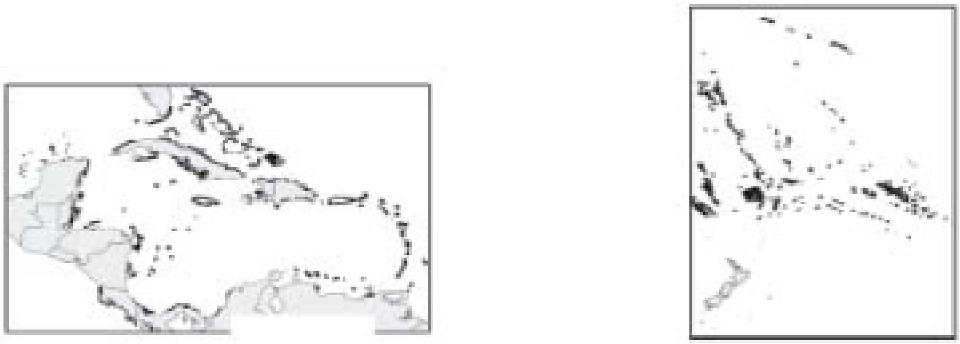
(a) East Indian and Western Pacific Oceans

(b) Middle East



(c) South Atlantic

(d) West Indian Ocean



(e) Caribbean

(f) Oceania

Modified from: UNEP-World Conservation Monitoring Centre, 2003 large, herbivorous vertebrates. Along with mangroves, seagrass is thought to be particularly important in providing nursery areas in the tropics, where it provides crucial habitat for coral reef fishes and invertebrates (Gray et al., 1996; Heck et al., 1997). This is a highly productive ecosystem, and an important source of food for many species of coastal and marine organisms in both tropical and temperate regions (Gray et al., 1996). Seagrass also plays a notable role in trapping sediments and stabilizing shorelines.

Seagrass continues to play an important ecological role even once the blades of grass are cut by grazers or currents and are carried by the water column. Drift beds, composed of mats of seagrass floating at or near the surface, provide important food and shelter for young fishes (Kulczycki et al., 1981). In addition, the deposit of seagrass castings and macroalgae remnants on beaches is thought to be a key pathway for nutrient provisioning to many coastal invertebrates, shorebirds, and other organisms. For instance, nearly 20% of the annual production of nearby seagrass (over 6 million kg dry weight of beach cast) is deposited each year on the 9.5 km beach of Mombasa Marine Park in Kenya, supporting a wide variety of infauna and shorebirds (Ochieng and Erftemeijer, 2003).

Tropical seagrass beds or meadows occur both in association with coral reefs and removed from them, particularly in shallow, protected coastal areas such as Florida Bay in the United States, Shark Bay and the Gulf of Carpentaria in Australia, and other geomorphologically similar locations. Seagrass is also pervasive (and ecologically important) in temperate coastal areas such as the Baltic Sea (Fonseca et al., 1992; Isaakson et al., 1994; Green and Short, 2003).

Offshore Open Water

The largest marine habitat by area or volume is offshore open water. This accounts for close to 55% of the earth's surface, providing nearly 90% of the living space of the biosphere. This offshore open water is not homogenous, however. Ocean circulation creates both pelagic water masses and dynamic frontal zones, both of which influence the distribution of communities of marine organisms. In the Mediterranean Sea, for instance, a frontal zone and associated upwelling area in the Ligurian Sea is distinctive because of the large diversity of marine mammals and other marine animals that congregate there to feed (see NCEP case study on *The Pelagos Sanctuary for Mediterranean Marine Mammals*).

The water column habitats of the world ocean can be subdivided into *biomes*. Although marine biogeographers have long struggled to classify the oceans according to not only the physical environment but also the biotic one, much as the Udvardy classification of terrestrial ecosystems, today the most widely accepted system is that of Longhurst (1998) who divides the world ocean into four major biomes (see Figure 3).

The Coastal Boundary Zone biome (10.5% of the world ocean) consists of the continental shelves (0-200 m) and the adjacent slopes, i.e., from the coastlines to the oceanographic front usually found along the shelf-edges (Longhurst, 1998). From a conservation point of view, this is the most important portion of the world ocean, since this is where human uses of, and impacts on, marine resources is the greatest.

The Trade-winds biome (covering 38.5% of the world's oceans) lies between the boreal and austral Subtropical convergences, where a strong density gradient hinders nutrient regeneration. The resulting low levels of new primary production make these zones the marine equivalent of deserts (MA, 2005c). Therefore, fisheries in this biome rely mainly on large pelagic fishes, especially tunas, capable of migrating over the long distances that separate isolated food patches. In the eastern tropical Pacific, a major portion of the tuna purse-seine catch results from exploitation of a close association with pelagic dolphins, which suffered severe depletion due to incidental kills in the tuna seines (Gerrodette, 2002). One exception to the general low productivity of the Trade-winds biome is around islands and seamounts, where physical processes such as localized upwelling allow for localized enrichment of the surface layer. Above seamounts, these processes also lead to the retention of local production and the trapping of advected plankton, thus turning seamounts into oases characterized by endemism and, when pristine, high fish biomass.

In the Westerlies biome (35.7% of the world's oceans), seasonal differences in mixed-layer depth are forced by seasonality in surface irradiance and wind stress, inducing strong seasonality of biological processes, characteristically including a spring bloom of phytoplankton (MA, 2005c). The fisheries of this biome, mainly targeting tuna and other large pelagics, are similar to those of the Trade winds biome.

The Polar biome covers 15% of the world ocean and accounts for 15% of global fish landings. The noteworthy productivity of this biome results from vertical density structure determined by low-salinity waters from spring melting of ice. The bulk of annual primary production occurs in ice-free waters as a short intense summer burst. Primary production under lighted ice occurs over longer periods, especially in Antarctica. The Antarctic krill, *Euphausia superba*, consumes the primary producers from both open waters and under the ice and then serves as food for a vast number of predators, notably finfishes, birds (especially penguins), and marine mammals (MA, 2005c).

Marine Ecology

Marine Population Ecology

Life history

Conservation and restoration decisions rest on understanding the processes that result in population changes, ecosystem stability, and succession. There are important thresholds in populations and ecosystems, relating to critical stages in the life histories of the populations, as well as to the roles populations play with regard to the resiliency of the ecosystems to natural and anthropogenic stress.

For marine systems such questions have focused on recruit-

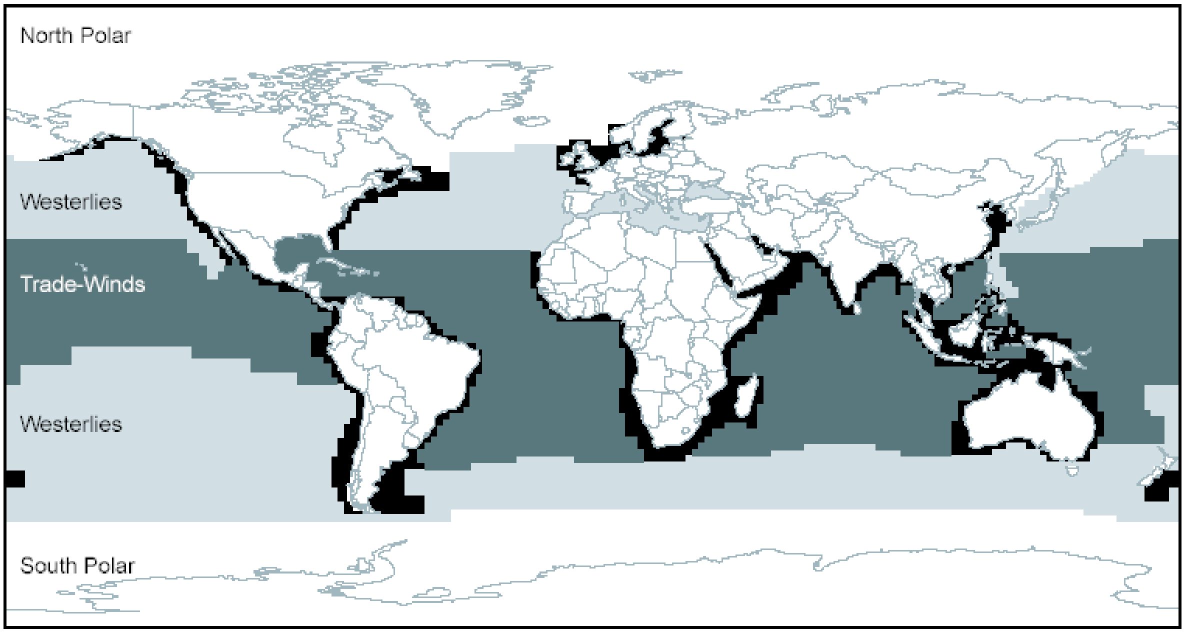


Figure 3: Longhurst classification of ocean biomes
The coastal boundary is indicated by a black border around each continent. Each of these biomes is subdivided into Biogeographical Provinces (BGP). The BGP of the coastal boundary biome largely overlaps with the LEMs identified by K. Sherman.

Taken from: MA, 2005c, adapted from Longhurst, 1998 ment dynamics, and while there are also many higher order processes such as productivity and turnover rates, understanding recruitment constitutes a logical beginning towards comprehending population and ecosystem thresholds (Dayton, 2003). Variously defined, ecologists have attempted to identify sources, sinks, and essential habitats as important factors of recruitment processes. Despite definitions, questions remain: how does one operationally define sources and sinks or rank habitat qualities? How can habitats be placed along a source-sink gradient? Critical periods and thresholds or bottlenecks can vary in time and space: how do we rank and study them with regard to declining populations and fragile ecosystems without understanding the relevant natural history? In most marine systems the following life-history components are important and have distinct thresholds (Dayton, 2003).

Reproduction

Fertilization of gametes is essential, and tactics for achieving this are well known for the birds and bees of the terrestrial world. Fertilization tactics are often very different in the sea, however, where dilution of gametes for broadcast spawners implies that individuals must release sperm and eggs within a meter or so of each other (Tegner et al., 1996). Fertilization of relatively sedentary species such as abalone, scallops, sea urchins, and bivalves often depends on the existence of dense patches of males and females, or en masse spawning. The *Allee effect* describes the relationship between high numbers of reproducing adults and successful subsequent recruitment of young – in some systems, management must take these Allee effects into account. In many cases, the feature that attracts spawning aggregations is a biologically produced physical structure, such as a coral reef. For example, Koenig et al. (1996) report that Florida groupers traveled over 100 miles to gather around deep-water Oculina coral reefs to spawn. Similar roles are likely to be played by other deep-water coral reefs, most of which have been virtually obliterated in the Aleutian Islands, Nova Scotia, Scotland, Norway, and especially the Southern Ocean seamounts.

How particular species are adapted to ecological conditions, including predation pressure and competition, is important for conservation and management (Dayton, 2003). As on land, marine species exhibit a wide variety of fertility patterns, which can be categorized as either R- or K- selected. R-selected species have high fertility and are usually free-spawning, with little to no parental care. K-selected species have significantly lower fertility (and usually longer life spans), but exhibit brooding and more parental care.

Larval ecology and recruitment

Critical periods in the planktonic life of fish and other marine larvae include time of first feeding, successful dispersal to appropriate habitats, settlement, and metamorphosis (Hjort, 1914). The first feeding periods are defined by the abilities of the larvae to handle prey, as well as sufficient density of appropriate prey. Invertebrates have much more complicated life history patterns and dispersal tactics, with post-fertilization and dispersal processes varying from seconds for brooding species, to many months for organisms with feeding larvae.

Most *propagules* depend on oceanographic transport. The larvae of most species with planktonic dispersal drift for periods of 3 to 60 days. Because of complicated coastal oceanography, the differences within this period of time often encompass complex and very different physical transport systems. This is especially true in the very near shore areas. These include those within/between bays, kelp forests, or unstable *gyres* where "relaxation" modes are important, and the oceanography is complicated. The variability in these factors complicates the definition of sources and sinks for species such as lobsters, and some echinoderms with very long larval periods (Dayton, 2003).

Dispersal processes are highly variable in evolutionary adaptations and the physical transport systems they utilize. Marine ecologists often focus on dispersal biology, but many systems, such as the clonal encrusting ones, have virtually no dispersal (Dayton, 2003). Most reproduce by budding or crawl-away larvae (Levin et al., 2001). In the same sense, many other soft-bottom groups including peraicarid crustacea and capitellid polychaetes are brooders and disperse as adults; their transport systems include the bottom *flocculent layer* or being picked up and carried by complicated breaking internal waves.

Successful settlement is another critical period (Tegner and Dayton, 1977). Food availability and temperature strongly influence the length of time spent in the water column. The period at which a larva becomes capable of settlement is known as the competent phase. The larva may continue to drift, exposing itself to increased risk of predation before it settles. Models of Jackson and Strathmann (1981) demonstrate that critical parameters are mortality rates, the length of the precompetent period, and the ratio of competent/precompetent time. These factors are poorly understood but extremely important and probably account for the common observation of episodic settlement.

Availability of appropriate settlement habitats or nurseries can be an important bottleneck, and much is left to chance (Sale, 1991). Many unanswered questions remain about how young locate appropriate settlement areas, especially those species that show natal homing. For instance, much as sea turtles return to the nesting beach where they were hatched in order to lay eggs, coral larvae also must find the reef after planktonic drifting. Recent research suggests that sound may have a role to play in coral settlement (Simson et al., 2005). Environmental inducements are sometimes needed for larvae to settle and metamorphose. According to Dayton, species with the longest precompetent periods also have very specific recruitment habitats that help avoid predation, disturbance, and stress (Dayton et al., 1995).

Indian lionfish (*Pterios muricata*) off of the Seychelles (Source: K. Frey)

Juveniles and adults often have different habitats. For example, nurseries of many Pacific rockfish are in kelp forests, and many other species rely on sea grass beds, mangroves, corals, various associations of encrusting species, or depressions in soft bottom habitats. In many cases the adults live in very different habitats and migration may be tenuous and risky. Without understanding this natural history, artificial settlement areas such as man-made reefs may simply be killing zones if the appropriate adult habitats are not available.

Community Ecology

Communities of organisms, whether in the sea or on land, respond in predictable ways to the forces of interspecific and intraspecific predation and competition. The intertidal communities of temperate regions provided many of the experiments that led to this understanding: most famous of all were the studies by Paine and colleagues, who removed the top predator *Pisaster* (a species of sea star) from intertidal rock pools and observed the decline in species diversity that resulted (see Paine, 2002, for a review of earlier studies and new results). Removal of predators can have this effect because top predators keep their prey populations down in number so that none can dominate. When this sort of predation pressure stops, species that were formerly controlled by predator populations are "released" and multiply, upsetting the original biodiversity balance. When such perturbations cause effects across the entire food web, they are known as "cascading effects," because impacting the top trophic level subsequently impacts the trophic levels below it.

Kelp forest communities are well studied in regards to cascading effects. At the bottom of the kelp community food web are seaweeds (kelps and other algae) and microscopic planktonic algae, both of which serve as the primary producers in this ecosystem. The planktonic algae support small planktonic invertebrates such as copepods, which in turn are consumed by filter-feeding sessile invertebrates such as hydroids, scallops, barnacles, sea anemones, bryozoans, and tube worms, as well as other smaller mobile predators like fish and certain crustaceans. The larger seaweeds are eaten both directly by a broad range of animals, including sea urchins, fishes, small snails, shrimp-like crustaceans, sea stars, and crabs, and indirectly (as large and small loose pieces of "drift") by abalones, sea urchins, mussels, and barnacles. Many of these animals are then consumed by mid-level predators, such as other sea stars, larger crabs, larger fishes, and octopuses.

The sea otter, at the top of the food web, acts as a "keystone species" in the community. Keystone species are ones that have, for various reasons, a substantial effect—disproportionate to their numbers—on the rest of the community. Because they lack the blubber of other marine mammals, individual sea otters need to consume a huge amount of food each day to stay warm and healthy. While a population of otters may eat many things, sea urchins are their favorite prey. Since sea urchins can have major effects on other species in the community, otter predation on them exerts a controlling influence on the ecosystem. When otters are removed from the community, or their numbers are diminished, urchin barrens can result, where urchins graze down everything including the kelp that provides the foundation for the other species to live (this effect is described in the *Introduction to Marine Conservation Biology* exercise; students are asked to predict what the effect of sea otter removal might be).

Predator/prey relations are thus important to understanding how communities of organisms are structured, and how populations of those organisms are maintained. Competition is also important, though probably a less dominant force in most marine communities. But impacts on community ecology are not only the result of perturbations involving predators – they can be felt with the removal of herbivores (or grazers) as well. In a recent study on coral reef community ecology in the Bahamas, Mumby (2006) studied the effects of removing parrotfish on the health and diversity of reefs across a wide area. Removing even small numbers of these grazers can have dramatic effects on reef communities, influencing the amount of coral cover, biomass of reef species, and reef species diversity. The reason for this is that herbivores like parrotfish keep algae from overgrowing the reef and diminishing the availability of niches for other reef species (including corals, sponges, crustaceans, mollusks, and fishes).

These community effects seem most pronounced in ecosystems that are relatively closed systems, and where food is a key limiting factor. In more open systems in which food is readily available, such as major upwelling systems like the Benguela or Peruvian upwellings, removal of one species likely has less discernable effects. But even open ocean systems can see dramatic changes to communities as a result of disturbance – for example, "trophic mining," in which industrial fisheries remove whole swaths of a trophic level and change the energetics of the entire community (Pauly et al., 1998).

Understanding why populations decline or why natural communities are disrupted is a critical facet of conservation. With well-studied ecosystems like coral reefs and kelp forests, the effects of perturbation can be anticipated. But even with well-studied communities, questions remain. And many, many ecological communities are not well studied at all.

Populations decline for a variety of reasons, and ecologists have debated the processes determining the distribution and abundance of individuals within populations. The debate includes disputes about the relative roles of density independent and dependent factors, the importance of interspecific and intraspecific competition, predation, parasites, and mutualistic relations. Dayton (2003) suggests the following list as a small sample of some of basic issues that need to be addressed in marine conservation biology.

Cumulative effects:

- How much is too much? What defines limits and thresholds?

- What describes species vulnerability?
- Are some species redundant and expendable?
- Can cumulative impacts of human perturbations be predicted?

Ecosystem or habitat stability and recoverability:

- How do we define and measure stress in multispecies systems?
- How do we define habitat or ecosystem health?
- Why do systems collapse? What are the thresholds?
- What are the processes that maintain stability?
- What are the processes that define recoverability?

Trend analysis:

- How do we differentiate human induced-trends from natural trends?
- What determines whether trends are general or peculiar to particular systems?
- What spatial and temporal scales are necessary for such trend analysis?
- How can society acquire trend data from already peturbed systems?

Restoration Ecology:

- How to define the desired state?
- What are realistic goals? How are they determined?
- How should we manipulate successional processes that are little understood?
- What are the most efficient means of restoration?

This extensive list of research questions demonstrates how little we actually know about marine community ecology, and how far behind the study of terrestrial ecology marine science lags. In some sense conservation is hindered by these gaps in knowledge and most management focuses on the simplest impacts. But innovative new management measures do allow applied information to be gained quickly through the process of adaptive management – and these approaches help overcome information constraints. Marine conservation will be greatly aided in coming years if applied research is directed at solving these basic questions.

Marine Resource Use and Conservation

Marine Resource Use

Coastal ecosystems are among the most productive, yet highly threatened systems in the world. They comprise heavily used coastal lands, areas where freshwater and saltwater mix, and nearshore marine areas. These ecosystems produce disproportionately more services relating to human well-being than most other systems, even those encompassing larger total areas. At the same time, these ecosystems are experiencing some of the most rapid environmental change: almost half of the world's mangroves have been lost or converted, and approximately 27% of coral reefs have been destroyed globally in the last few decades. Coastal wetland loss in some places has reached 20% annually (MA, 2005b).

Coastal areas are experiencing growing population and exploitation pressures; nearly 40% of the world population lives in this thin fringe of land (MA, 2005b). Demographic trends suggest coastal populations are rapidly increasingly, mostly through migration, increased fertility, and tourist visitation to these areas. Population densities on the coasts are nearly three times that of inland areas. Communities and industries increasingly exploit fisheries, timber, fuelwood, construction materials, oil, natural gas, sand and strategic minerals, and genetic resources. Additionally, demand on coastal areas for shipping, waste disposal, military and security uses, recreation, aquaculture, and even habitation are increasing.

Shoreline communities aggregate near those types of coastal systems that provide the most ecosystem services (MA, 2005b). These subtypes are also the most vulnerable. Within the coastal population, 71% live within 50 km of estuaries. In tropical regions, settlements are concentrated near mangroves and coral reefs. These habitats provide protein to a large proportion of the human coastal populations in some countries. Coastal capture fisheries yields are estimated to be worth a minimum of USD 34 billion annually. Marine ecosystems provide other resources as well: building materials (e.g., sand, coral), ores, and energy (hydrocarbons, thermal energy, etc.).

Marine systems also provide pharmaceuticals, and are highly valued for recreational, spiritual, and cultural reasons.

Sub-national sociological data suggest that people living in coastal areas experience higher well-being than those living in inland areas. The acute vulnerability of these ecosystems to degradation, however, puts these inhabitants at greater relative risk (MA, 2005b). The world's wealthiest populations occur primarily in coastal areas (per capita income being four times higher in coastal areas than inland). It is thought that life expectancy is higher, while infant mortality is lower, in coastal regions. However, many coastal communities are politically and economically marginalized, and do not derive the economic benefits from these areas. Wealth disparity has led to the limitation of access to resources for many of these communities. Access issues have in turn led to increased conflict, such as between small-scale artisanal fishers, and large-scale commercial fishing enterprises. Regime shifts and habitat loss have led to irreversible changes in many coastal habitats and losses in some ecosystem services. Finally, many degraded coastal systems are near thresholds for healthy functioning, and they are simultaneously vulnerable to major impacts from sea level rise, erosion, and storm events. This suggests that coastal populations are at risk of having their relatively high levels of human well-being severely compromised.

Threats to Marine Ecosystems and Biodiversity

General

Human pressures on coastal resources are compromising many of the ecosystem services crucial to the well-being of shoreline economies and peoples. While the ocean comprises nearly three-quarters of the Earth's surface area, it accounts for nearly 99% of its habitable volume. Thus, disruptions of marine and coastal ecosystem services have global consequences. Coastal fisheries have depleted stocks of finfish, crustaceans, and mollusks in all regions (MA, 2005b). Illegal and destructive fisheries often cause habitat damage as well as over-exploitation. Large scale coastal fisheries deprive shore communities of subsistence, and are causing increasing conflicts, especially in Asia and Africa (MA, 2005c). Demands for coastal aquaculture have been on the rise, partly in response to declining capture fisheries. The doubling of aquaculture production in the last 10 years, however, has also driven habitat loss, overexploitation of fisheries for fishmeal and fish oil, and pollution. Over-exploitation of other resources, such as mangrove for fuel wood, sand for construction material, seaweeds for consumption, etc., also often undermine the ecological functioning of these systems.

The greatest threat to coastal systems is development-related loss of habitats and services. Many areas of the coast are degraded or altered, such that humans are facing increasing coastal erosion and flooding, declining water quality, and increasing health risks. Port development, urbanization, resort establishment, aquaculture, and industrialization often involve destruction of coastal forests, wetlands, coral reefs, and other habitats. Historic settlement patterns have resulted in centers of urbanization near ecologically important coastal habitats. About 58% of the world's major reefs occur within 50 km of major urban centers of 100,000 people or more, while 64% of all mangrove forests and 62% of all major estuaries occur near such urban centers. Dredging, reclamation, engineering works (beach armoring, causeways, bridges, etc.) and some fishing practices also account for widespread, usually irreversible, destruction of coastal habitats (MA, 2005b).

Degradation is also a severe problem, since pressures within coastal zones are growing and these areas are also the downstream recipients of negative impacts of land use. Freshwater diversion from estuaries has meant significant losses of water and sediment delivery (30% decrease worldwide, with regional variations) to nursery areas and fishing grounds (MA, 2005b). The global average for nitrogen loading has doubled within the last century. This has made coastal areas the most highly chemically altered ecosystems in the world, with resulting eutrophication that drives coral reef regime shifts and other irreversible ecosystem changes. Nearly half of the global population living along the shore has no access to sanitation, and thus faces decreasing ecosystem services and increasing risks of disease (UNEP, 2002). Mining and other industries cause heavy metal and other toxic pollution. Harmful algal blooms and other pathogens, which affect the health of both humans and marine organisms, are on the rise. This can partly be attributed to decreased water quality. Invasions of alien species have already altered marine and coastal ecosystems, threatening ecosystem services.

The health of coastal systems and their ability to provide highly valued services is intimately linked to that of adjacent marine, freshwater and terrestrial systems, and vice versa. Land-based sources of pollutants are delivered via rivers, from run-off, and through atmospheric deposition. These indirect sources account for the large majority (77%) of pollutants (MA, 2005b). In some areas, pollution in coastal zones contaminates groundwater; this is a particular threat in drylands (MA, 2005b). Another linkage occurs between expanding desertification and pollution of coral reef ecosystems caused by airborne dust. Destruction of coastal wetlands has similarly been implicated in crop failures due to decreased coastal buffering leading to freezing in inland areas.

Though habitat conversion is the main driver behind coastal biodiversity loss, overexploitation of resources and, on continental shelves, fisheries-related habitat destruction, degradation driven by pollution, invasive species, and climate change play major roles. Trophic cascades and trophic mining result from overexploitation of fishery resources. This leads to biodiversity losses at the genetic, population, and even species levels. Marine ecosystems are less able to provide important ecosystem services (especially provisioning services) and often are less resilient as a result (MA, 2005b). Many of these impacts create negative synergies, in which multiple and cumulative impacts cause greater change to ecosystems and services than the sum of individual impacts would predict. At the same time, all ecosystems and the biodiversity they support are subject to multiple and cumulative impacts, both natural and anthropogenic. Some ecosystems face greater numbers of threats than others, particularly those that support a wide variety of uses/services (e.g. coastal ecosystems, islands). One effect of multiple impacts occurring simultaneously is to alter thresholds and increase the non-linearity of response (thus decreasing the predictability of environmental change) (MA, 2005a).

In addition to the proximate drivers, indirect drivers are behind each of these impacts. Population growth is said to be the main indirect driver behind all environmental change today. The link between sheer population number and environmental quality is not clear cut, however. Some authors argue that a direct link exists between the number of people and the quality of the environment or loss of diversity, irregardless of consumption patterns (McKee et al., 2004). Others argue that the number of households is better correlated to the environmental impact or *ecological footprint* left by humans (Liu et al., 2003). In the coastal zone, however, neither population numbers nor household numbers tell the full story. Patterns of consumption and other human behaviors greatly influence the ecological footprint left by communities, and migration and its effects often spell the difference between sustainable and unsustainable use (Curran and Agardy, 2002; Creel, 2003). Local resource use and migration patterns are also affected by local and international markets.

Habitat Loss and Degradation

The most serious consequences of biodiversity loss occur when changes are irreversible: e.g. habitat loss (especially complex habitats), species extinction, population extirpation, regime shifts. The most important driver behind these large scale impacts on biodiversity is land conversion (including coastal/marine habitat loss). However, the main drivers behind biodiversity loss are different in various ecosystems. The risks of abrupt/non-linear changes in species composition and the corresponding risks of abrupt or non-linear changes in ecological systems vary by species and ecosystem. Although natural systems contain significant redundancy in terms of ecological roles that species play in providing ecosystem services, there is no doubt that major decreases in species diversity (and thus the complexity of interactions between species) lead to potentially unstable, though often productive, ecosystems. Removal of species can cause cascading effects that alter productivity at various trophic levels. Such cascading effects are most acute when keystone predators are removed (see Finke and Denno, 2004 on predator diversity dampening trophic cascades, for example).

While the threat of greatest magnitude to coastal systems is development-related conversion of coastal habitats, degradation is a severe problem for biodiversity, since pressures within coastal zones are growing and because coastal zones are the downstream recipients of negative impacts of land use. Freshwater diversion from estuaries has meant catastrophic losses of water and sediment delivery (30% decrease worldwide) to nursery areas and fishing grounds. At the same time, external inputs lead to loss of biodiversity, reduction of ecosystem services, and declines in human well-being, especially in coastal communities.

Resource Extraction

Fishing and other extraction activities affect the stocks of living and non-living resources, the things that feed or are fed upon by those resources, and the habitat that supports marine life. In general, resource removal is detrimental when the amount of removal is greater than the capacity for the living resource to replenish itself (known as over-exploitation), when the resource being removed has a key role to play in community ecology, or when the method of removal is destructive. In essence, this boils down to three questions: 1) how much removal is sustainable?; 2) which resources can be removed sustainably?; and 3) how can resources be removed sustainably? (i.e. by what methods?).

While it would appear that significant concerns about fisheries impacts on the marine environment exist, most concern over the environmental effects of fishing has focused on nearshore habitats. In fact, the vast scope of ecological destruction of the full suite of marine habitats has only recently been documented. The removal of small-scale heterogeneity associated with the homogenization of habitats is an important cause of the loss of biodiversity in many marine systems (Dayton, 2003). And restoration of the system depends upon an understanding of structure in time and space, and of biological thresholds for all of the species that create and maintain the structure (Dayton, 2003).

There is now strong evidence of fisheries effects on seafloor communities that have important ramifications for ecosystem function and resilience. Given the magnitude of disturbance by trawling and dredging and the extension of fishing effort into deeper, more sensitive benthic communities, this type of human disturbance is one of the most significant threats to biodiversity and the provision of ecosystem services (Thrush and Dayton, 2002).

Invasive Species (Including Pathogenic Diseases)

Invasion of coastal and marine areas by non-indigenous or alien species is a major threat to marine biodiversity and ecosystem functioning, much as invasions are causing major ecological changes on land. Altering soft bottom habitat to hard bottom in the process often affects estuaries indirectly by creating conditions for new assemblages of species, and facilitating range expansions of invasive species (Ruiz and Crooks, 2001). The resulting ecosystems may have losses in some ecosystem services and biodiversity. In New Zealand invasive species have displaced commercially important mussel beds, resulting in significant economic losses for many mussel farmers (NOAA News Online, 2003).

Estuarine systems are among the most invaded ecosystems in the world, with exotic introduced species causing major ecological changes (Carlton, 1989, 1996). Often introduced organisms change the structure of coastal habitat by physically displacing native vegetation (Harris and Tyrrell, 2001; Grosholz, 2002; Murray et al., 2004). For example, San Francisco Bay (U.S.A.) has over 210 invasive species, with one new species established every 14 weeks between 1961 and 1995 (Cohen and Carlton, 1995, 1998). Most of these bio-invaders were borne by ballast water of large ships or occur as a result of fishing activities (Carlton, 2001). The ecological consequences of the invasions include: habitat loss and alteration; altered water flow and food webs; the creation of novel and unnatural habitats subsequently colonized by other exotic species; abnormally effective filtration of the water column; hybridization with native species; highly destructive predators; and introductions of pathogens and disease (Ruiz et al., 1997; Bax et al., 2003).

Climate Change

The geographically largest scale impacts to coastal systems are caused by global climate change, and since rates of warming are generally expected to increase in the near future, projected climate change-related impacts are also expected to rise (IPCC, 2003). Warming of the world's seas degrades coastal ecosystems and affects species in many ways: by changing relative sea level faster than most biomes can adapt; by stressing temperature-sensitive organisms such as corals and causing their death or morbidity (in corals this is most often evidenced by coral bleaching); by changing current patterns and thus interfering with important physiobiotic processes; and by causing increased incidence of pathogen transmission (MA, 2005b). Coral reefs may be the most vulnerable, having already evidenced rapid change, and some projections predict the loss of all reef ecosystems this century (Hughes et al., 2003). Global warming also changes the temperature and salinity of *estuary* and nearshore habitats, making them inhospitable to species with narrow temperature tolerances. Warming can also exacerbate the problem of eutrophication, leading to algal overgrowth, fish kills, and dead zones (Burke et al., 2001). Finally, warming is expected to further increase the transmission rates of pathogens and hasten the spread of many forms of human and non-human disease.

Climate change-related sea level rise will cause continued inundation of low-lying areas, especially in areas where natural buffers have been removed (Church et al., 2001). Sea level rise is due to thermal expansion of ocean waters and melting of land-based ice, and both expansion and ice melts are expected to increase (IPCC, 2003). In most if not all cases, global climate change impacts act in negative synergy with other threats to marine organisms, and can be the factor sending ecosystems over the threshold levels for stability and productivity. In limited cases, new habitats may be created. Changes in weather patterns modeled in some extreme scenarios of climate change, including increased precipitation in some areas, abrupt warming at the poles, and increased frequency and intensity of storm events, would affect oceanic circulation (perhaps even leading to the collapse of thermohaline circulation) and currents, and the ability of organisms to live or reproduce.

Most Threatened Areas

Island systems are especially sensitive to disturbances, and island biota particularly vulnerable to extinction, primarily driven by ecological changes wrought by invasive species. Many islands serve as important biological *refugia* for species that are either extinct or threatened on nearby continental landmasses. The habitat destruction and biodiversity loss on islands may therefore have more immediate and serious repercussions than on continental systems. With growing population and exploitation pressures, the impact on some island systems has exceeded the critical point. Invasive species are one of the most significant drivers of environmental change to islands over the world, and oceanic islands are more successfully invaded by vertebrates compared to corresponding continental areas.

Nearshore areas are particularly vulnerable to anthropogenic threats. The destruction of the natural watershed often results in the loss of most of the attributes of estuarine habitat, for instance. Poor management of watersheds, including poor grazing practices that destroy natural *riparian* habitats, results in floods and burial of the natural habitats under silt and enriched sediment. Often these impacts combine with severe nutrient loading, causing large coastal areas to become anoxic. An extreme example is the massive (up to 15,000 km^2) dead zone in the Gulf of Mexico (Turner and Rabalais, 1994). Urbanization of watersheds interrupts the flow of both essential fresh water and nutrients. Nutrient loading and eutrophication result in prolonged ecological degradation, as algae take over bottom habitats and the water column so that the entire ecosystem is altered (Levin et al., 2001).

Coral reefs and the ecosystem services they provide are especially threatened by anthropogenic forces (Birkeland, 2004). Ecosystem services provided by coral reefs include habitat and nurseries for fish, nutrient cycling and carbon fixing in nutrient-poor environments, wave buffering and sediment stabilization, and a number of cultural ecosystem services. These ecosystem services associated with coral reefs can only be maintained if: 1) the ecosystem remains intact, and 2) the interaction between corals and their obligate symbiotic algae is preserved.

Great attention has been paid to the decline in species diversity in terrestrial ecosystems, however it is apparent that there are substantial changes in diversity in deep ocean benthos – albeit changes that may not be so readily detected (Dayton, 2003). Direct killing and habitat loss are primary factors responsible for the global decline in diversity. Most bottom habitats are characterized by biological construction in which the organisms provide structure critical to many other parts of the ecosystem. Examples include reefs of mussels, oysters, sponges, corals (including some 700 species of deep-water corals that may tower more than 40 m above the sea floor), kelp forests, sea grass meadows, and even large single-celled *foraminiferans*, all of which fill important ecological roles within the community (Levin et al., 1986; Rogers, 1999). These roles include filtering the seawater and affecting its flow. The biological structure also serves to retain water masses with larvae, and it furnishes critical habitats and predator protection. The architectural complexity supports a diverse association of feedback loops that define the biological complexity of seafloor processes. These important ecological roles are as yet very poorly understood (Dayton, 2003). Physical disturbance by fishing, mining, etc. can thus significantly impact habitat, species diversity, and interlinked ecological processes.

Methods to Conserve Marine Biodiversity

There are many methods used in marine conservation; indeed, the toolbox is full, though seldom fully utilized. However, many of these tools can be discussed in the context of five major kinds of marine management: 1) spatial management through *marine protected areas*; 2) fisheries management; 3) restoration; 4) integrated coastal management; and 5) international treaties and agreements. These five major themes are presented not by order of importance but rather by the scale at which they are practiced, beginning with the smallest geographical scale and extending to the largest. Truly effective marine conservation requires that these sorts of initiatives be tied together in a holistic manner, so that not only individual sites are protected but the entire context in which such sites lie is protected as well. In many instances, however, a mismatch of scales occurs such that rather than complementing one another, these sorts of methods can impede one another – especially when marine conservation planning is focused only at a particular scale and not the hierarchy of scales that is reality (Agardy, 2005).

Spatial Management Through Zoning and Marine Protected Areas

Individual sites recognized for their valuable services are sometimes protected through zoning regulations and other spatial management interventions, such as marine protected areas (MPAs) (NRC, 2001). Such protected areas may be small fisheries reserves in which resource extraction is prohibited, or they may occur in the context of larger multiple-use areas. Increasingly, marine protected areas are being established in networks in order to safeguard key areas of the coastal and marine environment over a geographically large area (Agardy, 1999; Murray et al., 1999; Pauly et al., 2002). A prime example of this is the network of reserves encompassed by the newly re-zoned Great Barrier Reef Marine Park in Australia (Day, 2002).

In order for marine protected areas to succeed in meeting the objectives of conserving habitats and protecting fisheries and biodiversity, management seeks to address all relevant direct threats. In most habitats, these threats are multiple and cumulative over time. Thus, protected areas that address only one of these will usually fail to conserve the ecosystem or habitats and the services they provide.

Marine and coastal protected areas already dot the coasts of all the world's areas, and the numbers of protected areas continue to increase. The last official count of coastal and marine protected areas in 2003 yielded 4,116 (Spalding et al., 2003). This represents a marked increase over the 1,308 listed in 1995 (Kelleher et al., 1995). It is, however, a significant underestimate because unconventional protected areas that do not fit the IUCN categories for protected areas are typically not counted (see the *Marine Protected Areas and MPA Networks* module). By far the bulk of these protected areas occur in the coastal zone, and many include both terrestrial and aquatic components (MA, 2005b). Even with the large number of individual sites, however, coverage accounts for less than 0.5% of the world's oceans. Many marine protected areas occur in relatively close proximity to human settlements. In fact, nearly ten percent of the global human population lives within 50 kilometers of a marine protected area, and over 25% of the worldwide coastal population lives within 50 kilometers of a marine protected area (MA, 2005b). Management effectiveness of most MPAs remains questionable, and many of these have no operational management or enforced legislation at all. It is well established that marine protected area tools are not being used to their fullest potential anywhere in the world (Agardy et al., 2003).

Fisheries Management

Management of living marine resource use has been practiced for several centuries. Conventional fisheries management relies on fish population dynamics models that suggest *maximum sustainable yield (MSY)* for a particular stock. This information is then used to identify appropriate management regimes such as restrictions on catch (quotas, size limits, age class restrictions, etc.), gear, and harvest time (duration of fishing season). Fisheries managers also look to temporary, seasonal, rotating, or permanent MPAs as a way to target sustainability (MA, 2005c). Determining where to establish fisheries reserves requires an understanding of life histories and determination of essential fish habitat (EFH). These spatial management techniques are most successful in fisheries targeting species whose ecology is well known (Sale et al., 2005). However, even effective management of a single stock or species does not necessarily lead to conservation of the wider community or biodiversity of the region.

Resource use that is managed in a way that considers the impacts that resource removal has on all linked ecosystems and human well-being has proven to be more effective than sectoral or single-species management (Kay and Alder, 2005). Fisheries agencies and conservationists are promoting ecosystem-based fisheries management. This is management that looks at multispecies interactions and the entire chain of habitats these linked organisms need in order to survive and reproduce (Agardy, 2002). Due to the linkages between marine fisheries production and coastal ecosystem condition, the protection of coastal habitats figures very prominently in ecosystem-based fisheries management (Pauly et al., 2002). However, truly holistic integrated management also requires complementary watershed management and land use planning to ensure that negative impacts do not reach these areas from outside the coastal realm.

Implementation of ecosystem-based management (EBM) for fisheries requires a multi-pronged approach. Dinesen and Gribble (2005) explore the dual roles of modeling and policy development in enhancing EBM for Queensland-managed fisheries in Australia. ECOPATH software is used to simulate temporal and spatial reactions to commercial fishing and the imposition of a "no take" zone within an MPA. The addition of spatially explicit habitat data to the equilibrium GBR ecosystem model significantly buffered the predicted volatility in trophic guild biomass, by providing de facto spatial refugia from fishing pressure. The simulations showed that additional protected "no take" zones must be of adequate size to allow for "edge effects" caused by illegal fishing, particularly if sited in remote areas. Fishing tended to concentrate on the borders of the "no take" zone, which produced "gauntlet" effects to the movement of some groups. Vulnerable species did better within "no take" MPA areas, but scavenger/opportunistic species did worse.

Ecosystem-based fisheries management is currently *de rigeur*, even though some fisheries managers profess uncertainty about what the term actually means, and in what ways embracing the concept will change day-to-day operations of fisheries agencies (Lubchenco, 1998). Nonetheless, there are parts of the world where management is moving away from single species or even small-scale multi-species strategies to broader marine management. Many of these initiatives began as a result of regional fisheries agreements (Griffis and Kimball, 1996). A literature has begun to emerge on ecosystem-based fisheries management (e.g., Sinclair and Valdimaarson, 2003).

Arguably, the best example of ecosystem-based marine management is the Convention on Conservation of Antarctic Marine Living Resources (CCAMLR). Many regional fisheries agreements are delimited by the boundaries of large marine ecosystems (LMEs). These are regions of ocean space that extend from inshore to the seaward boundaries of continental shelves and seaward margins of coastal current systems (Kimball, 2001). There are 64 LMEs globally, averaging 200,000 square kilometers, and characterized by distinct *bathymetry*, hydrology, productivity, and trophically-dependent populations (Sherman, 1993; Wang, 2004). The LME concept originated from fisheries management. Even today most of these ecosystems are defined by physical oceanography and fisheries data, and not by other considerations of biodiversity. The LME concept was originally applied in the fisheries context under CCAMLR to take into account predator/prey relationships and environmental factors affecting target stocks. Thus, Antarctica became the first site of a truly ecosystem-based approach to fisheries management, and the target area was defined by the limits of the Antarctic LME. Several recent international instruments refer to LMEs. In addition, the geographic units serve as the basis for some global assessments, such as the UNEP's Global International Waters Assessment (GIWA; www.giwa.org). However, in many parts of the world, the political constituency for nations to cooperate to conserve the large scale ecosystems and marine species they share is limited, though this situation may be improving (Wang, 2004; see the *Marine Protected Areas and MPA Networks* module).

Restoration

Some key coastal habitats, such as mangrove forests, marshes, and seagrass meadows, can be, and are being, restored once degraded. The science of mangrove restoration is relatively advanced. This is especially the case when natural species diversity is low, and replanting a few species can restore ecosystems and most services quickly (Kaly and Jones, 1998). Marshlands are also relatively easily restored, as long as major alterations to hydrology have not taken place. Such initiatives are risky, however, since it has yet to be shown that the full range of ecosystem services can be supported by artificially reconstructed wetlands (NRC, 1992; Moberg and Ronnback, 2003). Coral reef transplantation, though technologically possible, can only be practiced at a small scale, and has had limited success (Moberg and Ronnback, 2003). Furthermore, the costs

Green moray eel (Source: K. Frey)

can be enormous, as the USD 7.8 billion price tag for the restoration of the Everglades cord-grass system in Florida (US) attests. In fact, most full-scale restoration (habitat reconstruction) is practiced in highly developed countries that are able to finance the high costs over the long time frames needed.

Restoration and subsequent management should be based on understanding the sources of propagules of the target species. Understanding propagule sources, however, requires understanding the strong interactions (Sala and Graham, 2002) and definition of target species in most urgent need of management. There is a pressing need to better understand the Allee effect (discussed above) in which sources of propagules, and the thresholds in their respective spawning aggregations, are defined. In addition, it is important to distinguish between larval nurseries and sinks, and establish the relative abundances of each. A clear understanding of successional processes is also important.

Integrated Coastal Zone Management

Complex problems require comprehensive solutions and an integrated management response is needed to conserve most aspects of biodiversity, especially at the ecosystem level. Sectoral approaches have been proven to have shortcomings in management of complex issues such as biodiversity. In marine environments, connectivity over large geographic distances requires a melding of a top-down management approach with the more local and national level approaches typical to most biodiversity conservation.

Integrated management of watersheds, land use planning, and impact assessment are key to protecting coastal ecosystems (Sorenson, 1997). For this reason, tackling the issues of loss and degradation of these areas by addressing single threats has not proven effective in the past. The holistic approach, looking at how human activities affect coastal ecosystems, identification of key threats, and implementation of management that is integrated across all sectors, is a relatively new focus. This is likely to produce much more effective decision-making. Successful management of these crucial areas means coordinated pollution controls, development restrictions, fisheries management, and scientific research.

Significant strides have been made in coastal management in the last few decades, in both the developed and developing world. Many of the earth's 123 coastal countries have coastal management plans and legislation, and new governance arrangements and regulations are being developed every year (Burke et al., 2001). In 1993, it was estimated that there were 142 coastal management initiatives outside the U.S.A. and 20 international efforts (Sorensen, 1993). By 2000, there were a total of 447 initiatives worldwide, including 41 at the global level (Hildebrand and Sorensen, 2001). This dramatic increase in activity was attributed both to new plans implemented since 1993, and to the improved ability to find relevant information using the Internet (Kay and Alder, 2005). The latest survey estimates that there are a total of 698 coastal management initiatives operating in 145 nations or semi-sovereign states, including 76 at the international level (Sorensen, 2002).

Yet even countries with well-developed coastal zone plans that have been in place for decades struggle with over-exploitation of resources, user conflict, habitat loss, and indirect degradation of ecosystems. These may involve activities occurring sometimes hundreds of kilometers away from the focal area. Management has not kept pace with degradation, as the number of interventions worldwide has only increased two or threefold over the last decade. In the same time period, degradation of many habitats, such as coral reefs and mangroves, has increased significantly more (Kay and Alder, 2005). There has been far too much emphasis on process rather than achieving results, and stakeholder participation is often seen as an end in itself instead of a critical step in a larger, more complex process.

Regional and International Agreements/Treaties

Many environmental issues, such as pollution, climate change, protection of marine and freshwater resources, and biodiversity conservation, are large scale topics that require multi-national governmental actions to address them. This is particularly true in the marine context. When resources are shared by more than one country, or consequences result from geographically removed actions, national action alone cannot suffice (Kimball, 2001). Most marine species cross boundaries of individual countries, and the regulation of these resources is beyond the control and responsibility of individual nations. In addition, the oceans contain vast areas that do not fall under the jurisdiction of any nation. These "high seas" are thus a *global commons* that cannot be addressed in any way other than international cooperation and global agreements (see *The Pelagos Sanctuary for Mediterranean Marine Mammals* case study). Such treaties and other agreements are the most frequent means of addressing the conservation of the 'global commons' and worldwide environmental problems. They foster a worldwide conservation ethic where the world's nations strive to conserve marine biodiversity and the environment by working together on global solutions (see the *International Treaties for Marine Conservation and Management* module).

International treaties provide a legal framework for marine conservation action, resource regulation, and scientific research on a broad scale. Such agreements exist at various scales, depending on the nature of the issue and the practicalities of fostering cooperation among countries. Some are global, involving virtually all nations; others are formulated with only those parties having coastal jurisdictions, while still others are regional and involve only countries bordering a particular ocean basin, semi-enclosed sea, or region. Thus, these treaties can be bilateral (between two countries or 'parties') or multilateral (between multiple countries). However, regardless of scale, these agreements legally mandate international cooperation to address complex environmental issues, aiming to promote sustainable utilization and protection of shared natural resources. They form the rules of conduct or behavior agreed upon by the signatory states to take actions that address a conservation and/or environmental issue. In the twentieth century, it has been suggested that environmental treaties are the best means of making law in our diverse world (see the *International Treaties for Marine Conservation and Management* module). But the question of who enforces international law remains a sticking point, and too often national laws are not harmonized to allow international agreement obligations to be carried out.

Global treaties that include all coastal and some riparian nations are crucial in addressing certain marine conservation issues. However, equally important marine agreements exist on the regional scale. Most important among these are the Regional Seas Agreements overseen by the United Nations Environment Programme (UNEP) and various regional fisheries agreements. Regional fisheries agreements such as the International Convention on the Conservation of Atlantic Tunas (ICCAT) allow countries to cooperate in managing shared fish stocks, as well as allowing fisheries management to become more holistic and thus effective by promoting ecosystem-based management approaches.

Constraints To Effective Marine Conservation

Just as marine ecosystems are complex, so do political, social and economic systems exhibit complex non-linear dynamics with thresholds. Social systems are constantly in flux – perhaps even more so than natural ones. Abrupt changes can occur in political (e.g., elections or revolutions), social (e.g., changes in fashions) or economic systems (e.g., technological changes leading to changes in what is produced or how it is produced). For example, an advance in fishing technology from dugout canoes to trawlers with long-line nets and GPS can cause massive changes in rates of resource exploitation. These jumps in exploitation rates often pass the threshold for sustainability, and may result in crashes in fish stocks and other profound alterations in marine ecosystems. These impacts may also be irreversible, since a return to previous low tech methods is unlikely, and fish stocks may be unable to recover even if fishing pressure is subsequently reduced.

Inertia is a fundamental characteristic of socio-economic and natural systems. There is typically a time lag between a perturbation to the system and the complete eventual effects. For example, a reduction in habitat may not result in immediate loss of species in a region. Population levels, however, will fall over time in response to the reduction in habitat. Eventually the population reaches a level where it is no longer sustainable and the species will suffer local extinction. This may occur many decades after habitat reduction (MA, 2005a).

Socio-economic institutions also illustrate considerable inertia. Culture and tradition may make societies reluctant to change practices, even in the face of altered environmental circumstances. Fixed investments in plants, equipment, and infrastructure make fundamental changes in production or consumption costly. New conditions may take place over time as fixed investments wear out and are replaced with new, better adapted investment. In many regions, population pressures on limited land and water resources, government policies impeding flexibility and adaptation, or limited access to information or financial resources make adaptation difficult or slow.

Anticipating major changes is complicated by lags in responses, complex feedbacks between socio-economic and ecological systems, and the difficulty of predicting thresholds prior to such benchmarks being passed. There are a number of intrinsic characteristics of ecosystems and of science that contribute to this. Ecological lag times often mean that responses to changes in biodiversity do not occur immediately; multiple impacts (especially the addition of climate change to the mix of forcing functions) can cause alterations in thresholds; and monitoring methods are often inadequate due to poor choice of indicators, inappropriate periodicity of monitoring, and infrequent analysis of results (MA, 2005a).

A mismatch exists between the dynamics of natural systems and human responses to those changes. Inertia and lag times in both natural and social arenas complicate the ability of humans to anticipate and develop adaptation strategies to cope with change. The result of our current inadequacies in understanding is increasing numbers of "ecological surprises" brought about by voluntary or accidental species introductions or removals. These illustrate how initially small changes in species richness (i.e. often just the addition of one species) can trigger dramatic effects, often with large losses in ecosystem services. For these reasons, conservation is best achieved by focusing on conserving or restoring the composition of communities, rather than simply maximizing species numbers. Particularly important is the preservation of the complex interactions among species, including links between pelagic and benthic organisms, keystone species, ecosystem engineers, and natural enemies of pests and human-disease vectors.

As conservationists, we must come to terms with the fact that considerable uncertainty exists in our understanding of what is in the oceans, how things interact, and how humans use and impact the ocean environment and biodiversity. This uncertainty is sometimes held up as an excuse for inaction – something that civil societies urge decision makers to resist. But the uncertainty can also be harnessed, in a sense, for conservation, by creating the conditions that allow conservationists to promote the precautionary principle. This principle essentially states that in the face of uncertainty, we should err on the side of conservation until better information is gained.

However, there is much political resistance to invoking the precautionary principle, especially in resource management circles that are time-bound by traditional management (especially fisheries management). Another constraint is that though the need to establish management regimes that are designed to further our ecological and sociological understanding is well accepted, developing such adaptive management methods is difficult, time consuming, and potentially costly.

Therefore, incomplete ecological understanding, and corollary incomplete sociological understanding, can be a major constraint in effective conservation. Other constraints include lack of funding for research to bolster that understanding and also funding to undertake monitoring and enforcement of regulations. Perhaps the biggest constraint of all is lack of political will, based in part in the misconception that the oceans are so large that humans could not possibly impact them, and in part in the sense that open access must be preserved in the oceans since they are indeed a global commons

(Agardy, 1997).

Conclusions

Ecological systems are extraordinarily complex and confusing. The populations that compose the systems often respond to environmental factors that are as yet virtually unknown. Yet they must be studied with the classical scientific techniques of simplification, analysis, and synthesis, and testing theory remains the cornerstone of science (Dayton, 2003). A trap exists, however, since bad assumptions can be quantitative and precise, esthetically pleasing, and appear heuristically useful, and experiments might make the right predictions for the wrong reasons (see Dayton and Sala, 2001).

Social systems are also extraordinarily complex. A promising new development in conservation, however, looks at the resilience of social systems as well as ecosystems (Adger et al., 2005). Developments such as these suggest that marine conservation seems at last able to couple human and natural systems and better understand the interactions between the two.

As in the terrestrial literature, the last century has produced a large marine literature. But the value for application to conservation of much of this literature is truncated by the limited appreciation of the important scales in time and space. While the focus on small scales is understandable for many practical reasons, arguably the most important lesson of the last several decades is the importance to local communities of oceanographic processes operating on much larger scales in time and space. With few exceptions, there are no time-series observations that allow a holistic definition of what is natural for the ocean ecosystem (Dayton, 2003).

Some systems are now almost as well understood as terrestrial systems that have been studied for centuries. Focusing on these systems allows us to make predictions about future condition of ecosystems and trends in populations of organisms, which are in turn needed to develop effective management regimes and bring about necessary policy changes. But making generalizations from a few well-known systems like tropical coral reefs is risky, given the structural and functional diversity that is exhibited by different portions of the oceans and coastal areas. Given that we cannot wait for perfect ecological understanding, however, marine conservationists would be best served by promoting adaptive management wherever possible, so we might learn as we go along. Adaptive management frameworks not only position us for more effective management, but also increase the speed with which critical new knowledge is gained.

Finally, integrated and holistic approaches that tackle the myriad, cumulative threats to marine systems are needed. In order to match the scale of these large, highly interconnected and in many cases open systems, international cooperation may be needed to achieve real conservation.

Terms of Use

"Agardy, T. 2007. Introduction to Marine Conservation Biology. Synthesis. American Museum of Natural History, Lessons in Conservation. Available at http://ncep.amnh.org/linc."

This material is based on work supported by the National

Oceanic and Atmospheric Administration Undersea Research Program (Grant No. CMRC-03-NRDH-01-04A)

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Glossary

Allee effect: the relationship between high numbers of reproducing adults and the successful subsequent recruitment of young.

Anadromous: fish that hatch their rear in freshwater, migrate to the ocean to grow and mature, and migrate back to fresh water to spawn.

Anoxic: without oxygen.

Ballast water: water taken up or released by a ship to stabilize it, or to raise/lower it in the water column.

Bathymetry: the measures of the depth of the ocean floor from the water surface; the oceanic equivalent of topography.

Benthos: the bed or bottom of a body of water, including the layers of much silt, or sand.

Biofouling: the formation of bacterial film (biofilm) on fragile reverse osmosis membrane surfaces.

Biome: an entire community of living organisms in a single major ecological area.

Biota: the animals, plants, and microbes that live in a particular location or region.

Cnidarian: a coelenterate. Radially symmetrical animals having saclike bodies with only one opening and tentacles with stinging structures. They occur in polyp or medusa forms.

Coalesced: grown together, fused or joined together into a whole.

Coastal zone: lands and waters adjacent to the coast that exert an influence on the uses of the sea and its ecology, or whose uses and ecology are affected by the sea.

Continental shelf: a submerged border of a continent that slopes gradually and extends to a point of steeper descent to the ocean bottom.

Copepods: a common herbivorous zooplankton. Small crustaceans found in either salt or fresh water.

Coriolis force: a force exerted on a parcel of air (or any moving body) due to the rotation of the earth. This force causes a deflection of the body to the right in the Northern hemisphere and to the left in the Southern hemisphere.

Crustacean: aquatic arthropods that are characterized by a segmented body, chitinous exoskeleton, a pair of often modified appendages on each segment, and two pairs of antennae. They include lobsters, shrimps, crabs, wood lice, water fleas, and barnacles.

Ctenophore: any of a phylum (Ctenophora) of marine animals superficially resembling jellyfishes but having biradial symmetry and swimming by means of eight meridional bands of transverse ciliated plates; also called comb jellies.

Dredge: equipment for collecting and bringing up objects from the seabed by dragging.

Echinoderm: a large group of animals characterized by five-fold symmetry and a skeleton of calcite plates. Examples include starfish, urchins, and sea lilies.

Ecological footprint: a calculation that estimates the area of Earth's productive land and water required to supply the resources that an individual or group demands, as well as to absorb the wastes that the individual or group produces.

Ecosystem engineer: any organism that creates or modifies habitats.

Estuary: the wide part of a river where it nears the sea, and fresh and salt water mix.

Eutrophication: over-enrichment of a water body with nutrients, resulting in excessive growth of organisms and the depletion of the oxygen concentration.

Extirpation: the elimination of a species or subspecies from a particular area, but not from its entire range.

Fecund: species that have a high reproductive output based on when and how often they reproduce.

Fiord: an estuary that occurs in a deep, narrow, drowned valley, originally formed by glaciers.

Flocculent layer: having a fluffy character or appearance.

Foraminifera: a class of animals of very low organization and generally of small size, having a jelly-like body, a surface from which delicate filaments can be given off and retracted for the prehension of external objects, and having a calcareous or sandy shell, usually divided into chamber and perforated with small apertures.

Global commons: natural assets outside national jurisdiction such as the ocean, outer space, and the Antarctic.

Gyres: currents moving in large circles in the Northern and Southern hemispheres.

Intertidal: the zone between high and low tide.

Keystone species: a species that plays a large or critical role in supporting the integrity of its ecological community, and whose removal leads to a series of extinctions within the ecosystem.

Lagoon: a body of comparatively shallow salt water separated from the deeper sea by a shallow or exposed sandbank, coral reef, or similar feature.

Longshore current: current located in the surf zone and running parallel to the shore as a result of waves breaking at angle on the shore.

Mangrove forest: an expanse of mangrove trees. Trees that live along the shore in tropical waters with their roots in the salt water.

Marine protected area: an area of sea especially dedicated to the protection and maintenance of biological diversity and of natural and associated cultural resources, and managed through legal or other effective means.

Marine snow: aggregates of detritus, visible to the naked eye, that consists of dead organisms, discarded feeding structures, fecal pellets, and other organic debris.

Marsh: a low-lying wetland with grassy vegetation, usually a transition zone between land and water.

Maximum sustainable yield: the largest average catch that can be taken continuously (sustained) from a stock under existing environmental conditions.

Meso-scale: the scale of meteorological phenomena that ranges in size from a few kilometers to 200 kilometers in horizontal extent, includes local winds, thunderstorms, and tornadoes.

Mollusk: an invertebrate animal with soft, unsegmented bodies, such as clams and snails, usually enclosed in a calcium shell.

Pelagic: fish and animals that live in the open sea, away from the sea bottom.

Photic zone: the layer of the ocean that is penetrated by sunlight, extending to a depth of about 200 meters.

Phyletic diversity: of or relating to the diversity of the evolutionary development of organisms.

Phytoplankton: Microscopic floating plants, mainly algae that live suspended in bodies of water and that drift about because they cannot move by themselves or because they are too small or too weak to swim effectively against a current.

Propagule: any part of a plant that can give rise to a new individual and aids in the dispersal of the species.

Protist: a heterogeneous group of living things, comprising those eukaryotes that are neither animals, plants, or fungi, or unicellular, or colonial organisms. Includes most protozoa and most algae.

Refugia: an area, untreated with pesticides, provided to preserve susceptible populations of pests.

Regime shift: a rapid modification of ecosystem organization and dynamices with prolonged consequences.

Riparian: relating to or living or located on the bank of a natural watercourse (as a river) or sometimes of a lake or tidewater.

Seiches: the oscillation of a body of water at its natural period. Coastal measurements of sea level often show seiches with amplitudes of a few centimeters and periods of a few minutes due to oscillations of the local harbor, estuary, or bay, superimposed on the normal tidal changes.

Spawn: the act of reproduction of fishes.

Sponge: a poriferan. Primitive, sessile, mostly marine, water dwelling filter feeders that pump water through their matrix to filter out particulates of food matter.

Stratification: the division into distinct layers (or strata).

Thermocline: a vertical negative teperature gradient in some layer of a body of water that is appreciably greater than the gradients above and below this level.

Thermohaline: the circulation path determined by temperature and salt, downwellings due to surface-water density created by low temperature and high salinity.

Trawl: a string of traps or nets connected by a line with two buoys marking each end that are dragged along the bottom to catch fish or towed at various depths above the bottom for the same purpose.

Upwelling: vertical currents that deliver cold, nutrient-rich bottom waters to the surface.

Zooplankton: small, usually microscopic animals (such as protozoans) that drift with the currents. May be either herbivores or carnivores.