BIODIVERSITY OF COASTAL-REALM WATERS

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Contents

Summary

This article is concerned with the structural-functional components of the coastal realm, unique land-air-sea interactions, and the natural history of its species. The coastal realm is composed of the earth's most diverse assortment of life, interacting with and regulated by a complex and functionally varied environment. Physically defined components, such as the coastal ocean, the benthos, and various coastal configurations, create a framework for addressing biodiversity. The coastal realm behaves as a morphodynamic feedback system, with loops among topography, fluid dynamics, and the biota, and tends to evolve from less stable to more stable states. The biota play significant roles in both structure and function, signifying that understanding biodiversity requires knowledge about the natural history of organisms. In this respect, biotic function is best conceived as a suite of constraints and trade-offs among many species and a variety of environments. Various theoretical concepts aid in this understanding: for example, concerning K- and *r*-selection, reproduction, dispersal, metapopulations, symbiosis, and biogenesis. It is also important to understand how species assemblages are biogeographically distributed. The conclusion is that the coastal realm is best viewed as a complex adaptive system on a global scale.

1. Introduction

Knowledge of planet Earth's biological diversity may be distorted by the fact that more land species than sea species have been described. However, the living volume of the oceans exceeds the thin veneer of life on land one hundred times. It hardly seems reasonable that the 1–2 million described species—most of them terrestrial, and mostly insects—paint a true picture of life on Earth.

Marine systems host all animal phyla described to date (Figure 1) and the coastal realm appears to have the greatest species diversity. Fishes are exemplary. They constitute about half of all vertebrates, with ~22 000 described species. About 12 900 species (~59%) are marine. The rest (~41%) live in freshwater. Most marine species, ~10 200 in all (~46% of all species, or >79% of marine species), are constrained within coastal waters, from the upper reaches of estuaries to the edge of the continental shelf. Only ~2700 (~12% of all species; 21% of marine species) are oceanic. One reason may be coastal productivity, which encourages diversity and has led to reentry into the sea of air-breathing sea turtles, sea snakes, and marine birds and mammals. Oddly, few insects have been able to adapt to marine environments.

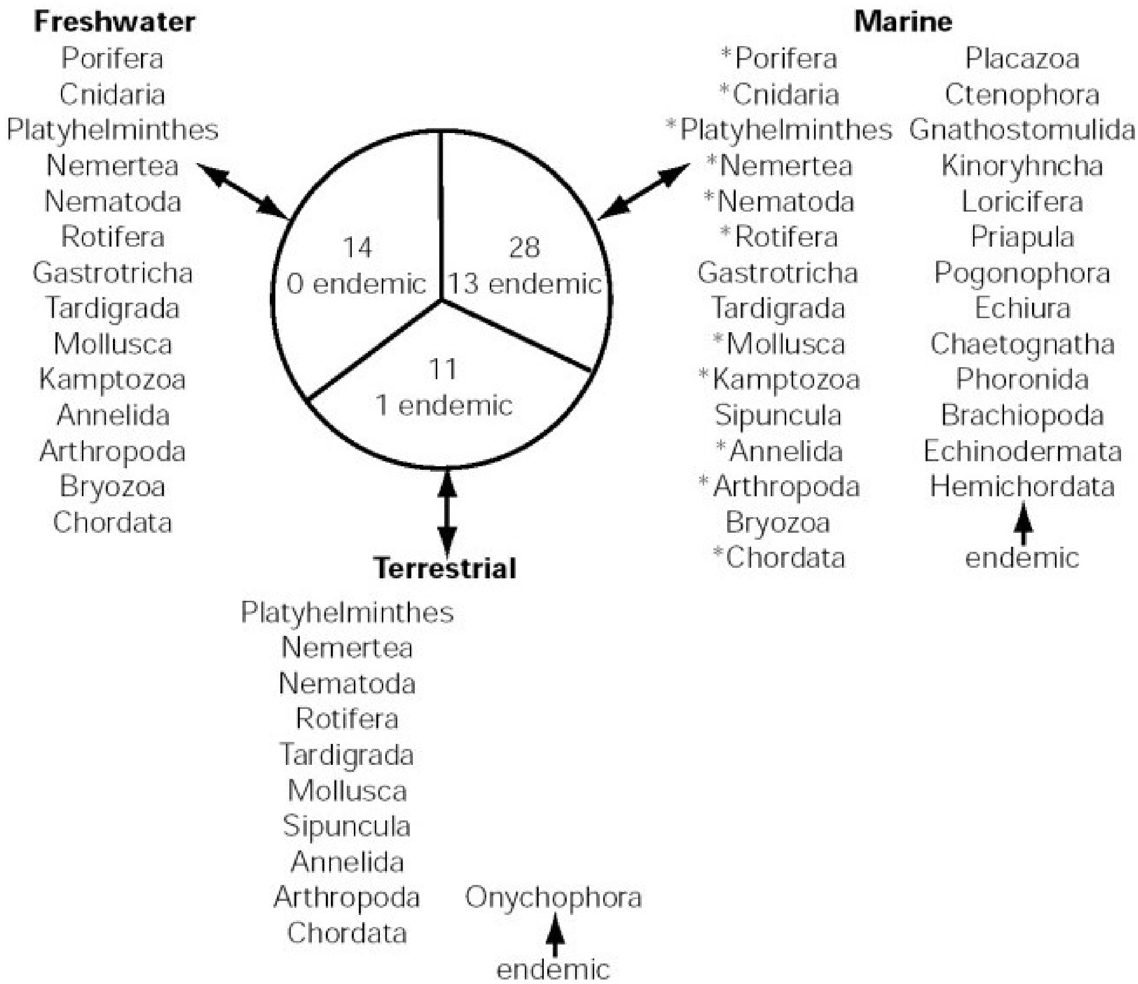

Figure 1. Phyletic diversity is richest in marine environments and poorest terrestrially. Eleven of the phyla shown have symbiotic species (*); an additional four phyla are exclusively symbiotic (Orthonectida, Dicyemida, Nematomorpha, and Acanthocephala). Some phyla have different names and different classifications exist, but the overall results are consistent with this listing. Adapted from R.M. May, How many species are there on Earth? *Science* 241 (1988), 1441–1449.

This article considers the structural-functional components of this realm and the natural history of its species. The coastal realm is best conceived as an ecosystem, composed of a diverse assortment of life interacting with and regulated by the structure and function of the biophysical system. Its behavior and the tempo and mode of its life emerge from land-air-sea interactions, as well as from processes of self-regulation, feedback, sensitivities to thresholds, regime changes, and changes in boundary conditions. In order to comprehend the distribution of life of the coastal realm, its boundaries, origination, and components must first be described.

2. The Coastal Realm

The marine portion of the coastal realm may be visualized as an irregular ribbon from 500 000 to 1 000 000 km long bordering the continents and island systems. It is a broad region that stretches from watersheds to coastal seas, and varies in width from hundreds of meters to more than 1000 km. It is where land, sea, and atmosphere interact with great intensity to create a unique realm. It encompasses islands and institutional jurisdictions and is generally defined by the following dynamic boundaries.

The *terrestrial boundary* is defined by (a) the inland extent of astronomical tidal and/or watershed influences, or (b) the inland limit of penetration of marine aerosols within the atmospheric boundary layer, including both salts and suspended liquids, whichever is greater. The *marine boundary* is defined by (a) the outer extent of the continental shelf (approximately 200 m depth), or (b) the extent of territorial waters or fishery zones, whichever is greater.

Both boundaries reflect patterns of zonation, and can be difficult to establish precisely. Terrestrially, aerosol and watershed influences are variable. The marine portion—the focus of this article—is easily delimited where continental shelves are wide and coastal waters are distinct from those of the open ocean. Where continental shelves are narrow, oceanic currents and upwelling systems are close to shore and may also be included as "coastal," although they are mostly dominated by open-ocean processes.

2.1. Coastal Realm Formation

Two long-term, global, processes are responsible for the physical conformation of the coastal realm. First, tectonics have moved the continents about, and tectonic processes have been major factors in development of continents and ocean basins. Three dominant coastal types exist, each with distinct characteristics for life. Narrow collision coasts occur on the leading edges of plates, and are often dominated by open-ocean processes, such as upwelling. Trailing-edge coasts occur on spreading plates and possess wide continental shelves and distinct coastal oceans, often in conjunction with extensive estuaries and lagoons. Marginal sea coasts lie behind continental-island arcs and are most complex, protected, and diverse, with curved coastlines that are frequently modified by large rivers and deltas. Other coastal formations do not fit neatly into these types. The Hawaiian Islands were formed by erupting hot-spots in Earth's mantle. Mantle material may also rise to form islands, as in the Mid-Atlantic Ridge. Large carbonate platforms, such as the Bahamas, are continuously created by combinations of physical and biological processes. The tropical Indo-Pacific has been formed by combinations of these processes, and is a present-day center for coastal-marine species diversity.

Global sea-level change is the second major process. Sea level has fluctuated widely in response to climate. During the past ~10 000-year interglacial period, sea level has encroached upon the land to drown ancient landforms. This has been modified by isostasy, which involves changes in land elevation through uplift and subsidence, and eustasy, which describes changes in sea level caused by alterations in the amount of water in the world's oceans. Both processes displace sea level relative to coasts. Additionally, sea-level change has influenced erosion and the movements of sediment, which have built coastal land- and sea-forms. From this viewpoint, the landward limit of the coastal realm may be set at ~50–100 m elevation, which represents the maximum level the sea has encroached on the coastal plain during interglacial periods. The outer continental shelf at depths of ~100–200 m marks sea level during the maximal reach of glaciers and ice sheets.

2.2. Large-Scale Physical Components

Physical processes establish integrated regional-scale structures that create a framework for addressing biodiversity. These include the coastal ocean, its underlying benthos, and terrestrial aquatic interfaces.

2.2.1. Coastal Ocean

The coastal ocean is where most commercial fishes aggregate and where the greatest variety and abundance of marine life exists. Its waters inundate the continental shelves, penetrate indented shores, and interact with terrestrial processes to yield a unique signature, different from the open ocean. The coastal ocean is a receptacle for salts and chemicals from the open ocean, detritus, sediment, and nutrients from freshwater, and a flush of precipitation from the atmosphere. It is also a source of dissolved and particulate matter to the open ocean. Regional differences in salinity, temperature, density, circulation patterns, fronts, and conditions of high turbulence or relative tranquility introduce considerable complexity, which generates a wide range of interactions and life forms.

The energetics of the coastal ocean are made vivid by the breaking of waves on shorelines, turbulent tides, and strong currents. The water column is usually separated into layers by density differences with varying capacities to mix, but due to the proximity of the surface and the bottom, vertical mixing and internal waves influence material exchanges throughout the water column and between the euphotic surface layer and the benthos. Additionally, inputs from watersheds introduce materials that are sorted, accumulated, physically altered, or dispersed by complex physical interactions. This complexity is amplified by interactions of currents with topographic features, circulation cells, plumes, and fronts. Thus, a wide range of interactions and phenomena create unique conditions for a diversity of life, including plankton and demersal and pelagic invertebrates, fishes, seabirds, and marine mammals.

2.2.2. Shelf Benthos

The sea's bottom can not be separated ecologically from the water above. Here, sediment and organic matter are deposited in great quantities, plants add detritus, planktonic diatoms and foraminiferans add tiny shells, and animals add feces and skeletons. These materials are subject to resuspension by currents, waves, and biological action. Of particular importance is a water mass known as the benthic boundary layer, which may extend ~20 m above the bottom, but which can influence the entire water column under turbulent conditions. Light penetration to the benthos is also critical, and can be limiting to life under turbid conditions.

Many forms of biological activity play prominent roles. Rooted plants recycle nutrients. Denitrification converts organic nitrogen into nitrogen gas. Biogenic structures, such as reefs, influence currents and contribute organic and inorganic matter. Burrowing by infauna allows oxygen to be distributed more deeply. Bioturbation by many invertebrates and some marine mammals has an important effect on benthic aeration, nutrient cycling, and the resuspension of particles. Many demersal fishes utilize both the water column and benthic environments at different stages of their life cycles.

2.2.3. Watersheds

These are the major sources of materials that connect the land to the productivity, structure, and evolution of the coastal ocean. Globally, watersheds contribute between about 7 billion and 13.5 billion tons of suspended sediment to the ocean yearly. Flood discharges may add an additional 1 billion to 2 billion tons. These discharges vary seasonally, annually, and by latitude. Rivers have the greatest, year-long impact on the ecology of the global ocean in wet, tropical regions where slightly more than half of the world's river water enters the oceans annually.

Freshwater discharge introduces dissolved and particulate materials and drastically modifies the structure and dynamics of the physical environment. River waters move through marshlands, seagrasses, and mud flats, all of which provide habitat for diverse arrays of organisms, and remove sediment, nutrients, pollutants, and materials. Wetland species play important roles in resisting erosion. Assemblages of organisms, such as snails, crabs, and bivalves, serve as "rip-rap" on channel banks and moderate erosion as they filter water and deposit materials otherwise carried to the ocean in turbidity flows. Depending on conditions of river flow and tides, rivers can penetrate offshore as plumes carrying terrestrial material. The ocean also influences watersheds by tidal action, salt intrusion, and anadromous species that carry nutrients upstream.

2.3. Protruding Coasts: Deltas and Headlands

2.3.1. Deltas

Deltas are created by watersheds, which deliver sediment faster than marine processes can carry it away. If watershed flow changes, the delta changes and so does the adjacent coastal ocean. Deltas usually contain extensive wetland habitat for many forms of life, including juvenile fish and shellfish of commercial importance. Deltas are also highly valued for port and urban development.

The best studied is the Mississippi River delta. Its watershed drains >3 million km^2 of the United States, delivering vast quantities of sediment, nutrients, and pollutants from farmland, urban centers, and industrial developments. This delta sustains an extensive marshland that is critical to migratory waterfowl, commercial fisheries, and recreational species. Recently, an extensive anoxic zone has occurred in summer offshore of this delta, when water is warm and oxygen demand is high. The result is a large region almost devoid of bottom-dwelling fishes and crustaceans.

2.3.2. Headlands

These are rocky and/or sandy protrusions of the land into the sea. They support a rich array of species adapted to the rugged conditions of a wave-swept environment.

Headlands vary in scale from small projections to large peninsulas and may result from erosion, isostasy, tectonics, or glacial processes. A drumlin is a headland composed of large mounds of poorly sorted gravel and boulders deposited on paraglacial coasts.

All headlands have important influences on tides, water patterns, sediment dispersal and deposition, and shoreline evolution. They tend to focus wave energy, and gyres and turbulent water are often created downstream by coastal currents. Behind headlands, sediment can be trapped by residual tidal flow and deposited in shoals, which can expand downstream of rapidly eroding coasts. These shoals affect tidal flow patterns and create quiet water for turbulence-sensitive organisms. These processes are three-dimensional, chaotic, non-linear, and can be of fundamental importance to the biota, especially for larval retention and dispersal and for transport of food and other materials.

2.4. Embayed Coasts

These semi-enclosed water bodies are conduits for exchanges of energy and materials between land and sea. They are protected from open-ocean forces, and provide a "climate" of relatively calm water that is nutrient rich, relatively shallow, and productive. They are greatly valued for commerce, recreation, and urban development, but are sensitive to erosion, pollution, and sedimentation.

2.4.1. Estuaries

Estuaries are semi-enclosed bodies of water that have a free connection to the open sea and in which seawater is measurably diluted with freshwater. They are among the most productive natural ecosystems and are subject to reworking by floods, storms, erosion, and sediment deposition. They support rich and diverse fisheries, wildlife populations, and are often bordered by marshes and wetlands. Many of the world's largest cities and ports have been built on drained marshes or filled land adjacent to estuaries.

Modern estuaries are the result of the latest major episodes of sea-level fall and rise, and are ephemeral, estimated to be only about 1% of the age of the shelf. There are four general types. Coastal-plain estuaries occur where seawater has invaded existing rivers due to sea-level rise. Fjords are U-shaped basins with a shallow sill near the mouth and steep, glaciated sides. Bar-built estuaries occur in flat, low-lying areas, behind sand bars lying parallel to the coast. Tectonic estuaries are a miscellaneous collection formed from faults or folding of the earth's crust. Combinations of these features result in highly varied distributions of sediment, phytoplankton, submerged aquatic vegetation, and biota.

2.4.2. Lagoons, Bays, Gulfs, and Sounds

These vary considerably in scale. The Bay of Bengal and Bay of Biscay are similar in scale to the Sea of Cortez and Gulf of Guinea. Large sounds often are estuary-like as, for example, Long Island Sound, New York. Lagoons are usually smaller structures.

Lagoons vary in type, but are almost universally rich. They are mostly oriented parallel to the coast, protected from the ocean by barrier reefs and shoals, and are no more than a few meters deep. Some have tidal inflow equal to outflow. Others have seawater inflow that exceeds outflow due to evaporation, and still others have outflow exceeding inflow due to freshwater input. These exchange regimes result in very different salinities, from those of a freshwater lake to a hypersaline pond, which determines the type of biological communities that may exist. Lagoons are most common where tides are relatively small, such as in the tropics and high latitudes. Hypersaline lagoons occur along semi-arid to arid coastal regions.

2.5. Wave-Dominated Open Coasts

The coastal ocean can act on open coasts rhythmically and gently, as with the breaking of low waves on a sandy beach, or violently, when stormy seas scour away loose sand and tear organisms from rocks. A wave ~12 m high can reach velocities as high as ~16 m/s, and accelerations as high as 1000 m/s^2, or ~100 times the acceleration of gravity. Between the wave-dominated shore and a frontal boundary at the ~10–20 m depth contour, great turbulence may cause sediment suspension and mixing to extend to the bottom. The effect of waves diminishes in deeper waters where the bottom is less directly influenced by wind and wave stress.

Waves are modified by coastal morphology. As shallow water is encountered, waves are refracted at an angle, bending until their crests are parallel to shore. If waves encounter an object, such as an island or headland, wave crests will be diffracted to wrap around the object. Waves may also be reflected from relatively linear shorelines or obstacles, and if the reflected waves travel in exactly the opposite direction than the original, standing waves can develop. All of these characteristics have important consequences for life, mainly on larval dispersal and by altering habitat.

2.6. Islands

Islands and their surrounding waters are unique yet vulnerable habitats. They are isolated, thereby allowing evolutionary processes to create diverse forms. Continental islands are parts of continents, such as the Canadian Archipelago. Marginal islands circumscribe regional seas and have been formed by tectonic movements. Bermuda and the Hawaiian chain are oceanic. Other island systems have been formed by complex processes; Indonesia and the Philippines are large island systems where tectonics, vulcanism, sedimentation, coral-reef formation, and other processes have combined.

The biota of island types can be markedly different. Continental fishes are influenced by continental processes, such as sediment and turbidity from watersheds. This is very unlike atolls and carbonate karst formations, such as the Bahamas in the western Atlantic, which have been formed from chemical-physical processes and from reef development, and are devoid of true rivers.

2.7. Ice-Influenced Seas and Coasts

Glaciers consist of compacted snow and frozen fresh water. They have affected many portions of the coastal realm and have left a legacy of fjords, moraines, drumlins, and ice-scoured coasts. Sea ice, conversely, is frozen seawater and can be habitat for many forms of marine life. Marginal sea ice, at the edge of the ice pack, is seasonally variable; in the Arctic, it increases annually from summer to winter about 35%, while that of the Antarctic changes 85%. Several species of marine mammals rest and breed on sea ice. On its undersurface, diatoms accumulate and fish and crustaceans find refuge. But although sea ice hosts much biota, it can be inimical to shore life. It scours shorelines, prohibiting growth of algae or attachment of sessile organisms. Nevertheless, abutment of sea ice on shores can be of advantage to polar bears, which hunt on sea ice for seals.

2.8. Land- and Seascapes

These describe the smaller scale habitat anatomy of the coastal realm. Near the land-sea interface, coastal wetlands are frequent. Their net production is very high. Three essential ingredients are water, hydric substrate, and biota, although surface water may not always be present. Temperate marshes are a form of wetland that is dominated by grasses and sedges. These wetlands improve water quality and provide nutrients to adjacent waters and habitat for a wide diversity of organisms. Coastal swamps are defined by trees and shrubs and largely occur in warm temperate areas and the tropics; mangroves are typical and are composed of a few species of several families that share saltwater tolerance.

Rocky shores are mostly high-energy environments. They support a high diversity of sessile species and the greatest variety of macroalgae of any environments. Tide pools that are flooded by tides host a variety of life. Unconsolidated substrates, such as beaches, are usually crescentic in shape and support relatively few, but distinctive, species. Sand and mud flats, on the other hand, are generally low-energy habitats. They support a wide variety of epifauna and infauna, such as crabs, snails, shrimps, burrowing worms, mollusks, and fishes. Algal mats are also common in quiet waters.

On the submerged side, the surf zone lies just offshore and is an important habitat for the young of many coastal fishes, especially where "wrack" (dead marine vegetation) accumulates. Offshore in deeper waters, a host of habitats exist, from benthic sedimentary plains to coral and oyster reefs, most of which are species rich. Even the continental slope fauna, in water >200 m depth, can be extraordinarily species-diverse.

3. Coastal Realm Life

Life originated in coastal seas perhaps a billion or more years ago and has evolved into an astounding array of forms. However, factors responsible for diversity and abundance in the coastal realm are not clearly understood, in part because many coastal environments have been greatly altered by human activities.

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Biographical Sketches

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