

Final Report for “Ecological Functions of Hudson River Shorelines” (HRF 009/07A)

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Chapter 1: Ecology of freshwater shore zones

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Abstract

Freshwater shore zones are among the most ecologically valuable parts of the planet, but have been heavily damaged by human activities. Because the management and rehabilitation of freshwater shore zones could be improved by better use of ecological knowledge, we summarize here what is known about their ecological functioning. Shore zones are complexes of habitats that support high biodiversity, which is enhanced by high physical complexity and connectivity. Shore zones dissipate large amounts of physical energy, can receive and process extraordinarily high inputs of autochthonous and allochthonous organic matter, and are sites of intensive nutrient cycling. Interactions between organic matter inputs (including wood), physical energy, and the biota are especially important. In general, the ecological character of shore zone ecosystems is set by inputs of physical energy, geologic (or anthropogenic) structure, the hydrologic regime, nutrient inputs, the biota, and climate. Humans have affected freshwater shore zones by laterally compressing and stabilizing the shore zone, changing hydrologic regimes, shortening and simplifying shorelines, hardening shorelines, tidying shore zones, increasing inputs of physical energy that impinge on shore zones, pollution, recreational activities, resource extraction, introducing alien species, changing climate, and intensive development in the shore zone. Systems to guide management and restoration by quantifying ecological services provided by shore zones and balancing multiple (and sometimes conflicting) values are relatively recent and imperfect. We close by identifying leading challenges for shore zone ecology and management.

Introduction

Shore zones are among the most productive and most threatened habitats on our planet. Natural shore zones are the sole homes of many distinctive plants and animals, and as transition zones between aquatic and terrestrial ecosystems, can contain highly diverse biological communities as well as hot spots of biogeochemical activity. Intact shore zones also regulate exchanges between aquatic and terrestrial ecosystems, contributing to the normal functioning of both. Shore zones can be one of the most valuable parts of the world in terms of the ecological services that they provide – habitat for many species, recreation, harvestable resources, production and processing of organic matter, dissipation of wave energy, flood protection, maintenance of water quality, and dispersal corridors for plants and animals.

Humans have used shore zones intensively for thousands of years, which has greatly reduced their ability to provide these ecological services. Many of the world's great civilizations arose in the shore zone, most of the world's great cities still depend on the shore zones in which they are located, and more than half of the world's population lives in or near the shore zone (Airoldi and Beck, 2007). Humans use shore zones for land- and water-based transportation; as a source of water for domestic, industrial, and agricultural use; for waste disposal; as a place to harvest plants, animals, and geologic resources; for recreation and aesthetic and spiritual inspiration; and as desirable sites for building homes and factories. Human pressure on shore zones will increase in the future as the human population grows, as an increasing fraction of that population moves into the shore zone and adjacent areas (Airoldi and Beck, 2007), as new building is increasingly focused in the shore zone (Glasby and Connell, 1999), as economic growth places more demands on shore zones, as increasingly affluent populations demand more water-based recreation, and as engineers work to protect property from rising sea level on

oceanic shores (Nicholls et al., 1999; IPCC, 2007) and changing water levels on inland waters resulting from climate change.

Thus, ecologists, engineers, managers, and planners will be challenged to maximize ecological functioning while maintaining human uses of shore zones. At present, ecological functioning of shore zones often is neglected in favor of engineering or economic concerns (Ostendorp, 2008). We need better designs for engineered structures in the shore zone, better laws to protect the shore zone, better systems of protected conservation areas, and better ways to rehabilitate ecologically degraded shore-zone ecosystems. All of these solutions will require us to understand the functioning of shore-zone ecosystems, both natural and engineered. The purpose of this review is to summarize what is known about the ecological functioning of shore-zone ecosystems in fresh water.

The shore zone

The **shoreline** is the infinitesimally thin line that separates the water from the land. It is well known that the precise location, length, and shape of the shoreline depends on the scale of the observation (Mandelbrot, 1967), but despite these nuances, the definition of the shoreline is clear enough.

It is impossible to offer such a clear, unambiguous definition of the **shore zone**. In broad terms, the shore zone is the region in which interactions with the land have a strong influence on ecological processes and structures in the water, and *vice versa*. The ideal definition of the shore zone depends however on the subject of the study. A geologist studying sand transport might define the shore zone as extending from the landward limit of active sand dunes to the greatest depth at which waves suspend submarine sands. However, a fish ecologist interested in the use of woody debris by lake-dwelling fishes might define the shore zone as extending a distance of

the height of the tallest tree in either direction from the shoreline (i.e., the terrestrial zone which supplies wood to the lake plus the aquatic zone that receives that wood). There is no reason to suspect that different definitions of the shore zone adopted by investigators working on different subjects will be even approximately congruent (cf. Ostendorp, 2004). Indeed, previous authors have used several definitions and subdivisions of the shore zone (Fig. 1). We doubt that it will be possible (or even desirable) to reconcile these various systems to reach a single, unambiguous definition of the shore zone that will be useful across all subjects and study sites.

Instead, we propose a broad definition: *the shore zone is the region closely adjoining the shoreline in which strong and direct interactions tightly link the terrestrial ecosystem to the aquatic ecosystem, and vice versa*. We think it is useful to exclude some kinds of strong aquatic-terrestrial interactions from this definition. For instance, it seems unnatural to define the inland forests of the Pacific Northwest as being in the shore zone of the Pacific Ocean, despite the fact that marine-derived nutrients carried by salmon have an important influence on these forests (e.g., Naiman et al., 2002). We do not deny the importance of such long-distance interactions, but they are so spatially incongruent with the other interactions between the Pacific Ocean and the land (e.g., wave wash, wrack deposition, salt spray) and so far removed from the use of “the shore” in common language that it would seem to overstretch the idea of the shore zone to include them.

Because of the enormous diversity of shore zones, and because many kinds of shore zones have been reviewed well by others, we focus here on the ecology of freshwater shore zones in which wave energy is an important factor. This includes lakes and rivers large enough to have substantial waves driven by the wind or from recreational boating or commercial shipping; very roughly, lakes larger than ~10 ha and rivers more than 100 m wide.

We exclude marine shore zones, because they have been very well treated by others (e.g., Denny, 1988; Paine, 1994; Bertness, 1999; Brown and McLachlan, 2002; Thompson et al., 2002; McLachlan and Brown, 2006; Airolidi and Beck, 2007; National Research Council, 2007), and because they are quite different from their freshwater counterparts. Marine shore zones often are subject to tides and high wave energy, and support a distinctive biota. We also exclude freshwater shore zones that are subject to low wave energy. Shore zones of smaller bodies of water are extensive and ecologically important, but have a different character from wave-swept shore zones. These include the riparian zones of small streams and rivers, as well as many wetlands, which were recently addressed by Naiman et al. (2005) and Mitsch and Gosselink (2007). Although we do not address marine shore zones or freshwater shore zones with low wave energy in detail, we bring in data and ideas from these habitats where they are relevant.

Special characteristics of the shore zone

Before describing the ecological functions performed by the shore zone, it is worth emphasizing some of the unusual characteristics of the shore zone: it is a phase boundary between land, air, and water; it is a zone of energy dissipation; it is a characteristically heterogeneous environment; and it often is a large, spatially continuous habitat and therefore a dispersal corridor for plants and animals.

The shore is a phase boundary between land, water, and air

The shore zone is defined as a boundary region between land and water (and of course, air). The juxtaposition of these three realms has several important ecological consequences. Two of them, energy dissipation at the shoreline and habitat heterogeneity, are important enough to be discussed individually below. In addition, shore zones are sites where buoyant materials (driftwood, wrack, plastic trash, ice, and hydrophobic liquids such as oil) accumulate. Floatable

materials can be washed into the shore zone more or less permanently, or they can be very transient, washing up in one storm and leaving a few days later in the next. The expansion and contraction of the sheet of ice covering a lake or river can bulldoze shoreline materials into a ridge along the shore and destroy vegetation (Begin and Payette 1991). Alternatively, when the ice sheet breaks up, winds, currents, and flood waters can push large mounds of ice onto the shoreline, moving materials and destroying plants and animals. Shallow-water sediments may freeze into an ice sheet and be rafted away when the ice breaks up in the spring (Reimnitz et al., 1991; Dionne, 1993). Thus, ice can be an important geomorphic agent along shore lines in cold regions (Forbes and Taylor, 1994).

The shore is a zone of energy dissipation

Waves break on the shore, dissipating a large amount of energy in a focused area. This energy dissipation has several important ecological consequences – it suspends shallow-water sediments (making them available for transport by currents and decreasing water clarity in the shore zone), erodes the shore, increases turbulence, drives water movement through nearshore sediments, and produces strong and highly variable forces on the organisms that live in the surf zone (Denny, 1988). All of these processes affect biodiversity and biogeochemical processes in the shore zone. Especially if water levels fluctuate, wave energy is part of the dynamic by which sediments and organic matter are suspended, transported, deposited, and temporarily stored in the shore zone.

The importance of energy dissipation varies enormously across time and space in freshwater shore zones. Wave energy is negligible in small or sheltered fresh waters, but can reach values as high as hundreds of kilowatts per meter of shoreline during storms on large lakes (Fig. 2). Wave energy tends to be very variable over time in freshwater shore zones, falling to

zero for part of the time in all freshwater shorelines, in contrast to marine shores that are subject to regular, incessant swells. Some shorelines (e.g., gently sloping beaches) dissipate nearly all incident wave energy, whereas others (e.g., vertical seawalls) reflect nearly all incident wave energy.

The shore zone is a heterogeneous environment

Shore zones are always regions of high environmental contrast and heterogeneity (e.g., Pieczyńska, 1972; Amoros and Bornette, 2002; Robinson et al., 2002; Ostendorp et al., 2004; Arscott et al., 2005). This stems partly from the simple juxtaposition of a terrestrial ecosystem with an aquatic ecosystem, and partly from large variations in inputs of physical energy. By definition, shore zones contain both aquatic and terrestrial parts, and these adjacent parts have highly contrasting biotas and environmental conditions (e.g., temperature, redox potential, physical forces, disturbance regimes). In particular, shore zones frequently contain closely juxtaposed aerobic and anaerobic zones. As in other ecosystems, the biota and underlying geology contribute to additional environmental heterogeneity. Most importantly, the high physical energy (waves, currents) in the shore zone interacts with these geological and biological structures to produce an environment that is highly heterogeneous on all spatial scales, from scour and deposition around a rush stem to islands formed in the lee of woody debris. The heterogeneity of the shore zone includes many environmental variables, including substratum granulometry, water and soil chemistry, temperature, light, disturbance rates, predation rates, amount and quality of organic matter, rates of water movement, and many others. Although the most obvious direction of heterogeneity is across the shore zone, heterogeneity along the shore zone may be large and ecologically important, particularly if there is a directional flow of water or if the underlying geology is variable.

Shore zones usually are also regions of high temporal variability, as a result of temporal variation in water level, wave energy, biological activity, and climatic conditions. Again, this temporal heterogeneity occurs across all time-scales, from ephemeral changes in physical energy and sediment suspension in a breaking wave, to annual cycles of biological activity and soil biogeochemistry associated with flooding, to long-term evolution of shore zone geomorphology following changes in climate or land use in the watershed. All of these forms of temporal heterogeneity shape the ecology of the shore zone.

The shore zone is a dispersal corridor

Shorelines are corridors for movement and dispersal of biota, for several reasons. First, many species have their main habitats in the shore zone. For these species, habitats outside the shore zone are inhospitable, so dispersal takes place chiefly within the shore zone. Second, shorelines are more or less impassable boundaries for many members of both the aquatic and terrestrial biota. When such species move across the landscape or through the water and encounter a shoreline, they must turn and follow the shoreline (or retrace their path), resulting in a concentration of migrating individuals along the shore zone. Third, the physical structure of the shore zone often facilitates dispersal. Shore zones along large lakes and especially rivers are physically continuous over long distances. Further, many species of terrestrial plants and animals are dispersed by currents, either as floating seeds (or other propagules) or on rafts of floating debris or ice (e.g., Hill et al., 1998; Nilsson and Svedmark, 2002; Jansson et al., 2005; Thiel and Gutow, 2005). As a result, breaks in the shore zone, whether natural or human-made, can seriously impede the movement of the biota and fragment populations.

Ecological services provided by shore zones

Shore zones perform many ecological functions that humans value (“ecological services”). We briefly review the most important and well-studied of these ecological services, describing the importance, regulating factors, and human impacts on each.

Support of biodiversity

One of the most important ecological functions that shore zones provide is to support biodiversity. This includes species that are harvested by humans (waterfowl, fish, shellfish, timber, reeds, etc.), species that we value for recreational or aesthetic purposes (birds, catch-and-release fisheries, wildflowers), imperiled species that live chiefly in the shore zone, and species that perform important biogeochemical functions (e.g., riparian vegetation).

Shore zones can support a rich biota of both aquatic and terrestrial species, including bacteria, fungi, protozoans, plants, and animals. Barren, frequently disturbed shore zones (such as those bordering hydropower reservoirs) may have a poor biota, but many kinds of natural shore zones have remarkably rich biotas, containing a very large fraction (>25%) of all of the species in the regional species pool (e.g., Oborny et al., 1995; Nilsson and Svedmark, 2002). There are no complete inventories of the biotas of freshwater shore zones, but such rich zones are likely to support hundreds to thousands of species, excluding bacteria. Shore zone habitats are highly varied, and different kinds of shore zone support different kinds of plants and animals (e.g., Bänziger, 1995; Madjczyk et al., 1998; Lewin et al., 2004; Brauns et al., 2007). Consequently, it is difficult to make any generalizations about the “typical” shore zone biota. Nevertheless, we can make a few interesting general points about the shore zone biota.

Many species are more or less restricted to the shore zone, or at least depend completely on the shore zone for part of their life cycle. These shore zone endemics include many plants (e.g., dune grasses, floodplain specialists, most aquatic plants), invertebrates (including

specialists that depend on shore zone plants), and vertebrates (e.g., many fishes, amphibians, turtles, shorebirds, terns, waterfowl). The transformation of shore zones by humans has especially serious consequences for the continued survival of these species; it is no surprise that several of these shore zone specialists in the United States are now extinct or imperiled (e.g., Pitcher's thistle *Cirsium pitcheri*, the decurrent false aster *Boltonia decurrens* (Smith et al., 1998), the piping plover *Charadrius melanotos*, and the least tern *Sterna antillarum*).

The terrestrial side of the shore zone often contains large numbers of predators and scavengers that feed on wrack or carrion that is washed up onto the shore, or on emerging aquatic insects. This guild includes predatory arthropods like spiders and carabid beetles (e.g., Polis and Hurd, 1996; Kleinwächter et al., 2005; Paetzold et al., 2005), insectivorous birds and bats (Gray, 1993), scavenging invertebrates like dipterans, isopods, and grasshoppers (e.g., Backlund, 1945; Behbehani and Croker, 1982; McLachlan, 1983, 1985; Bastow et al., 2002), predatory and scavenging mammals (Moore, 2002; Carlton and Hodder, 2003), and others. This subject will be discussed in more detail in the section on accumulation and processing of organic matter.

Wave-swept shores support many organisms that usually are thought of as stream-dwellers, such as heptageniid mayflies, stoneflies, elmid beetles, pleurocerid snails, and filamentous green and red algae (Brinkhurst, 1974; Barton and Hynes, 1978; Brittain and Lillehammer, 1978; Dall et al., 1984; Meadows et al., 2005). This group of animals is especially conspicuous at sites where wave energy is high, such as the exposed shores of the Laurentian Great Lakes.

Controls on biodiversity

Much has been written about which features of the shore zone determine which species live there, and ecologists have identified a very wide range of controlling factors. Some factors that surely are important in controlling the distribution and abundance of species in the shore zone (e.g., climate) have received little attention. Here, we briefly review some of the factors that have received most attention from shore zone ecologists.

Physical complexity

Physically complex shore zones usually support a richer biota than simple ones. Comparisons of different kinds of shore zones usually show that density (Jenkins and Wheatley, 1998; Barwick, 2004; Barwick et al., 2004; Toft et al., 2007), biomass (Barwick, 2004; Lewin et al., 2004), body size (Madjeczyk et al., 1998), or species richness (Jenkins and Wheatley, 1998; Jennings et al., 1999; Barwick 2004) of fishes is greater in structurally complex habitats than in simple habitats (Fig. 3). Working at larger spatial scales, Benson and Magnuson (1992) reported that β -diversity (site-to-site variation in species composition) of fish communities in Wisconsin lakes was correlated with the amount of physical heterogeneity across sites. Further, structurally complex habitats may support distinctive communities of fish (Jenkins and Wheatley, 1998; Madjeczyk et al., 1998; Long and Walker, 2005). Growth rates of fishes may be higher in structurally complex habitats as well; Schindler et al. (2000) found that the growth rate of bluegills was correlated with the amount of coarse woody debris in lakes (Fig. 3), and Sass et al. (2006) showed that growth rates of largemouth bass fell when woody debris was experimentally removed from a lake. There are exceptions to these patterns, of course. Juvenile Chinook salmon were more likely to be found over gravel bottoms than in structurally complex riprap in a western reservoir (Garland et al., 2002), consistent with the observation that added artificial structure rarely enhances local densities of salmonids in lakes (Bolding et al., 2004).

Experimental additions of structure usually increase the local density (Barwick et al., 2004; Bolding et al., 2004), spawning (Vogele and Rainwater, 1975), and growth and survival (Bolding et al., 2004) of fishes. The strength of this effect depends on the species of fish and the amount of structure available in the surrounding area (Bolding et al., 2004; Wills et al., 2004). There is an active debate about whether such artificial structures actually increase population size, or merely attract fish from other areas. Added structure may also encourage anglers to overharvest fishes, lead to stunting of prey species, be ugly, or pose a hazard to navigation, so fisheries managers must carefully consider whether adding structure will help them attain their goals for recreational fisheries (Bolding et al., 2004).

Conversely, experimental removal of structure may harm fish populations. Sass et al. (2006) removed most of the coarse woody debris from half of a Wisconsin lake, and found that populations of yellow perch fell drastically. (Because this experiment covered an entire lake basin, we know that populations of perch actually fell, not just moved to other areas.) In response to the loss of this important prey item, predatory largemouth bass shifted their diets, and their growth rates fell.

Habitat structure interacts with other factors in interesting ways. For example, MacRae and Jackson (2001) found that fish densities were higher in structurally complex habitats only in lakes where a large predator (smallmouth bass) was present (Fig. 3). Likewise, Wolter and Arlinghaus (2003) suggested that structure could reduce the deleterious effects of commercial navigation on nearshore fish communities by providing physical refuges against wakes and currents. It therefore seems likely that the per-structure value of structural complexity to fish is greatest in habitats where physical forces are large, predators are abundant, and structure is scarce.

Evidence on the effects of structural complexity on other organisms is consistent with, but scarcer than, data on fish. Structural complexity or high spatial heterogeneity is typically correlated with high densities (Lewin et al., 2004; Kostylev et al., 2005) or species richness (Moon, 1934; Le Hir and Hily, 2005; Kostylev et al., 2005; Moschella et al., 2005; Brauns et al., 2007) of aquatic invertebrates. Just as with fish, structurally complex shore zones protect invertebrates from the damaging forces of waves (Gabel et al., 2008). On the terrestrial side of the shore zone, Paetzold et al. (2008) found that channelization, which simplifies the structure of the shore zone, reduced abundance and richness of terrestrial arthropods, and some vertebrates preferentially use complex shore zones (e.g., Stickney et al., 2002). Structurally complex shore zones also support rich plant communities (Fig. 4; Everson and Boucher, 1998; Pollock et al., 1998; Naiman et al., 2005). In addition to these specific studies, many authors (e.g., Obrdlik et al., 1995; Nilsson and Svedmark, 2002; Arscott et al., 2005; Brauns et al., 2007) have made the general claim that high physical heterogeneity of the shore zone is responsible for its high biodiversity, without offering direct evidence.

A few studies have investigated the details by which physical complexity affects the biota. Le Hir and Hily (2005) suggested that species richness was not driven by physical complexity *per se*, but rather by the provision of special microhabitats (e.g., cavities) that support particularly distinctive or rich biotic communities (cf. Chapman and Bulleri, 2003). Some studies have suggested that the size of the roughness elements is related to the size of the organisms that inhabit the shore zone. Thus, the size of fish that use artificial structures depends on the size of the interstitial spaces that these structures provide (Bolding et al., 2004), and small-bodied invertebrates were especially important on structurally complex marine shores that contained many small crevices (Kostylev et al., 2005).

Hydrologic regime

The hydrologic regime, i.e., the pattern of change in water level over time, strongly influences the composition and activities of the shore zone biota. Shore zone vegetation is tied in several ways to the hydrologic regime (Keddy and Reznicek, 1986; Hill et al., 1998; Johnson, 2002; Coops et al., 2004; Strang and Dienst, 2004; Van Geest et al., 2005). Cottonwoods and other important shore zone plants germinate and establish on exposed soils (Keddy and Reznicek, 1986; Nishihiro et al., 2004; Naiman et al., 2005). Saturated, reduced soils produced by high water levels can kill terrestrial vegetation such as shrubs, which would otherwise shade out herbaceous plant species near the water's edge. High water levels also reduce light penetration to underwater sediments, reducing growth rates or killing light-limited submersed aquatic vegetation. Prolonged low water levels can kill vegetation through desiccation. Many plants of the shore zone are thus adapted to moderately fluctuating water levels, which may maximize the extent and species richness of plant cover in the shore zone (Keddy and Reznicek, 1986; Hill et al., 1998). Species richness and the area occupied by aquatic plants can be reduced by decreasing, increasing, or changing the seasonal pattern of water-level fluctuations (Hill et al., 1998). Thus, Keddy and others (Keddy and Reznicek, 1986; Hill et al., 1998) have suggested that the hydrological regime is a master variable that controls the character of the shore zone vegetation (Fig. 5).

Shore zone animals also are affected by the hydrologic regime. Predictable changes in water level allow animals to access different habitats over the course of the year. For example, fishes such as northern pike and yellow perch spawn on seasonally flooded vegetation (Wilcox and Meeker, 1992; Farrell, 2001) or forage in floodplains (Junk et al., 1989). Amphibians and many other species live in habitats such as shore zone pools whose very existence depends on

water-level fluctuations (Robinson et al., 2002). On the other hand, unpredictable changes in water levels can make parts of the shore zone unsuitable for animals or kill them outright. Bowers and de Szalay (2005) suggested that irregular fluctuations in water level resulting from wind-driven seiches kept zebra mussels from colonizing shallow substrates along the shore of Lake Erie. Wind-driven waves or wakes can strand young fish on the shore and dewater nests (Adams et al., 1999; Wolter and Arlinghaus, 2003). The same effects can be produced by rapidly falling water levels downstream of peaking hydropower dams (Cushman, 1985). Conversely, rapid rises in water level, whether natural or anthropogenic, can drown terrestrial animals along the shore (Moon, 1935), and Paetzold et al. (2008) found lower abundance and species richness of riparian arthropods along the shores of rivers with peaking hydropower dams.

As a result of the close relationship between shore zone hydrology and the biota, human-induced changes in shore zone hydrology may lead to rapid and profound changes in the biota. Regulation by hydropower dams changed species composition and reduced species richness of shore zone vegetation along Swedish rivers (Nilsson et al., 1991). Shore zones with artificially stabilized water levels may have lower species richness and higher cover of the invasive plants than those with more natural hydrology (Hill et al., 1998; Van Geest et al., 2005; Boers and Zedler, 2008). Bunn and Arthington (2002) suggested that artificially altered hydrologic regimes generally favor alien species. Human regulation of water levels, whether resulting in increased or decreased variability in water levels, also has deleterious effects on fish, waterfowl, and mammals of the shore zone (e.g., Wilcox and Meeker, 1992; Farrell, 2001).

Elevation (or bathymetry)

Biological communities and distributions change regularly along an elevational gradient (or its underwater equivalent, the bathymetric gradient), from offshore waters onto the shoreline,

and then upslope into upland communities (Fig. 6; Šapkarev, 1975; Dall et al., 1984; Keddy and Reznicek, 1986; Strayer and Smith, 2000; Bulleri et al., 2005). This elevational zonation is so universal and conspicuous that almost all subdivisions of the shore zone are based on elevation (Fig. 1). Elevation is an indicator for changes in many variables that affect the biota, such as frequency and timing of inundation or desiccation; grain size, nutrient and organic content, and redox state of soils and sediments; intensity of predation and other biological interactions; frequency and intensity of disturbance by different agents; and inputs of organic matter from aquatic primary production, terrestrial primary production, and wrack deposition (Fig. 7). As a result, there frequently is a regular zonation of vegetation across the shore zone, from woody plants, to emergent graminoid species such as *Typha* (cattail) and *Phragmites* (common reed) around the shoreline, to low-growing rosette plants just below the shoreline, to floating-leaved species such as *Nymphaea* (white water lily), *Nuphar* (spatterdock), and some of the *Potamogeton* spp. (pondweeds), and finally to fully submerged vascular plants, charophytic algae, and mosses. Because vegetation has such strong effects on animal communities and biogeochemical processes, this vegetational zonation contributes to zonation of many other ecological properties along the elevational gradient.

Slope, a variable closely related to the elevational gradient, may also affect shore zone biodiversity. It is perhaps obvious that slope is important because it determines the width and therefore the area of the shore zone (Fig. 8), which are centrally important to many ecological functions. Slope can also determine the suitability of the shore zone for organisms, for instance as nest or foraging sites for birds (Maccarone et al., 2005; Neuman et al., 2008).

While coarse-scale elevational profiles have received the most attention from ecologists, local elevations (i.e., meso- to microscale roughness) also strongly affect shore zone biodiversity

(Fig. 4). For instance, Chapman and Bulleri (2003) suggested that one of the main reasons that constructed sandstone seawalls support different species from natural sandstone shores is that the latter contain small pools and crevices that are absent from the seawalls. Likewise, small shoreline pools lying just landward of the lake shore support a rich biota and are metabolically very active (Pieczyńska, 1972).

Human actions that change the large-scale shore zone profile or small-scale roughness are likely to have profound effects on the distribution and abundance of species within the shore zone. Such actions, including dredging, filling, and grading, are very common, and probably represent one of the major human impacts on shore zone ecosystems.

Exposure and disturbance

Many studies point to the importance of exposure in determining the character of the shore zone biota, although this variable is rarely defined and even more rarely measured. Generally what is meant is exposure to the forces of wind and waves (or sometimes currents). Although there are devices to measure exposure as either peak wave energy (Bell and Denny, 1994; Guinez and Pacheco, 1999) or dissolution rate of a substance such as gypsum (Pettigrew and Kalff, 1991; Thompson and Glenn, 1994; Porter et al., 2000), these methods are rarely used in fresh water. Instead, exposure usually is estimated by measuring the wind fetch at a site (Keddy, 1982; Brodersen, 1995; Ekebom et al., 2003), if it is estimated at all. Exposure acts as a disturbance (e.g., Keddy, 1983) that dislodges or kills organisms. High wind and wave energy also can winnow fine particles out of sediments, thin benthic boundary layers and drive mass flow of water and solutes (e.g., oxygen) through sediments, increase turbulent mixing in the water column, increase passive dispersal of organisms and non-living particles, and overwhelm the swimming or flying abilities of animals.

Many biologists have noted that the composition of the shore zone biota varies along exposure gradients (Fig. 9; Moon, 1934; Keddy, 1982, 1983; McLachlan, 1983; Dall et al., 1984; Kennedy and Bruno, 2000). Rooted aquatic plants often are absent from nearshore areas of highly exposed sites (Chambers, 1987) because they are uprooted, damaged, or grow poorly (e.g., Coops et al., 1991, 1994; Doyle, 2001). The density and species richness of marine invertebrates is lower on reflective beaches than on dissipative beaches (Fig. 13; Brazeiro, 2001; Brown and McLachlan, 2002), presumably as a result of the disturbance regime. It is otherwise difficult to generalize about the effects of exposure except to note that species composition usually varies along an exposure gradient, and that numbers and species richness of organisms may be low at highly exposed sites. In this latter respect, freshwater shores may differ from their marine counterparts, in which even very highly exposed shores support a rich and distinctive biota, at least on stable bedrock or boulders. There seems to be no close freshwater equivalent to the biota of exposed marine rocky shores. Some ecologists (Keddy, 1983; Tabacchi et al., 1996) have suggested that species richness should peak at intermediate levels of exposure, but this idea seems not to have been accepted as generally true (Riis and Hawes, 2003; McClintock et al., 2007).

Several other variables interact with exposure to affect biological distributions in the shore zone. Although fine-grained sediments support high densities of macrofauna in sheltered sites (e.g., McLachlan, 1983), they can be very poor in highly exposed sites (Barton and Hynes, 1978), presumably because they are stable in sheltered sites but mobile in exposed sites. Thus, the stability of a sediment may be more important than its grain size or the exposure of the site *per se*. As already suggested, provision of physical shelter may have much greater effects on an exposed shore than on a sheltered shore. Access to quiet-water areas during storms or floods

may allow the biota to survive these events (e.g., Quist et al., 1999; Rempel et al., 1999). Likewise, the effects of exposure may depend on the biota of a site, as some plants and sessile animals are able to ameliorate the effects of exposure for other organisms (Fig. 10, Brodersen, 1995; O'Donnell, 2008).

Disturbances other than wind and wave action also are important. Ice and low temperatures can be important agents of disturbance along cold shorelines (Dall et al., 1984; Begin and Payette, 1991; Pugh and Davenport, 1997). The importance of flooding and desiccation has already been discussed. Disturbances caused by humans (e.g., recreational vehicles) are an important factor in modern shore zones, and will be discussed in a later section on human impacts on the shore zone.

Species richness or density of aquatic animals may be reduced in very shallow water (e.g., Brinkhurst, 1974; Šapkarev, 1975; Burlakova and Karatayev, 2007), presumably as a result of disturbance by waves, ice, or frequent desiccation, or predation by terrestrial predators. It seems likely that there might be a corresponding depression in richness or density of some terrestrial organisms immediately uphill of the shoreline because of frequent inundation or disturbance.

Wrack deposition is an important disturbance on many shores. Heavy wrack kills vegetation (and presumably sessile or slow-moving animals), and can prevent a successional dominant from monopolizing the shore zone. Experimental work on marine shore zones shows that wrack deposition has strong effects on vegetational succession and composition, and favors fugitive species (Tolley and Christian, 1999; Minchinton, 2002).

Several common human activities change inputs of wave energy onto the shore zone. Breakwaters and other coastal defenses reduce inputs of physical energy. Less obviously,

several common human activities (e.g., building the shore out into the water, dredging, seawall construction, boat wakes) increase energy inputs to the shore zone. The ecological effects of such changes probably are common and important.

Biological interactions

Although shore zones often are thought of as stressful habitats, leading to the possibility that biological communities are controlled primarily by stress rather than biological interactions, there is ample evidence that biological interactions structure shore zone communities. We will not document all of these interactions, but simply cite a few examples to show the strength and diversity of these interactions. Aquatic and terrestrial plants support animal communities that differ from those of unvegetated sediments, and often differ across plant species (e.g., Moon, 1934; Brodersen, 1995; Radomski and Goeman, 2001; Romanuk and Levings, 2003; Salovius and Kraufvelin, 2004; Kraufvelin and Salovius, 2004). Consequently, invasions of alien plants frequently not only push out native plants but also change associated animal communities (e.g., Ailstock et al., 2001; Strayer et al., 2003). Predation by terrestrial predators (birds and mammals) may be so intense that it reduces the density of aquatic prey near the water's edge by direct consumption or intimidation (Power, 1984; Power et al., 1989; Burlakova and Karatayev, 2007). Similarly, terrestrial predators may take large numbers of emerging aquatic insects (Paetzold and Tockner, 2005), and aquatic predators affect the distribution, abundance, and behavior of their prey (Fig. 3). Interestingly, the emergence of aquatic insects may increase the populations of terrestrial predators in the shore zone enough to suppress populations of terrestrial herbivores (Henschel et al., 2001). Backlund (1945) reported extraordinarily high levels (86-100%) of parasitism by wasps among wrack-dwelling dipterans. By absorbing wave energy, *Spartina* (cordgrass) moderates the environment enough to allow other plants to persist (Fig. 10,

Kennedy and Bruno, 2000). Thus, biological interactions in shore zones are varied, and often strong enough to affect the distribution and abundance of species, just as they are in other habitats.

Inputs and stocks of organic matter

Animal and microbial populations often are controlled by the amount and quality of organic matter (Cole et al., 1988; McNaughton et al., 1991; Wallace et al., 1999). Considering the enormous range in organic inputs from open sandy beaches to wrack-covered shores, to wetlands covered by emergent plants to shores stacked with driftwood, it is reasonable to expect that the quantity and quality of organic matter controls the composition, abundance, and activity of many shore zone consumers. Densities of macroinvertebrates in the shore zone increase with organic content of the sediments (e.g., Brittain and Lillehammer, 1978; McLachlan, 1983; Dall et al., 1984), and experimental additions of wrack increase animal densities (Rossi and Underwood, 2002). Likewise, tidying beaches by removing wrack reduces populations of terrestrial and aquatic consumers (Malm et al., 2004).

Other physical and chemical controls

A large number of other physical and chemical factors control the shore zone biota, but we will mention just a few of the most important: grain size, content of nutrients and organic matter, and redox status of the soil or sediment, and nutrient loading. Animal densities and community composition often vary with sediment grain size (e.g., Barton and Hynes, 1978; McLachlan, 1983; Dall et al., 1984; Rodrigues et al., 2006), although it may be difficult to disentangle the effects of grain size from those of sediment stability. Grain size affects substratum roughness, soil cohesion (and therefore its suitability for burrowing), and often is correlated with the content of organic matter. Grain size and organic content affect the ability of

soils to hold water and nutrients, and should affect plant communities as well (Naiman et al., 2005).

The redox status of soils and sediments affects the shore zone biota in several ways.

Soils and sediments with low redox potential (e.g., soils that are saturated, fine-grained, or have a high organic content) are poor habitat for most animals (e.g., McLachlan, 1983) because dissolved oxygen is low or absent, and toxic substances such as sulfide and ammonia may be present. Although plant nutrients (ammonium, soluble reactive phosphorus) may be readily available in soils with low redox potential, the scarcity or absence of dissolved oxygen may stress or kill plants as well, unless they have special physiological adaptations for coping with these conditions (e.g., Sorrell et al., 2000).

Nutrient loading has strong direct and indirect effects on the shore zone biota. The direct effects of nitrogen or phosphorus loading are important to the shore zone vegetation. For instance, high loads of nitrogen from developed shore zones favor monocultures of *Spartina* (cordgrass) or *Phragmites* (common reed) in estuarine shore zones (Bertness et al., 2002; Chambers et al., 2008). High levels of phosphorus, whether from external loading or recycling by shore zone consumers, can favor the development of nuisance blooms of the macroalga *Cladophora* in fresh or slightly brackish water (Hecky et al., 2004; Kraufvelin et al., 2006). In addition to these direct effects, excessive nutrient loading can increase phytoplankton populations. Although phytoplankton is an important food for some shore zone animals (e.g., zebra mussels, net-spinning caddisflies), dense phytoplankton populations reduce water clarity, and therefore reduce the extent and productivity of submersed vegetation, with consequent effects on shore zone animals.

Shore zones as habitat complexes

Many animals use different parts of the shore zone during different parts of their life cycle, or move between the shore zone and nearby habitats. In this sense, the individual parts of the shore zone may function as parts of habitat complexes. There are many examples. Northern pike, yellow perch, and many other fish species use the shore zone as spawning or nursery areas, moving into the open waters of lakes or rivers as they mature. Some fish species use different parts of the shore zone during different juvenile stages (Scholten, 2002). As a consequence, the overall composition of the shore zone, and connectivity among the parts of the shore zone and between the shore zone and other nearby habitats may be vital to maintaining biodiversity (Fig. 11; Amoros and Bornette, 2002; Robinson et al., 2002).

Energy dissipation

Waves, currents, and wakes may focus enormous amounts of energy onto shore zones (Fig. 2), much of which can be dissipated by drag against the bottom, turbulence, suspension of sediments, or absorption. The amount of energy that is dissipated by the shore zone versus reflected back into the body of water varies greatly, depending on the slope, roughness, and composition of the shore zone, including its biota. Shore zones with steep slopes often reflect more energy than flatter shore zones. Marine geomorphologists and ecologists make a fundamental distinction between typically steep, coarse-grained *reflective* beaches and typically flat, fine-grained *dissipative* beaches (Figs. 12, 13). Roughness, such as vegetation, bedforms, boulders, or engineered structures can be important in dissipating energy (Zhu and Chang, 2001).

Shore zone vegetation may absorb significant amounts of wave energy, thereby reducing erosion along the shore (Fig. 14, Coops et al., 1996) and allowing other species to survive (Fig. 10, Kennedy and Bruno, 2000). As a result of this reduction in physical energy, shore zone vegetation changes flow patterns, reduces near-bed shear stresses, and may cause local sediment

deposition and change mesoscale geomorphology (e.g., bar formation) (Jordanova and James, 2003; Baptist et al., 2005; Naiman et al., 2005). Roots of shoreline vegetation also can stabilize banks and provide a stable substratum for other species in the physically stressful shore zone (Gregory and Gurnell, 1988; Sweeney, 1993). If the protective shore zone vegetation is lost, whether from excessive energy inputs or other causes, it may be necessary to construct artificial barriers, which often are expensive and ineffective (Johnson, 2002).

In other cases, shore zone vegetation may focus water flow to increase shear stress and erosion (Widdows et al., 2008). The amount of energy that is absorbed or focused by the vegetation, along with the consequent erosion or deposition, will depend on the details of the structure of the vegetation and the local flow environment.

Accumulation and processing of organic matter

The shore zone accumulates and processes large amounts of organic matter. Some of this organic matter originates from on-site primary production in the shore zone, which can be among the highest recorded from any habitat (Wetzel, 1990). Of course, on-site primary production in other shore zones (highly exposed rocky or sandy shores, or many engineered shore zones) may be negligibly small.

In addition to this on-site primary production, large amounts of organic matter can be washed into and retained by shore zones from adjacent ecosystems. This matter can be focused onto narrow bands (“wrack”) along the shore, and so reach enormous densities. Deposition, decomposition, and animal communities of wrack have been well studied by marine ecologists, who have recorded deposition rates as high as 2920 kg wet mass per meter of shoreline per year (Backlund, 1945; McLachlan, 1983; Polis and Hurd, 1996; Colombini and Chelazzi, 2003; Orr et al., 2005). Typically, marine wrack is dominated by kelp and other macroalgae, but it may be

dominated by vascular plants (e.g., eelgrass, *Spartina*) or wood at sites near major rivers. Inputs of animal carrion may also be significant (>100 g dry mass/m-yr; Colombini and Chelazzi, 2003). Wrack seems not to have been much studied in fresh water, although it may be an important source to freshwater shore zones as well. Wrack accumulations as high as ~5 kg dry mass/m² (chiefly *Vallisneria americana* or wood) are common along the shores of the freshwater tidal Hudson River, which is 60-fold higher than plant biomass in living *Vallisneria* beds (Strayer et al., unpublished). Much greater accumulations surely exist along freshwater shores. The amount of wrack that is deposited and retained on a shore depends on the amount of organic matter that is generated locally, the hydrologic regime, and the slope and roughness of the shore (Fig. 15; Backlund, 1945; Orr et al., 2005).

Wrack is an important source of organic matter to shore zones, especially where on-site primary production is small (e.g., sand beaches), and may be an important source of soil organic matter (McLachlan, 1983, 1985; Rossi and Underwood, 2002). Although some of this organic matter is exported from the shore zone (wrack accumulations in particular can be very ephemeral – Backlund, 1945; Orr et al., 2005), much of it is decomposed on site, supporting very high rates of respiration and production by microbes and animals (McLachlan, 1985; Polis and Hurd, 1996; Jedrezejczak, 2002a,b; Coupland et al., 2007). Initially, large amounts of dissolved organic matter are leached from the wrack (Jedrezejczak, 2002a), which can be an important source of dissolved organic matter to the shore zone soils (Malm et al., 2004) and nearshore waters. Marine wrack is rapidly colonized by both microbes and invertebrates (Backlund, 1945; Jedrezejczak, 2002b), which together decompose the organic matter. Animals often prefer to feed on aged wrack (Backlund, 1945; Pennings et al., 2000), probably because it contains higher microbial biomass and lower concentrations of defensive chemicals than fresh wrack. The

nitrogen and phosphorus released in the mineralization of wrack can be an important source of nutrients to nearshore microbes and phytoplankton (Malm et al., 2004), as well as terrestrial microbes and vegetation.

By virtue of its complex physical structure and high food availability, marine wrack supports large populations of invertebrates, typically dominated by dipterans, enchytraeid oligochaetes, collembolans, mites, and amphipods (e.g., Backlund, 1945; Behbehani and Croker, 1982; McLachlan, 1983, 1985; Marsden, 1991; Jedrezejczak, 2002a,b; Romanuk and Levings, 2003; Garbary et al., 2004). Most of these species are detritivores or bacteriovores, and many are good colonizers, and so are able to take advantage of ephemeral wrack accumulations. Large populations of predators, both invertebrate (e.g. carabid beetles, spiders – Backlund 1945, Paetzold et al., 2008) and vertebrate (e.g., shorebirds – Elias et al., 2000; Dugan et al., 2003) feed on these primary consumers.

Apart from its importance in shore zone food webs, the physical structure of wrack may affect shore zone geomorphology, biogeochemistry, and biodiversity (Backlund, 1945; Pieczyńska, 1972). Temperature and moisture are moderated within and beneath a wrack bed (Backlund, 1945; Coupland et al., 2007), and dense wrack may impede oxygen diffusion, leading to hypoxia or anoxia. This leads to steep vertical gradients in environmental conditions, biodiversity, and biogeochemical processes within a wrack bed (e.g., Backlund, 1945). Some birds nest in and around wrack (Smith and Renken, 1991; Maccarone et al., 1993). Floating wrack may be an important means of dispersal for shore zone organisms (Backlund, 1945; Salovius et al., 2005; Minchinton, 2006).

Humans often remove wrack from the shore zone, formerly as a resource to fertilize fields, thatch roofs, and build fences (Backlund, 1945), and now to tidy beaches (e.g., Dugan et

al., 2003). In addition to any effects resulting from sediment compaction from machines used to remove wrack, wrack removal can reduce organic matter in shoreline soils and sediments (Dugan et al., 2003; Malm et al., 2004), reduce nutrient concentrations offshore (Malm et al., 2004), and reduce microbial and animal numbers, biomass, or production in the terrestrial and aquatic parts of the shore zone (Dugan et al., 2003; Malm et al., 2004). Other human modifications of the shore zone (destruction of seagrass beds, replacement of gently sloping shores with vertical seawalls, removal of shore zone vegetation and other roughness elements) probably have greatly reduced wrack accumulation on many shores, with large ecological consequences.

The combination of saturated soils and high organic matter makes shore zones ideal habitats for anaerobic processes such as denitrification, sulfate reduction, and methanogenesis. Ecologists have reported high rates of these processes in shore zones, especially in plant beds or wrack accumulations where labile organic matter is abundant (e.g., Juutinen et al., 2003; Kankaala et al., 2004; Hirota et al., 2007). Notably, many of the products of anaerobic metabolism, including methane, sulfide, hydrogen, and ferrous iron, can themselves be used as a source of energy by microbes with access to oxygen. Because aerobic and anaerobic microhabitats are closely juxtaposed in most shore zones, there is often close coupling between aerobic and anaerobic processes. This coupling can lead to high rates of biological activity and rapid decomposition of organic matter.

Wood in the shore zone

Woody debris often accumulates in freshwater shore zones. Although it is not usually an important source of energy to the shore zone biota (but see Hoffman and Hering, 2000; Benke and Wallace, 2003; Wondzell and Bisson, 2003 for examples of wood-eating insects), this dead wood plays several important ecological roles. Some of this wood originates locally, from

riparian trees that fall into the water and decay in place. Because of bank instability and exposure to high winds, inputs of wood from shore zone forests presumably are much greater than in most upland forests. However, in large lakes and rivers, currents and waves may transport wood considerable distances. The amount of wood along shorelines varies over wide ranges (Gurnell, 2003; Marburg et al., 2006). Wood tends to accumulate in characteristic locations – on the upstream end of islands and bars, in strands parallel to and above the water line (especially on low-slope shores), at the mouths of side channels, or around retentive structures such as standing tree trunks and bridge abutments (Gurnell, 2003).

Woody debris structures the morphology of the shore zone, at micro- to mesoscales (Gurnell et al., 2005). Woody debris encourages island formation, armors shores where large accumulations occur, and tends to increase mesoscale spatial heterogeneity (Piegay, 2003; Gurnell et al., 2005). Wood accumulations retain smaller particles of organic matter (Wondzell and Bisson, 2003), and may therefore be sites of high food availability for detritivores and decomposers. At small scales, flow patterns around pieces of wood produce local variations in topography (including small pools), sediment grain size, and organic content. All of this wood-induced heterogeneity provides a rich array of meso- and microhabitats for the shore zone biota, and must have large effects on species composition and richness.

Woody debris has other strong effects on the shore zone biota. Where the primary substratum is unstable (e.g., sand in high-energy environments), wood snags offer stable substrata, and may support very high densities of invertebrates (Benke and Wallace, 2003; Wondzell and Bisson, 2003). Wood also simply increases surface area available for bacterial and algal biofilms, as well as invertebrates. Coarse woody debris shelters fishes from predators; provides visual isolation from competitors, allowing higher local densities of competitors;

provides food and foraging sites; offers shelter for nests and young; and provides visual landmarks for homing or site recognition (Vogele and Rainwater, 1975; Crook and Robertson, 1999; Benke and Wallace, 2003; Zalewski et al. 2003). Some species spawn around woody debris (e.g., Vogele and Rainwater, 1975; Cochran and Cochran, 2005). Experimental addition of woody debris decreased predation rates on grass shrimp in a Maryland estuary (Everett and Ruiz, 1993), and high densities of woody debris may enhance growth rates of fish (Fig. 3; Schindler et al., 2000). Aquatic insects use terrestrial wood for emergence, oviposition, and resting sites (Benke and Wallace 2003), and terrestrial vertebrates use wood accumulations as sites for perching and basking and shelter for nests and dens (Steel et al., 2003). Consequently, densities of animals often respond to increases or decreases in availability of woody debris (Fig. 3; Everett and Ruiz, 1993; Scholten et al., 2003; Sass et al., 2006). Like other physical structure in the shore zone, the importance of wood varies with the availability of other structure; wood usually has the greatest ecological effect in shore zones where other structure is lacking (Crook and Robertson, 1999; Benke and Wallace, 2003). Finally, floating wood can raft species from place to place in the shore zone (Gurnell et al., 2005; Thiel and Gutow, 2005), and thus contribute to dispersal and connectivity across shore zone populations.

There has been relatively little work comparing the ecological value of woody debris from different species of trees. Fresh debris from some tree species (poplars and willows) can reroot after it is transported, so such debris is more stable and less subject to subsequent transport than debris from other species (Gurnell et al., 2005). Bark roughness, wood hardness, and the age of the wood may affect aquatic invertebrates (Bowen et al., 1998; Magoulick, 1998), and the size of the hiding spots in wood accumulations affects the species and sizes of fishes that use these accumulations (Bolding et al., 2004).

Several human activities have greatly reduced the amount of shore zone wood, so that modern shore zones contain substantially less wood than natural shore zones. Humans remove wood from river channels to improve recreational and commercial navigation (Angradi et al., 2004), to tidy the appearance of shoreline properties (Christensen et al., 1996; Francis and Schindler, 2004), or to reduce the likelihood of damage to infrastructure. Humans have cut many riparian forests, removing the source of wood to the shore zone (Christensen et al., 1996; Angradi et al., 2004; Francis and Schindler, 2004; Scholten et al., 2005). Reservoirs act as traps for wood (Piegay, 2003), and stabilized river flows tend to reduce bank-cutting, which is an important source of wood to rivers, as well as reducing the ability of the river to transport wood (Angradi et al., 2004). Humans also remove much of the roughness from shore zones, decreasing their ability to retain floating wood (Piegay, 2003). All of these activities have greatly reduced stocks of woody debris, especially in large rivers (Figs. 2, 16). These large losses may have important consequences for the functioning of shore zone ecosystems.

Other kinds of organic matter may accumulate in the shore zone as well. Just as wave energy focuses wrack into small areas, insect emergence can funnel animal biomass into the shore zone. These inputs can be considerable in large lakes and rivers, and support large populations of terrestrial predators in the shore zone, including carabid beetles, spiders, insectivorous birds, and bats (Backlund, 1945; McLachlan, 1983; Gray, 1993; Paetzold and Tockner, 2005; Paetzold et al., 2005; Smith et al., 2004, 2007). This enhancement of predator populations in the shore zone may be large enough to suppress populations of terrestrial prey as well (Henschel et al., 2001). Animals that spawn in the shore zone (e.g., yellow perch, sunfishes) may also focus large amounts of very labile organic matter into the shore zone. In

addition floatable organic pollutants (plastics, oils) often accumulate in shores zones; their effects will be addressed briefly under “Human impacts on the shore zone” (below).

Processing of nutrients

Shore zones frequently support high rates of nutrient cycling (McClain et al., 2003). Shore zones intercept nutrients that are moving from the land into the water, capture nutrients from the water, and liberate nutrients in the process of decomposition of organic matter. The first of these has received the most attention because of the interest in using riparian zone buffers to reduce nutrient loading (especially nitrogen) to surface waters (e.g., Lowrance, 1998). The plants and microbes of the shore zone can be very effective in capturing incoming nitrate and ammonium and converting it into biomass, detrital organic nitrogen, or N₂ gas (via denitrification). Likewise, phosphorus can be retained by shore zone plants, microbes, or soils. Although much attention has been focused on terrestrial plants, aquatic plants and microbes also can retain nutrients (Wetzel, 1990). These valuable functions can be disrupted if the shore zone vegetation is removed or if patterns of water flow through the shore zone are changed (e.g., by construction of impermeable barriers such as seawalls or other coastal defenses, or by changing water levels – Groffman et al., 2003). Humans commonly make such changes to shore zones, and probably have compromised the abilities of many shore zones to trap nutrients.

Nutrients from the water likewise may be taken up and incorporated into organic matter or denitrified by shore zone plants and microbes. Marine ecologists have emphasized the importance of wave-driven water movement through permeable sediments in boosting uptake of nutrients and organic matter by interstitial microbes (McLachlan, 1983). Some of these water-derived nutrients may be moved uphill into terrestrial ecosystems by insect emergence, uptake by terrestrial plants, or consumption of aquatic prey by terrestrial predators.

As was discussed earlier, nitrogen and phosphorus are liberated as organic matter is decomposed. Because the amount of organic matter that is decomposed in the shore zone may be very large, either from on-site primary production or wrack deposition, correspondingly large amounts of inorganic nitrogen and phosphorus may be released. These nutrients may be exported to nearshore waters (e.g., Malm et al., 2004) or taken up by the shore zone biota (Addy et al. 2005).

Corridors

For reasons already noted, shore zones can be important corridors for the movement of both plants and animals, knitting together different populations of a species into a functional metapopulation, or allowing animals to exploit different regions in different seasons. Thus, many migrating birds follow shorelines, and shore zone plants can be dispersed along the shore by floating (Jansson et al., 2005) or ice-rafting (Hill et al., 1998). Fish likewise may disperse along the shore zone rather than in the open water (Reichard et al., 2004).

The value of different shore zones as corridors must vary widely, depending on their length, orientation, availability of cover, and water movement. Long, nearly linear shore zones such as those along major rivers must be much more important as dispersal corridors than the small, closed shore zones around small isolated lakes. The orientation of the shore zone relative to the direction of animal migration must also affect the extent to which it is used as a dispersal corridor, although not always in a straightforward fashion – a shore can be used heavily because it is along the direction of movement (the north-south Mississippi River for migrating birds) or because it lies across the direction of movement (the east-west shores of Lake Erie for migrating birds). The presence of nearshore currents must greatly increase the value of shore zones as dispersal corridors by providing a mechanism for passive dispersal of the biota (Hill et al., 1998;

Nilsson and Svedmark, 2002; Jansson et al., 2005). The availability of logs, wrack, ice, and plastic may affect dispersal as well, because these floatable platforms may be important in dispersing terrestrial organisms (Hill et al., 1998; Gurnell et al., 2005; Salovius et al., 2005; Thiel and Gutow, 2005).

Human activities have greatly changed the value of many shore zones as dispersal corridors. Dams and habitat destruction fragment freshwater shore zones, and presumably greatly reduce their value as dispersal corridors. Reservoirs in particular can act as traps for biota dispersing along river corridors (Jansson et al., 2005). On the other hand, marine ecologists have suggested that coastal defense structures such as groynes and breakwaters serve as stepping stones and enhanced dispersal of organisms that use the hard surfaces and quiet backwaters created by these structures (Thompson et al., 2002; Airoldi et al., 2005; Bulleri and Airoldi, 2005). Presumably these same effects occur along large lakes and rivers that have been protected by similar structures.

What sets the character and functioning of the shore zone?

It should be apparent that from this brief review that many factors control the structure and function of freshwater shore zone ecosystems. Nevertheless, by analogy with Jenny's (1941) analysis of state factors for soil development, we can think of the ecological character and function of shore zones as being determined chiefly by six interdependent classes of factors (cf. Meadows et al., 2005): inputs of **physical energy** to the shore zone; the geological or engineered **structure** of the shore zone and its environs; the **hydrology** of the shore zone; inputs of **nutrients**; the **biota** of the shore zone; and the **climate** to which the shore zone is exposed. We are not suggesting that these factors completely determine the character of every freshwater

shore zone, but taken together they capture most of the variation in freshwater shore zones. We discuss each of these six factors briefly below.

Physical energy regime

One might be tempted to see the physical energy regime as *the* master variable that controls the ecological character of the shore zone. In this view, given enough time, the materials and morphology of the shore zone would adjust to the energy regime. Materials fine-grained or light enough to be suspended by the ambient energy regime would be swept away, while materials too large or heavy ever to be moved would be covered by mobile particles. Thus, low-energy beaches would be dominated by fine-grained sediments, and high-energy beaches by coarse-grained sediments. Bedforms (e.g., ripples) and shore zone slopes also would adjust to match the energy regime, so the physical structure of the shore zone would depend only on the energy regime. One might also view the biota as ultimately dependent on energy inputs. This view is analogous to the idea of the graded alluvial river that has been widely discussed in stream geomorphology and ecology (e.g., Leopold et al., 1964).

Real shore zones are so far from this ideal world that the idea of equilibrium with the energy regime would seem to have little use, except perhaps as an ideal standard against which real shore zones can be compared. Even in open marine beaches, perhaps the case that most closely approaches the ideal, the idea of an equilibrial beach profile has been sharply criticized (Pilkey et al., 1993). Many natural shore zones other than sandy beaches contain materials that are far too coarse to be transported by the ambient energy regime (e.g., boulders or bedrock), have an insufficient supply of fine materials that could be deposited or sculpted by the ambient energy regime, or have energy inputs that are so variable over time that the shore zone structures never “catch up” to reach equilibrium with the instantaneous energy regime. Deviations from

the ideal world are even more pronounced along human-dominated shore zones, where humans often introduce materials or structures that are deliberately designed to be immobile under the ambient energy regime (seawalls, riprap), or alter the energy regime (dredging, filling, breakwaters, etc.). The physical structure of these human-dominated shore zones often is far out of equilibrium with the energy regime. Thus, it seems impossible to treat the character of the shore zone as depending solely on the energy regime, and it will be necessary to include the physical structure of the shore zone as a separate controlling factor.

Nevertheless, even if the energy regime is not *the* master variable that sets the character of shore zone ecosystems, it surely must be considered as *a* master variable. The energy regime does have strong effects on the physical structure of the shore zone (particle sizes, bedforms, slope), even if it does not completely determine it. Physical structure in turn has strong and pervasive effects on biodiversity and biogeochemistry, through its effects on factors like the disturbance regime, retention of wrack and woody debris, etc. The energy regime also affects turbulent mixing in nearshore waters and sediments, as well as pumping of water through nearshore sediments by wave action, with consequent effects on biogeochemical processes. The energy regime also directly affects the behavior, movement, passive dispersal, and morphological structure (e.g., Puijalon et al., 2008) of the shore zone biota. Consequently, there are very pronounced differences in ecological structure and function between low- and high-energy shore zones (cf. Figs. 12, 13). Many of the most important human effects on shore zone ecosystems are a result of changes to the energy regime.

Structure

“Structure” includes a wide range of attributes of the shore zone that affect ecological functioning, including the grain size of the soil or sediment, the types of materials that constitute

the soil or sediment, the surface topography or roughness of the shore zone at various scales, the slope of the shore zone, and the plan view shape of the shoreline. Grain size affects the permeability (and therefore water movement and redox potential), water-holding capacity, internal surface area (and therefore exchange capacity), cohesion, and stability of soils and sediments, and so has large, pervasive effects on biological distributions and biogeochemical processes. Given the same grain size distribution, different materials produce different ecological effects. For instance, materials with different specific gravities differ in their mobility and susceptibility to disturbance, and materials of different chemical composition will differ in their fertility to support plant growth. Of course, different materials weather differently as well, so that they produce different grain size distributions even when exposed to the same environmental settings. Surface topography determines the availability of micro- and mesohabitats in the shore zone, some of which (e.g., crevices, supralittoral pools) are hot spots for biodiversity and biogeochemical processing (e.g., Pieczyńska, 1972; Chapman and Bulleri, 2003; Le Hir and Hily, 2005). A high diversity of micro- and mesohabitats encourages high biodiversity (Figs. 3, 4) and close coupling of biogeochemical cycling (such as nitrification-denitrification in adjacent oxic and anoxic microhabitats). Topographic roughness also increases retention of organic matter and other materials (Fig. 15). The slope of the shore zone affects its ability to dissipate or reflect wave energy (Fig. 12) (and therefore the frequency and intensity of disturbance), the area of the shore zone (Fig. 8), the ability of the shore zone to retain wrack and wood, and the relationship between fluctuations in water level and area inundated. The plan view of the shoreline has effects that are analogous to topographic roughness, and also determines the provision of micro- and mesohabitats and the retention of organic matter and other materials. Consequently, the structure of the shore zone has large effects on its ecological

functioning. Human activities such as dredging, channelization, filling, grading, and shoreline armoring have had large effects on shore zone structure, and therefore shore zone ecology.

Hydrologic regime

By “hydrologic regime”, we mean the temporal pattern of water-level fluctuations along a shoreline. Shoreline hydrology could be described in several ways. Perhaps the simplest would be a plot of water levels over time (Fig. 17). More useful in comparing two or more shorelines, or in assessing the effect of human-induced changes to hydrology, would be a plot giving the amplitude of water-level fluctuations at various frequencies (waves, tides, daily changes, seasonal changes, etc.). Frequency-amplitude plots like those of Sabo and Post (2008) could be applied to shore zone water level data to allow for easy comparison across sites or time (Fig. 17). However, even this detailed plot lacks important information about the hydrologic regime; in particular, the timing of water-level fluctuations. Thus, for some applications, it will be useful to take into account fluctuations at certain, critical times of the year, or to look specifically for shifts in timing of key events. The literature on hydrologic alteration in stream flows (Richter et al., 1996; Olden and Poff, 2003) may be a useful model for more detailed analyses of shoreline hydrology.

Hydrology has large and pervasive effects on the functioning of shore zone ecosystems (Wantzen et al., 2008). Obviously, the water level determines the precise location of the shoreline, with everything that implies for energy dissipation, sediment dynamics, biogeochemical processes, and the location and quality of various microhabitats along the shore. Bodies of water in which the water level has been artificially stabilized can lose the rich array of ephemeral habitats along their margins (Robinson et al., 2002). These habitats often are sites of high biogeochemical processing (Fig. 18; Pieczyńska, 1972) and biodiversity.

Gradual long-term rises in water level frequently lead to erosion along the shoreline, whereas long-term falls in water level often lead to sediment deposition in the shore zone (e.g., Lorang et al., 1993; Lavalle and Lakhani, 2000). Raising or lowering water levels quickly may greatly increase erosion, as soils and sediments that were not previously exposed to currents, wave action, and ice are now subjected to increased physical forces (e.g., Lorang et al., 1993). This erosion may be exacerbated if the new hydrologic regime discourages colonization by vegetation (Walker et al. 1994), which can stabilize soils and sediments, as in the case in flood-control or hydropower reservoirs.

The hydrologic regime also strongly influences biogeochemical processes in the shore zone. Most importantly, oxygen diffusion is orders of magnitude slower in water than in unsaturated soils, and leaching is much higher in the water than in soils. Consequently, reducing conditions are likely to occur in underwater sediments or saturated soils, leading to increased availability of soluble phosphorus, a predominance of ammonium over nitrate, and increased concentrations of the reduced form of metals such as ferrous iron and manganous manganese, and anaerobic metabolism. The alternation or close physical juxtaposition of oxidizing and reducing conditions can lead to coupling of aerobic and anaerobic biogeochemical processes, and rapid and efficient biogeochemical cycling (Baldwin and Mitchell, 2000). Leaching is partly responsible for the more rapid disappearance of organic matter underwater than on nearby terrestrial soils (Langhans and Tockner, 2006), and may be an important source of DOC to rivers and lakes. Thoms (2003) suggested that cutting linkages between a regulated river and its floodplain could reduce DOC inputs to the river. The alternation of wet and dry periods along the shore zone can speed the decay of organic matter, especially in standing waters where the supply of oxygen to underwater sediments may limit decomposition (Battle and Golladay, 2001;

Langhans and Tockner, 2006). Indeed, it has been suggested that the “moving littoral” of rivers with large, predictable water-level fluctuations is responsible for the high biodiversity and productivity of these ecosystems (Junk et al., 1989; Bayley, 1995; Hamilton et al., 1995).

The hydrologic regime is therefore one of the most important determinants of the ecological character of the shore zone. Humans have altered the hydrologic regimes of many shore zones, either by increasing fluctuations in water levels (flood-control or hydropower reservoirs), stabilizing water levels (lakes used for recreation), or changing the timing of water-level fluctuations (Walker et al., 1994; Hill et al., 1998; Wantzen et al., 2008). These human-induced changes can have large ecological effects on nearly all aspects of the shore zone ecosystem, and so are regarded as one of the largest current threats to the shore zone and its inhabitants (e.g., Schmieder, 2004; Winfield, 2004).

Nutrients

Nutrients often control the quantity and quality of biological production in the shore zone. In natural shore zones, nutrient inputs are controlled largely by the geological structure of the shore zone and its surroundings, but modern shore zones often are dominated by human inputs from sewage, urban and agricultural runoff, and atmospheric deposition. Even small changes in the inputs of phosphorus and nitrogen can affect the species composition and productivity of macrophytes and algae (e.g., Bertness et al., 2002; Hecky et al., 2004; Boers and Zedler, 2008; Rosenberger et al., 2008).

Biota

Although the biota often is considered to be a variable that depends on the character of the shore zone, it also helps to determine the character of the shore zone, and is not completely dependent on other variables. The biota provides structural roughness that dissipates energy and

retains organic matter, stabilizes sediments against erosion, provides materials (woody debris, wrack, shells) that structure the shore zone, produces and decomposes organic matter, carries oxygen into anoxic sediments and reduced substances into the oxic zone (e.g., Dacey, 1981; Wigand et al., 1997; Wang et al., 2001), and cycles nutrients. Biota-biota interactions are among the most important determinants of biodiversity. Thus, the composition of the biota has broad and deep effects on the character of shore zone ecosystems and the ecological services that they provide (Jenkins et al., 2008).

Because of dispersal limitations, shore zones that are geographically distant from one another typically support different biotas, even if local environmental conditions are similar. As a result, it is impossible to precisely predict the shore zone biota solely from local environmental conditions.

The importance of these dispersal limitations and the role of the biota in the functioning of shore zone ecosystems is demonstrated by the large number of alien species that humans have introduced into shore zones and the large ecological changes that have followed these invasions. If biogeographic barriers were unimportant, species would have already occurred in all suitable sites, and human activities would be unable to expand their ranges; this is clearly not the case. Likewise, if the biota were unimportant to shore zone functioning, then species invasions wouldn't cause any changes in ecological functions or services. As will be discussed below, this also is untrue. For all of these reasons, it seems necessary to include the biota as one of the master variables that determines the character of shore zone ecosystems.

Climate

Climate exerts its influence on shore zone ecosystems in large part by acting through one of the other four controlling factors, and so it might not be necessary to include it as a separate

controlling factor. For instance, climate has a strong influence on the hydrologic regime and the biota of the shore zone, so climatic effects are partly accounted for when we consider hydrologic regime and biota. Nevertheless, some climatic influences on shore zone ecosystems are not expressed through hydrology or the biota. Ice rafting and ice-push affect shore zone morphology, transport sediment (Dionne, 1993), and disturb the biota (e.g., Begin and Payette, 1991); the occurrence and severity of these effects depends on climate. Likewise, climate sets the length of the growing season and metabolic rates, and so can affect the functioning of shore zones independent of the composition of the biota. Climate will affect the rate at which coarse woody debris enters the shore zone via windthrow. As a result, although climate works partly through hydrology and the biota, its influence is not expressed entirely through these other factors, and it seems useful to retain it as an independent factor determining the character of shore zone ecosystems. Human-induced climate change probably did not have large effects on shore zone ecosystems in the past, but is likely to be an important factor in the next few decades, particularly as it stimulates new human modifications of shore zones.

Human impacts on the shore zone

Human activities have profoundly affected shore zone ecosystems and threaten the ability of these ecosystems to provide valued ecological services (Brown and McLachlan, 2002; Thompson et al., 2002; Tockner and Stanford, 2002; Ostendorp et al., 2004; Airoldi and Beck, 2007). We briefly review the most important of these impacts.

Compression and stabilization of the shore zone

Despite the many ecological services that they provide, shore zones often have been seen as waste lands, to be improved or replaced. Consequently, humans have dredged shallow waters to make them useful for navigation, and filled terrestrial parts of the shore zone, built levees, and

regulated river flows to keep flood waters away from the landward portion of the shore zone. These activities have stabilized the location of the shoreline and reduced the width or area of the shore zone. These effects can be very large (Fig. 20; Hein et al., 2005; Miller et al., 2006); Tockner and Stanford (2002) reported that the ratio of the area inundated during high water to the area inundated at low water fell from 16.8 to 4.9 following human-induced modifications to the Mississippi River. Although the overall ecological consequences of the compression and stabilization of the shore zone have not been estimated, they must be very large. Compression of the shore zone of course reduces its area, but also probably reduces some of the habitats and the heterogeneity of the shore zone, both of which should have large effects on biodiversity and biogeochemical processes.

Fixing the location of the shoreline can also lead to the problem of “coastal squeeze”, in which the shore zone narrows further if water levels change in the future. This effect has been recognized chiefly as a threat to marine shore zones, which will be narrowed or eliminated as shore zones are squeezed between a rising sea and fixed coastal defenses (such as levees) (Airoldi and Beck, 2005; Winn et al., 2005; Fujii and Raffaelli, 2008). Substantial coastal squeeze has already occurred along some marine shores as a result of rising sea levels (NRC, 2007). An analogous squeeze can occur in fresh waters as a result of either rising (squeeze between a landward levee and an advancing shoreline) or falling (squeeze between a dredged navigation channel and a receding shoreline) water levels. The more we try to narrow the shore zone and fix the location of the shoreline, the more likely that coastal squeeze will threaten shore zone ecosystems.

Changes to the hydrological regime

Humans have changed the hydrologic regime of many freshwater shore zones through water diversions, dams that regulate water flow (e.g., for flood-control or peaking hydropower), or water-control structures (low outlet dams on many lakes). Because of the importance of hydrologic regime as a master variable that controls many aspects of shore-zone ecosystem functioning (Fig. 5), these changes in hydrologic regime have led to large changes in shore zone ecology. The effects of changing hydrologic regime on the ecology of freshwater shore zones probably will increase in the 21st century as human demands for fresh water rise and as climate change affects hydrology.

Shortening and simplification of the shoreline

By eliminating small irregularities in the shoreline (bays, peninsulas), straightening channels, and removing islands and side channels, humans have greatly shortened the length of many freshwater shorelines (Fig. 19), simplified their structure in map view, and reduced long-shore habitat heterogeneity. Dramatic changes have been documented in many large rivers (e.g., Sedell and Froggatt, 1984; Gurnell and Petts, 2002; Tockner and Stanford, 2002; Jungwirth et al., 2005; Scholten et al., 2005; Miller et al., 2006). Presumably, similar but smaller changes have occurred along lake shorelines. Shortening and simplifying the shoreline probably has strong effects on the ecology of the shore zone because it reduces the area of the highly interactive land-water interface, eliminates sites of long hydraulic retention (backwaters), and reduces the habitat heterogeneity of the shore zone. Changes as large as those shown in Fig. 20 must have had very large ecological effects, even though these effects seem not to have been quantified. Some restoration projects are specifically designed to add back some of this shoreline complexity to enhance biodiversity (Hein et al., 2004; Chovanec et al., 2005).

Hardening of the shoreline

Humans have hardened many shorelines to protect them against erosion. Hardening may involve the construction of seawalls or revetments of concrete, stone, or steel; wooden bulkheads; armoring the shore with riprap or dressed stone, or other devices. Such shoreline modification has been extensive in many parts of the developed world, to the extent that artificially hardened shores dominate many shorelines. For instance, ~50% of the shoreline of Sydney Harbor and the freshwater tidal Hudson River, and 80% of the shoreline of the Lake of Geneva is artificial (Bänziger, 1995; Moreira et al., 2006; HRNERR, unpublished); most of this change involved shoreline hardening. Artificially hardened shorelines can differ dramatically from their natural antecedents in many ways, depending on their construction. Most artificially hardened shorelines reflect more energy than natural shorelines, which may increase sediment resuspension and scour the nearshore zone, thereby altering the biota and biogeochemistry of this region. In most cases, the hardened shoreline provides a vastly different habitat than the natural shoreline it replaced, in terms of slope, particle size, nutrient content, organic content, and physical complexity. It usually can be expected to produce a largely novel shoreline biota (except in cases where a stone or bedrock shore is replaced by an artificial hard shore, but even in such cases the biota on the artificial shoreline often is distinctive – Chapman, 2003; Bullieri et al., 2005; Moschella et al., 2005). By design, hardened shores are more stable than the natural shores that they replace; because disturbance plays an important role in the functioning of shore zone ecosystems, this stability also will change the shore zone biota and biogeochemistry. Further, it seems likely that hardened shores generally impede exchanges between the aquatic and terrestrial parts of the shore zone (e.g., groundwater flow, migration of aquatic biota such as nesting turtles onto the shore, use of the water by terrestrial biota). Thus, the artificial hardening

of shorelines probably has profoundly influenced shore zone ecosystems, although this has not been well quantified.

Tidying of the shore zone

Humans tidy shore zones, especially those used for recreation or housing. This tidying may involve removal of wrack, woody debris, or terrestrial or aquatic vegetation. It is well established that wrack, woody debris, and vegetation all play important ecological roles in the shore zone (see above), so it is unsurprising that shore zones that have been tidied for recreation or housing have a different ecological structure and function than natural shore zones (Fig. 3; Christensen et al., 1996; Malm et al., 2004).

Increasing inputs of physical energy

High inputs of physical energy endanger many human uses of the shore zone. It is therefore ironic that several common human activities tend to increase inputs of energy onto the shore. For example, we often build shorelines out into higher energy settings away from the existing shoreline. Nearshore dredging removes shallow-water sediments and vegetation that could have dissipated wave energy (cf. Miles et al., 2001; Miles and Russell, 2004). Seawall construction deepens the region in front of the seawall, again removing sediments and vegetation that could have absorbed wave energy. Seawalls also reflect wave energy to a much greater degree than most natural shores. Of course, wakes from recreational boating and commercial navigation may significantly increase energy inputs to the shore (e.g., Bauer et al., 2002; Hofmann et al., 2008). As a result of all of these actions, we turn shorelines that did not need protection against erosion into shorelines that need engineering protection from increased wave energy.

Increasing physical energy in the shore zone also has ecological consequences.

Vegetation will be uprooted or prevented from establishing, and the animals that depend on this vegetation will decline. If it is not protected, erosion of the shoreline will disrupt the terrestrial side of the shore zone and increase turbidity on the aquatic side of the shore zone, further endangering submerged vegetation and the fauna that it supports. High inputs of energy may prevent animals from maintaining desired positions in the water or even wash them onto the shore (Adams et al., 1999; Wolter and Arlinghaus, 2003).

Pollution

Shore zones are subject to all of the kinds of pollution that other ecosystems receive, but also are particularly subject to pollution by materials that float on the water. This includes plastics, which are ubiquitous and abundant in many marine shore zones (e.g., Derraik, 2002; Thompson et al., 2004), as well as oil and other hydrophobic liquids. Plastics are unsightly, and kill marine animals by entangling them or blocking their digestive tracts (Derraik, 2002). Microscopic plastic particles, such as those used in “scrubbers” (plastic particles <0.5 mm, used in hand cleaners, cosmetics, and cleaning media) or resulting from the fragmentation of larger items or the degradation of some “biodegradable” plastics, are abundant in marine shore zones (Derraik, 2002; Thompson et al., 2004). These small particles can be ingested by many kinds of animals, possibly moving PCBs and other contaminants into the food web (Derraik, 2002). Plastic contamination of freshwater shore zones seems not to have received much study. The amount and kind of plastics should be very variable across freshwater shore zones, depending upon the activities in the catchment. Of course, oils and other hydrophobic liquids end up in the shore zone, where they can kill animals and contaminate the biota (Thompson et al., 2002).

Recreational activities

Recreation and tourism are now regarded as leading threats to shore zones in both marine and fresh waters (Thompson et al., 2002; Schmieder, 2004). Visitors attracted to popular sites in the shore zone may cause substantial ecological damage (e.g., Povey and Keough, 1991; Brosnan and Crumrine, 1994; Eckrich and Holmquist, 2000; Pinn and Rodgers, 2005; Davenport and Davenport, 2006; Rossi et al., 2007). Trampling damages vegetation; kills or dislodges plants and animals from the rocky intertidal, shifting community structure from branching algae to encrusting or turf species; and kills subtidal seagrasses and bivalves. Damage to subtidal communities may be more severe in soft muds than in firm sands (Eckrich and Holmquist, 2000). Hikers, swimmers, and bird-watchers sometimes (but not always) reduce populations of birds in the shore zone (van der Zande and Vos, 1984; Cardoni et al., 2008; Trulio and Sokale, 2008). Likewise, off-road vehicles kill beach vegetation, crush animals (Schlacher et al., 2008), and compact sediments. Some of these damaged communities recover within months after trampling or vehicle traffic is stopped, but in other cases recovery may take several years. Damage from trampling and vehicles is regarded as a serious and growing problem along marine coasts, and has led to regulation and public education. Little attention has been paid to how trampling or vehicles might affect biogeochemical functioning in the shore zone. Likewise, almost all of the research on the impacts of trampling or vehicles has been conducted along marine shores. While it seems likely that many of the same impacts occur along freshwater shores (Schmieder, 2004), some of the impacts that have been described pertain specifically to the distinctive marine intertidal biota, which has no analogue in fresh water, and may not occur along freshwater shores.

Wakes from recreational boats (as well as commercial ships) cause shoreline erosion and increase nearshore turbidity (Asplund, 2000; Bauer et al., 2002; Hofmann et al., 2008). Further,

turbulence and wakes from recreational boats and ferries damage aquatic vegetation (Ali et al., 1999; Asplund, 2000; Doyle, 2001; Eriksson et al., 2004; Sandström et al., 2005) and thereby reduce populations of fish that depend on this vegetation (Sandström et al., 2005), and alter macroinvertebrate communities (Bishop, 2007). In very shallow water, propeller scarring may be important (e.g., Asplund, 2000; Burfeind and Stunz, 2006; Hammerstrom et al., 2007). Recreational watercraft (small outboards and personal watercraft) may disturb animals using the shore zone (Asplund, 2000; Rodgers and Schwikert, 2002; Stolen, 2003) and produce pollution as well (Lico, 2004). Emission controls on the small engines that power these craft often are poor (Davenport and Davenport, 2006), and the large amounts of unburned hydrocarbons and PAHs released by these engines may contaminate shore zone sediments and biota. In lakes and rivers that are heavily used by recreational boaters, these combined impacts may be substantial, although they seem not often to have been assessed.

Extraction of resources from the shore zone

Humans have extracted resources from freshwater shore zones for thousands of years. Some of the most important of these resources are sand and gravel, wrack, driftwood, various kinds of plants (timber, reeds, edible plants), shellfishes, fishes, turtles, waterfowl, wading birds (for plumes), and fur-bearing mammals. Harvest rates have been very large in some times and places, and probably exceeded the threshold of sustainability. Many of these extractive industries have dwindled or disappeared in Europe and North America, but continue in other parts of the world. The individual or combined effects of these extractive uses on ecological functioning of freshwater shore zones seem not to have been well studied.

Alien species

Introductions of alien species (species that are deliberately or accidentally moved out of their native ranges by human actions) have large ecological and economic effects in ecosystems around the world (e.g., Lodge et al., 2006; Lockwood et al., 2007), and freshwater shore zones now support many alien species with strong impacts (e.g., zebra mussels in North America, muskrats in Europe, tamarisk in the American West, common carp in North America and Australia, invasive clones of *Phragmites australis* in North America). Some ecologists (Pyšek and Prach, 1993; Planty-Tabacchi et al., 1996; Hill et al., 1998; Bunn and Arthington, 2002; Airoldi and Beck, 2007) have suggested that shore zones are particularly prone to invasion because of high rates of natural and human-caused disturbance, close contact between humans and shore zones, and effectiveness of the shore zone as a dispersal corridor for alien species. For instance, Planty-Tabacchi et al. (1996) found that 23-30% of the plant species in riparian zones in France and the Pacific Northwest were aliens, and alien species constituted 56% of species and 40% of cover in marine shore zones in Rhode Island (Bruno et al., 2004).

Regardless of whether shore zones are more susceptible than other types of ecosystems to invasion or impacts of alien species, it is clear that shore zones have been strongly affected by alien species, and that these impacts are likely to intensify in the future as new aliens establish themselves, and established aliens spread throughout shore zones. Eradication or management of established alien species can be difficult or impossible (Rejmanek et al., 2005; Lodge et al., 2006), so some (e.g., Winfield, 2004) have argued that it is important to prevent aliens from getting established in the first place.

Climate change

Humans have now begun to affect the climate, and these effects are projected to accelerate over the next few decades (IPCC, 2007). Anthropogenic climate change will affect

shore zone ecosystems in several ways. Sea-level rise, projected to at least 18 cm and perhaps much more in the 21st century (IPCC, 2007) will affect marine shore zones as well as coastal or tidal freshwater shore zones. Sea-level rise should raise mean water levels, increase the frequency of floods, increase salinity, and increase sedimentation in these shore zones. Rising air temperatures should accelerate rates of biogeochemical processes in many freshwater shore zones. Other important effects on freshwater shore zones are likely to occur, but will be more idiosyncratic and difficult to predict. Changes in temperature and precipitation will cause water levels to rise or fall, and some have projected that extreme events (droughts and floods) will become more frequent and more severe. Both changes in climate and subsequent changes in hydrology will probably have strong effects on the composition, distribution, and abundance of the shore zone biota (e.g., Hijmans and Graham, 2006), but the details of such changes and the changes that they will in turn cause to shore zone morphology and biogeochemistry are unknown. Humans will almost certainly respond to climate change by intensifying management and engineering of shore zones to protect property. It is possible that the effects of human engineering responses to climate change (e.g., coastal squeeze, shoreline hardening, levees, hydrological modifications) will cause greater ecological changes to freshwater shore zones than the direct effects of climate change itself.

Building in the shore zone

The intensification of human development in the shore zone will have a number of important ecological effects, in addition to effects addressed above. The increase in impervious surfaces will tend to increase local flooding and alter pathways of groundwater flow in the shore zone, with consequent effects on biogeochemical processing and habitat quality. Human activities will provide a local source of toxins, including pesticides, petroleum products,

pharmaceuticals, and many other compounds to developed shore zones. Rates of introductions of alien species to the shore zone will increase as these species are used in landscaping, released from captivity, or are transported in commerce. The increased artificial lighting associated with human settlements and buildings will affect the shore zone biota, perhaps leading to nuisance accumulations of emerging aquatic insects (Rich and Longcore, 2005). Structures built along dispersal corridors in the shore zone may kill birds and other migrating animals.

Engineering shore zones to enhance ecological services

Humans have long engineered shore zones for specific purposes (e.g., to prevent erosion or flooding, to enhance crop production). As the ecological services provided by shore zones have received greater visibility, it has been natural to ask whether shore zones could be engineered to increase the ecological services that they provide while at the same time satisfying human needs for flood control, etc. The ecological engineering of shore zones is still a young field, and has been focused mainly on marine shores (e.g., Airolidi et al., 2005; Martin et al., 2005; National Research Council, 2007; Chapman and Blockley, 2009). Marine ecologists have made suggestions about which design features of engineered structures will affect their ecological value (Table 1), as well as principles that might be used to manage shore zones taking ecological services into account (Table 2). There have been a few attempts to assess the ecological value of different kinds of structures in freshwater shore zones as well (Fladung, 2002; Scholten, 2002; Chovanec et al., 2005; Kleinwächtler et al., 2005; Scholten et al., 2005).

There would seem to be considerable potential to incorporate ecological considerations into the design of engineered structures in freshwater shore zones (cf. Engel and Pederson, 1998). It is far too early to give firm recommendations about how best to design such structures to maximize desired ecological services, but the results reviewed above suggest some possible

directions. For instance, structures that are rough or irregular in topography or plan view are likely to support higher biodiversity and biogeochemical function than perfectly smooth structures. Engineered structures that have slopes very different from the natural shore zones that they replace are likely to induce large changes in ecological function. Very steep structures not only reduce the area of the shore zone (Fig. 8), but also generally increase reflection of wave energy, which usually is undesirable. Structures that block the movement of organisms, water, or other materials, whether across the shore zone (impermeable vertical seawalls) or along the shore zone, are likely to be undesirable from an ecological point of view. Hydrological regimes that deviate greatly from the natural regime, either in magnitude or timing of water-level fluctuations, can be expected to degrade ecological functioning (cf. Poff et al., 1997; Hill et al., 1998). Likewise, structures that reduce the ability of the shore zone to produce or retain organic matter, including woody debris, may have undesirable consequences. In addition, as Doyle et al. (2008) pointed out, replacement, repair, or removal of aging infrastructure in shore zones may offer promising opportunities to improve the ecological functioning of engineered shore zones.

One concern that may arise as shore zones are deliberately engineered to provide ecological services is whether such artificially provided ecological services are as valuable as those provided by a natural shore zone (Angermeier, 1994). For instance, high biodiversity is considered to be a desirable goal of ecosystem management. However, novel and highly artificial substrata introduced into a shore zone often support species that occur nowhere else in the system, including on natural substrata (Fig. 21). Are the species that occur on these artificial substrata valuable, or should they be dismissed as “artificial biodiversity” of little value (Angermeier, 1994)? Likewise, would completely artificial structures that captured floating organic matter be considered as valuable as woody debris, from the viewpoint of organic matter

retention and nutrient cycling? Such issues will need to be resolved by stakeholders and managers before engineering projects to enhance ecological services are undertaken.

Values of different kinds of shore zones

Individual ecological services

From the viewpoint of shore zone management, it would be useful to be able to estimate the ability of a particular shore zone to provide various ecological services (e.g., primary production, nitrate removal, habitat for a sport fish, etc.). This might be done by classifying shore zones into a manageable number of classes (e.g., dissipative sandy beaches, vertical seawalls, etc.) and constructing a table that gives the typical amount of each ecological services that is provided by each kind of shore zone (Table 3), or by treating shore zones as continuous and constructing a multivariate equation of the form

$$v_i = f(C_1, C_2, \dots, C_n)$$

where v_i is the amount of the i th ecological service (e.g., habitat provision for a particular sport fish) and the C are the important characteristics of the shore zone (e.g., slope, complexity, hydrology, etc.). At present, neither of these approaches is feasible for freshwater shore zones because of inadequate information. Many ecological services and types of shore zones have been very poorly studied, and the information we do have has been insufficiently organized and analyzed. Marine ecologists have attempted to assess the ecological services that different kinds of shore zones provide (Table 3), but these approaches still are rough, even for marine shores.

Another difficulty in estimating the ability of a shore zone to provide a particular ecological service, apart from the problem of insufficient information, is that the value of an individual bit of the shore zone depends on the context into which it is placed (Airoldi et al., 2005; Martin et al., 2005; Toft et al., 2007). The overall composition of habitats within the

larger system and the strength of linkages among these habitats will help to determine the value of a unit of shore zone habitat. Thus, a hectare of rocky shoreline may provide far more value in terms of system-wide ecological services when it occurs in a predominately muddy estuary than when it occurs in an entirely rocky one. For these and other reasons, the ability of a unit of habitat to provide an ecological service often will be a nonlinear function of the amount of that habitat (cf. Barbier et al., 2008), so it will be impossible to assign a unique per hectare value to a habitat type. This is a problem of special significance when considering cumulative losses of habitat or the marginal value of restoring habitat. For the many species or ecological processes that depend on more than one habitat (e.g., Irlandi and Crawford, 1997; Amoros and Bornette, 2002; Robinson et al., 2002; Scholten, 2002; Winfield, 2004), the details of the spatial structure of the system will modify the ability of a unit of habitat to provide ecological services. Consequently, it seems unlikely that a general approach like that shown in Table 3 will ever be able to precisely estimate the value of a particular piece of the shore zone. Instead, if a precise estimate of value is needed, a special study will have to be made of each shore zone and the setting into which it is placed.

It is certainly too early to make a comprehensive assessment of the ecological values provided by different kinds of freshwater shore zones, when many of ecological functions and shore zone types have not been studied. Nevertheless, we have made a very tentative assessment of the ability of different kinds of freshwater shore zones to provide ecological services (Table 4). This assessment should be taken as hypothetical, and tested before it is applied.

Integrating multiple ecological services

Because shore zones provide so many kinds of ecological and economic services, it would be useful to be able to produce a single index of the overall ecological value of a shore

zone to aid in prioritizing sites for conservation or management, assessing alternative plans for management or rehabilitation, or other purposes. There have been several attempts to produce such indices (e.g., Ostendorp, 2004; Hostmann et al., 2005; Ludwig and Iannuzzi, 2006; Reichert et al., 2007; Barbier, et al. 2008), but all suffer from more or less serious difficulties.

Broadly speaking, such indices combine information about provision of various ecological services by a shore zone with human valuation of those services. The first difficulty with such an approach is in estimating all of the ecological services provided by a particular bit of the shore zone. As we have seen, the services that shore zones provide are numerous and highly varied (biodiversity of various taxa, biogeochemical transformations of various substances, recreation, etc.) and have probably never been adequately estimated for any specific shore zone. Consequently, attempts to consider multiple ecological services (e.g., Ludwig and Iannuzzi, 2006) typically have been based on a limited range of services.

Second, it can be tricky to convert from ecological services, however estimated, and human valuation of those services. One approach is to consider the overall value of a shore zone to be the weighted sum of the values of all of the ecological services that it provides. Thus,

$$V(S_j) = \sum_i w_i v_i(a_{ij})$$

where $V(S_j)$ is the overall value of the j th shore zone, w_i is the weight (relative value) that stakeholders place on the i th ecological service relative to other services provided by that shore zone, and $v_i(a_{ij})$ is the value function for the i th ecological service (i.e., the relative value of different amounts a_{ij} of that particular service). In theory, this approach (which follows Hostmann et al., 2005) allows one to calculate the relative value of different shore zones, different rehabilitation proposals, etc. In fact, this approach can be difficult to apply in practice. In addition to the difficulties just discussed in estimating the a_{ij} , it is necessary to estimate the

value functions for each ecological service as well as the relative weights of the different services. Value functions and weights often will vary greatly across stakeholders (bird biodiversity will be highly valued by some users of the shore zone but not by others) and are assumed not to interact (i.e., the value of a shore zone for recreational angling is assumed not to depend on the aesthetic appeal of the site). Hostmann et al. (2005) dealt with the former problem by estimating value functions and weights independently for different stakeholder groups (recreationalists, farmers, government officials). This reasonable solution then leads to another problem – how to resolve the inevitable differences in $V(S_j)$ estimated by the different stakeholder groups. Again, Hostmann et al. (2005) discussed the merits of different ways to resolve such conflicts.

It would be very helpful to have practical, reliable approaches to estimate or at least rank the overall value of different kinds of shore zones to guide planning, protection, management, and rehabilitation. Such approaches will need to be based on good estimates of the ecological services provided by different shore zones (including a broad range of services), careful consideration of the values that different stakeholders place on these services, and some system of conflict resolution.

Conclusions

Enough is known about freshwater shore zones and the ecological services that they provide to improve the protection, management, and rehabilitation of these important ecosystems. Nevertheless, there are prominent gaps in our knowledge. We mention just three of these gaps, and highlight an opportunity to fill these gaps.

First, much of our knowledge is too general to be applied to the management of specific sites and services. Management questions often are very specific (will restoring 0.6 ha of marsh

at site X on river Y increase the population size or growth rate of fish species Z?). Few of our theories about the workings of shore zones are so powerful and free of context-dependence that they can provide adequate answers to such specific questions. Instead, we should expect to have to conduct site- and species-specific studies if we really want precise answers to many management questions. Perhaps it will eventually be possible to build general empirical models that provide sufficiently precise answers, but at present it seems likely that precise questions will require site-specific analyses.

Second, because the ecology of marine shore zones is so much better understood than that of freshwater shore zones, there will be a natural tendency to apply ideas and models developed for marine shore zones to freshwater shore zones. There are both significant similarities and significant differences between marine and freshwater shore zones. Which marine paradigms can be safely applied to freshwater shore zones, which must be modified, and which should be rejected? For instance, can interannual fluctuations in water level be substituted for relative tidal range in models of shore zone morphology and ecology? We suggest that freshwater ecologists and managers actively seek out and use ideas from marine ecology, but insist that these ideas be tested on freshwater shore zones before they are widely applied.

Third, almost all studies of shore zones, whether marine or freshwater, have focused on individual bits of the shore zone, rather than on a larger system (a biological population, a coastal habitat complex, etc.). Yet it is the larger system that is most often the target of our management efforts, and which is vulnerable to the cumulative effects of changes in many bits of the shore zone or the effects of a change that are propagated to distant parts of the system by physical or biological vectors (currents, migrations). This is a hard problem that applies to many parts of ecology (Lovett et al., 2005), and appears to have no easy solutions. The fact that the problem is

difficult does not excuse us from addressing it. Shore zone ecologists will need to develop ways to understand how changes in individual bits of the shore zone alter the larger system of interest.

People are conducting countless experiments on shore zones every day, in the name of management or development activities. These activities offer powerful opportunities for rapid scientific progress. If we are serious about learning enough about shore zone ecosystems to manage them intelligently, then we need to take better advantage of these opportunities. When shore zones are developed, coastal defenses are built, or habitats are restored, we should treat them more like scientific experiments. We should insist that good pre- and post-project data on ecological functions are collected, and look for opportunities to include experimental treatments as part of routine activities in shore zones. For instance, if a revetment is built to protect a shoreline from erosion, perhaps a small section could be built of a different material or a different roughness thought to improve ecological functioning. Collecting such data more systematically could trigger a quantum advance in the understanding and management of shore zones.

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Table 1. Design features of low-crested coastal defense structures that affect their ecological functioning (modified from Airoldi et al., 2005).

Feature	Effects
Amount	If structures are numerous, they can have large-scale effects
Location	Geographic context and local habitat set local species pool, which affects ecological responses to added structure
Spatial arrangement	Distance from other artificial structures and similar natural habitats affects dispersal of species onto added structure
Height, size, and porosity	Affects local hydrodynamics and sediment dynamics, which affect ecological responses
Lifetime and structural integrity	Frequent disturbance favor opportunistic species
Material and physical complexity	Affect local distribution of biota and biogeochemical activities

Table 2. Suggested principles for the sustainable management of shore zones using low-crested coastal defense structures and other coastal defenses (modified from Airoldi et al., 2005).

Action	Comments
Clearly define management goals	Allows development of predictions of effects of added structure and evaluation of effectiveness
Consider regional context	If context is not considered carefully, undesirable downstream and cumulative effects can occur
Minimize downstream effects	Downstream effects can magnify the original problem and lead to proliferation of structures
Avoid proliferation of structures	Proliferation of structures can cause large-scale, long-term effects
Consider alternatives	Alternative solutions (including “do nothing”) may have fewer undesirable effects, and should be considered early in planning process
Monitor effects	Sound long-term monitoring allows future management to be improved
Preserve native assemblages and processes	
Minimize hydrodynamic disruption	Reduces ecological changes
Minimize ongoing maintenance	Allows development of mature ecological assemblages

Manage human access and use	Severe human disturbance can negatively affect zoobenthos and plants
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Table 3. Example of a tentative assessment of the amount of various ecosystem services provided by different kinds of marine shore lines (modified from National Research Council, 2007). Higher numbers indicate greater provision of services.

	Sandy beaches	Sand dunes	Mudflats	Marshes and mangroves	Seagrasses and macroalgae	Bluffs	Bulkheads and seawalls	Revetments	Groins	Breakwaters and sills	Planted marshes /mangroves
Fish habitat	1	1	2	3	3	1	1	2	1	3	3
Mollusk habitat	3	1	3	3	3	1	2	2	2	2	3
Crustacean habitat	2	1	2	3	3	1	0	1	1	1	3
Turtle habitat	3	2	0	1	2	1	0	0	0	0	1
Bird habitat	2	3	3	3	1	3	0				3
Nutrient processing	2	1	2	3	3	1	1	1	1	1	3
Food production	1	1	2	3	3	2	1	1	1	1	3
Wave attenuation	2	3	1	2	2	3	1	2	2	3	2
Sediment stabilization	0	3	2	3	3	0			2	3	3
Gas regulation	1	0	1	3	3	0	0	0	0	0	3
Biodiversity	2	3	2	3	3	3	1	1	1	1	3
Recreation	3	3	1	3	3	2	2	1	2	2	3
Raw materials	3	3	1	3	3	3	1	1	1	1	3
Aesthetic value	3	3	2	3	3	3	0	0	0	0	3

Table 4. Tentative assessment of the ability of different kinds of freshwater shore zones to provide ecological services (cf. Table 3).

	Unvegetated mud flat	Unvegetated sand beach	Cobble or bedrock	Vegetated sand or mud	Marsh	Riprapped revetment	Steel or concrete seawall
Habitat for aquatic plants	0	0	+	+++	+++	+	0
Habitat for aquatic invertebrates	++	++	+++	+++	+++	++	+
Habitat for fishes	+	+	++	+++	+++	++	+
Habitat for birds	++	++	++	+++	+++	++	0
Energy dissipation	++	++	++	+++	+++	++	+
Primary production	+	+	+	+++	+++	+	0
Retention or decomposition of organic matter	++	++	++	+++	+++	++	0
Nutrient transformation	++	++	++	+++	+++	+	0
Biotic dispersal	++	++	++	+++	+++	++	+

Figure legends

Fig.1. Examples of three classifications of the shore zone, showing the diversity of approaches and defining variables. From top to bottom: Hutchinson's (1967) classification of lake zonation; Osterdorp et al.'s (2004) classification of the shore zone of lakes; McLachlan's (1983) classification of zonation along a marine sandy beach.

Fig. 2. Very rough estimates of peak wave heights offshore (solid line) and peak wave energy impinging on shorelines (dashed line) as a function of fetch. Axes are logarithmic. Based on formulas of Denny (1988), assuming that wave height = 0.05 wavelength (Wetzel, 2001).

Fig. 3. Responses of fishes to structural complexity in the shore zone; a: abundance and species richness of fishes as a function of the density of large wood (cover classes as follows: class 1 = no wood, class 2 = 0-5% cover of wood, class 3 = 5-15% cover of wood, class 4 = >15% cover of wood) in French rivers (Piégay, 2003); b: numbers of nests plus schools of young fry of three species of black bass (*Micropterus*) in Bull Shoals Reservoir along shores with and without experimentally added brush piles, from data of Vogege and Rainwater (1975); c: numbers of small fishes using simple and complex littoral habitats in Ontario lakes with and without smallmouth bass, from data of MacRae and Jackson (2001); d: reductions in density of coarse woody debris and growth rates of bluegills ($\pm 1\text{SD}$) in Wisconsin lakes with increasing human development, from Schindler et al. (2000).

Fig. 4. Plant species richness increases with structural complexity (topographic variation, measured as spatial variation in flood frequency) on floodplains in Alaska ($r^2=0.52, p<0.01$; Pollock et al., 1998).

Fig. 5. Hypothesized relationships between within- and among-year water-level fluctuations and shoreline vegetation in Nova Scotia (modified from Hill et al., 1998). The stippled area shows the floras with the highest species richness.

Fig. 6. Density of different kinds of invertebrates (+1SE) along a rocky shoreline in the freshwater tidal Hudson River, as a function of elevation (Strayer and Smith, 2000). “High” = 38 cm above mean low water level, “mid” = mean low water level, and “low” = 38 cm below mean low water level. Note the different scales along the y-axes of the different panels.

Fig. 7. Cartoon showing how some important controls on biodiversity vary with elevation along the shore zone. The horizontal line is the mean water level. This diagram is not comprehensive (i.e., many factors are omitted) and is very approximate.

Fig. 8. An example showing how the slope of the shore zone influences its width and area. In this example, the shore zone is defined as the region extending from the -2m contour to the +2m contour. Flat shore zones are very wide, whereas steep shore zones (like those typically made by humans) are very narrow. Both axes are logarithmically scaled.

Fig. 9. Characteristics of “low mixed vegetation” in the shore zone of Lake Wanaka, New Zealand, as a function of exposure (Riis and Hawes, 2003). Species richness and cover are estimated for the region between 25 cm above median water level to 1 m below median water level; sampling transects were placed where maximum vegetation cover occurred within a 50-m long section of shore.

Fig. 10. Vegetational zonation along a marine cobble beach, showing the colonization of the shore zone by forbs just landward of a *Spartina* (cordgrass) bed, which stabilizes the cobble sediments (Kennedy and Bruno, 2000).

Fig. 11. Idealized relationships between species richness of aquatic biota and degree of hydrological connectivity of various bodies of water on a riverine floodplain ranging from the main channel of a river to remote floodplain pools (redrawn from Amoros and Bornette, 2002, after Ward and Tockner 2001).

Fig. 12. Diagram to determine whether a beach is reflective, dissipative, or intermediate on the basis of breaker height (m), wave period (T, in seconds), and fall velocity (m/sec) or grain diameter (ϕ) of the beach particles (Short, 1996). Reflective beaches (for which the dimensionless fall velocity $\Omega < 1$) lie below the solid line for a given wave period, dissipative beaches ($\Omega > 6$) lie above the dashed lines for a given wave period, and intermediate beaches ($\Omega = 1-6$) lie between the two lines.

Fig. 13. Idealized relationships between beach geomorphology, ecological processes, and aquatic macroinvertebrates along sandy beaches (modified from Defeo and McLachlan, 2005). Beach types are arranged from highly reflective to highly dissipative.

Fig. 14. Effects of *Phragmites australis* on wave attenuation and bank erosion in an experimental wave tank (Coops et al., 1996). Waves approach from the right.

Fig. 15. Standing crop (upper) and daily input (lower) of wrack on beaches of different grain sizes in British Columbia. Data are medians + median absolute deviation (n=3 samples), from Orr et al. (2005).

Fig. 16. Density of coarse woody debris (pieces >5 m long and >0.3 m in diameter) along the shores of the upper Missouri River, as a function of bank type and adjoining land cover (modified from Angradi et al., 2004). The natural condition of most of this shore zone would have been alluvial and forested (the bar on the far left).

Fig. 17. The water-level regime along three shorelines: the freshwater tidal Hudson River near Poughkeepsie, NY; Lake Erie at Toledo, OH; and the Missouri River at Toston, MT. The upper panels show an entire year (calendar year 2003) the lower panels show finer-scale variation (the first week in May), and the lower panels show a spectral analysis of the long-term record (5-10 years). The hydrologic regime along the Hudson is dominated by great variation at short time-scales (a result of twice-daily tides, peaks “t” on the spectral analysis) and smaller annual cycle (peaks “a” on the spectral analysis); that of Lake Erie shows limited variation at longer time-scales, and occasional extreme water levels, presumably resulting from wind-driven seiches; and that of the Missouri River is dominated by annual spring snowmelt (peaks “a” on the spectral analysis, showing the annual peak as well as related peaks at 365/n days), with occasional stormflows through the rest of the year. Data were taken every 15 minutes (Hudson, Missouri) or 60 minutes (Erie), and therefore don’t show short-term variation in water levels from wind-driven waves and boat wakes. Data from NOAA (2008) and USGS (2009a,b).

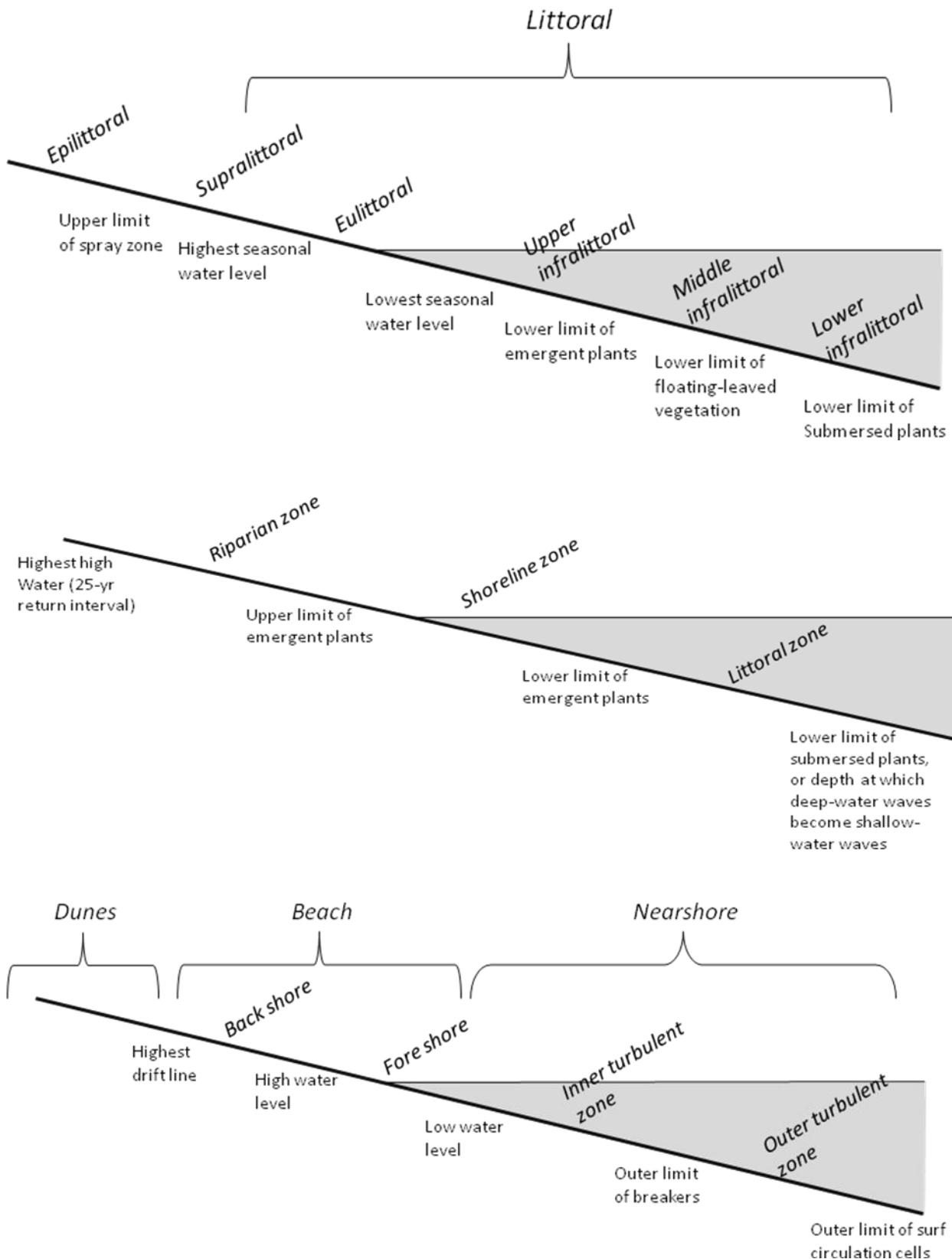
Fig. 18. Decomposition rate of two kinds of plant litter at various sites along a Polish lakeshore; the elevational gradient runs from high ground on the left to deeper water on the right (from data of Pieczyńska, 1972).

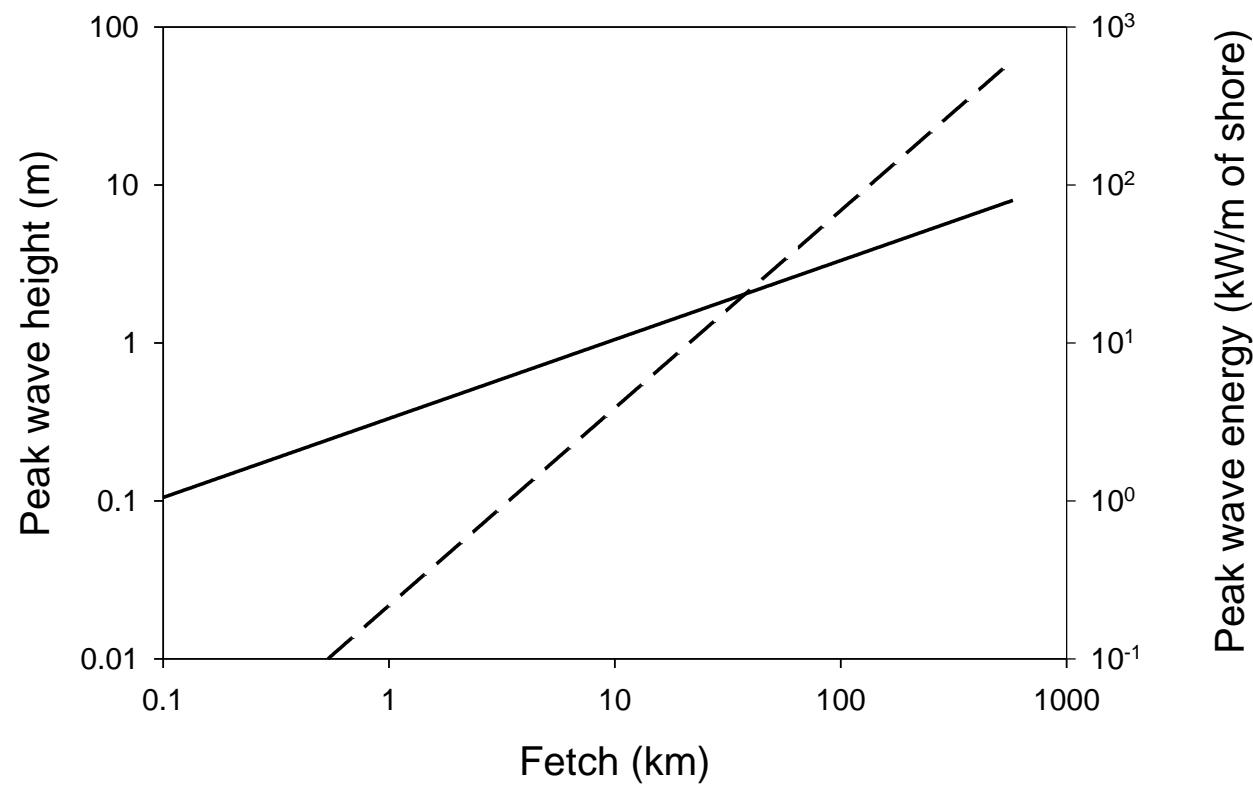
Fig. 19. Modification of the shore zone of a 5-km reach of the freshwater tidal Hudson River between 1820 (left) and 1970 (right). Red = dry land, yellow = intertidal zone (the tidal range is 1-2 m), light blue = shallow water (<1.8 m deep at low tide), dark blue = deep water (>1.8 m deep at low tide), heavy black lines = dikes or bulkheads. From Jackson et al. (2005), after Ladd, Miller, and Nieder.

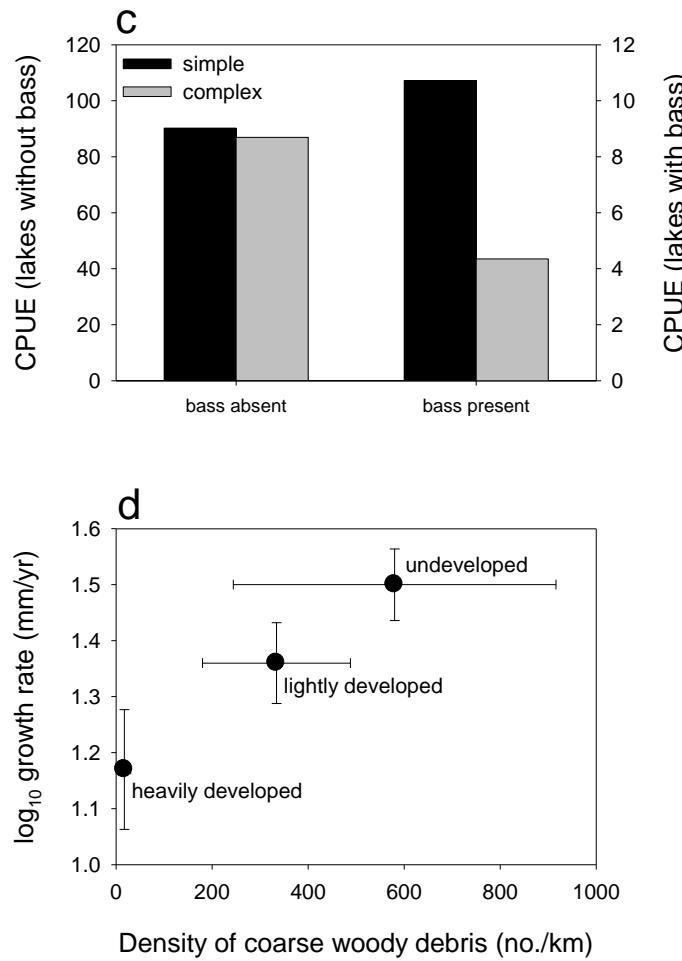
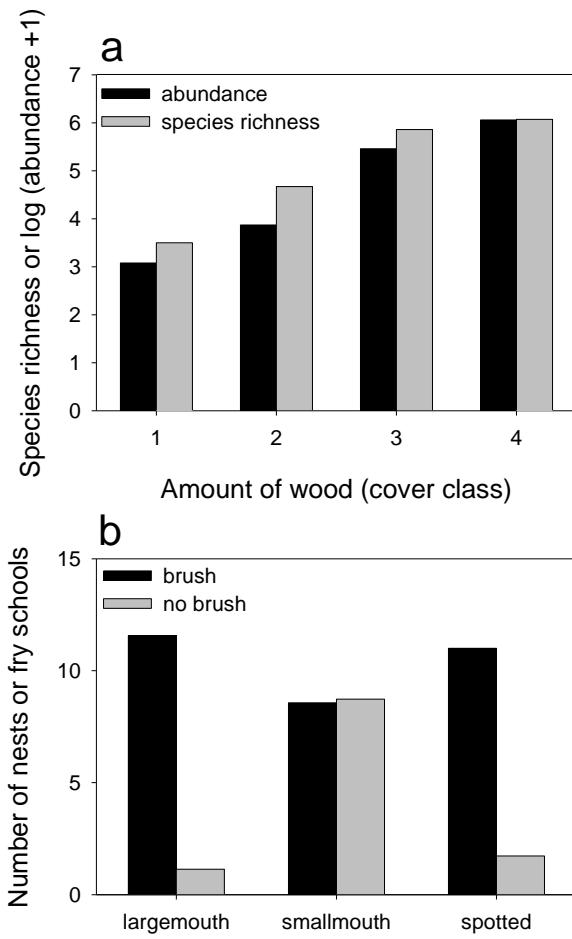
Fig. 20. Seasonal changes in the shoreline length (km of shoreline per km of river) in a natural river (Tagliamento), a modified river (Danube), and a channelized river (Rhone), showing the

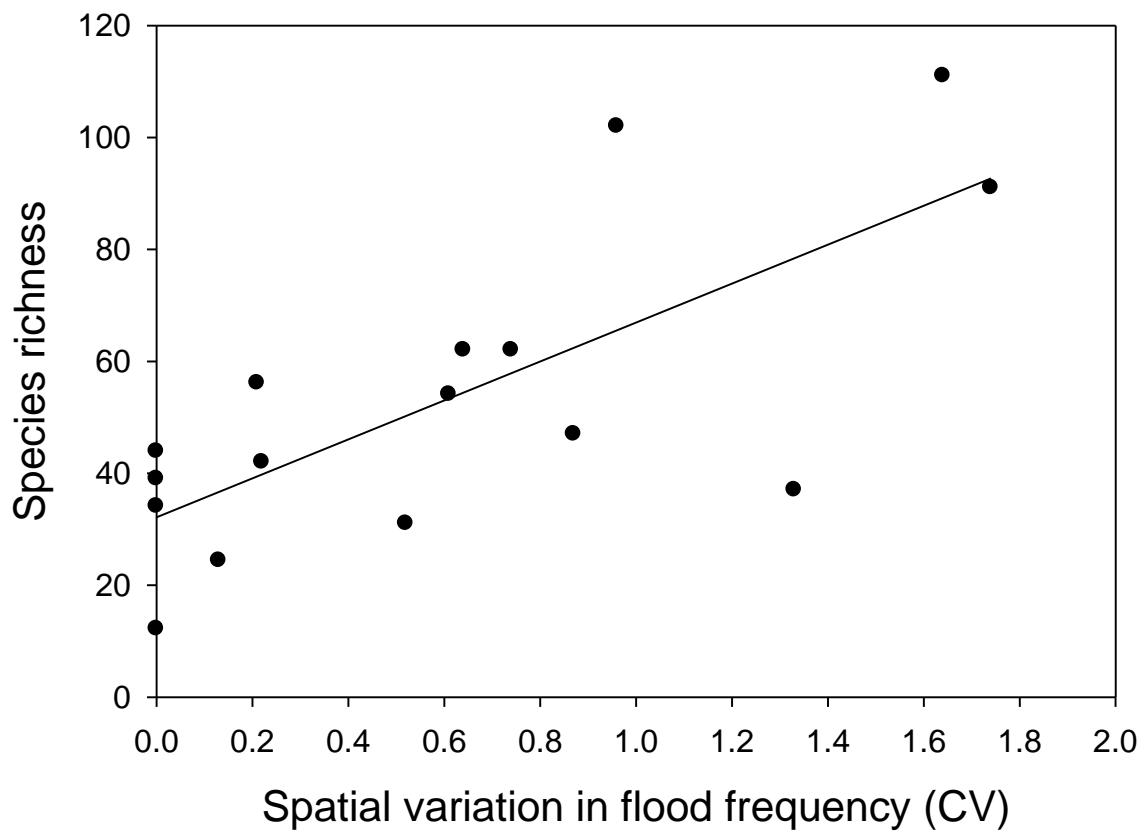
huge reductions in shoreline length caused by human modifications (Tockner and Stanford, 2002).

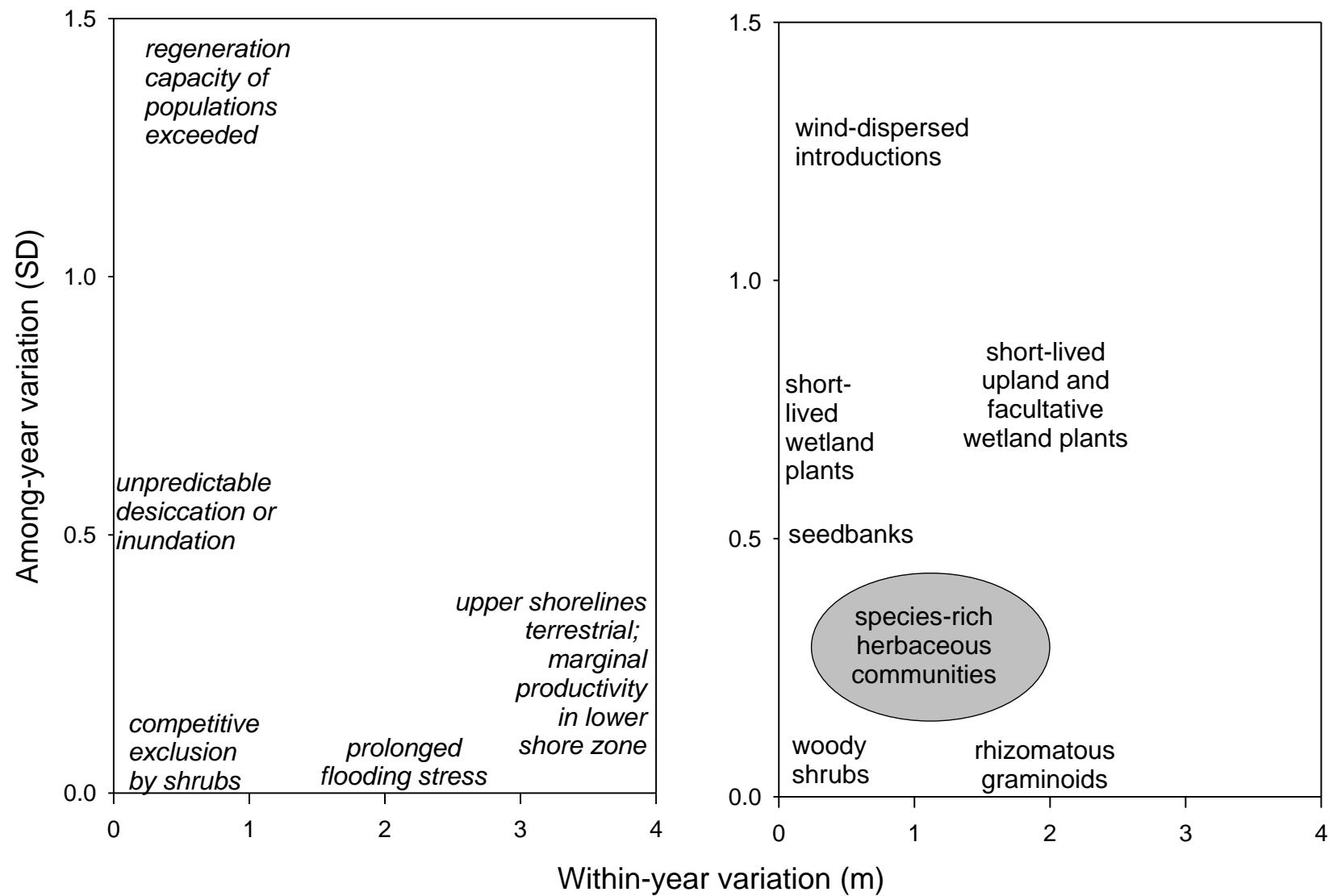
Fig. 21. Number of taxa of common macroscopic algae and animals occupying natural rocky reefs and various artificial substrata in Sydney Harbor, Australia. “New taxa” means taxa that do not occur on the natural rocky reefs, and indicate the potential of artificial substrata to enhance biodiversity at the cross-habitat scale (from data of Glasby and Connell, 1999).

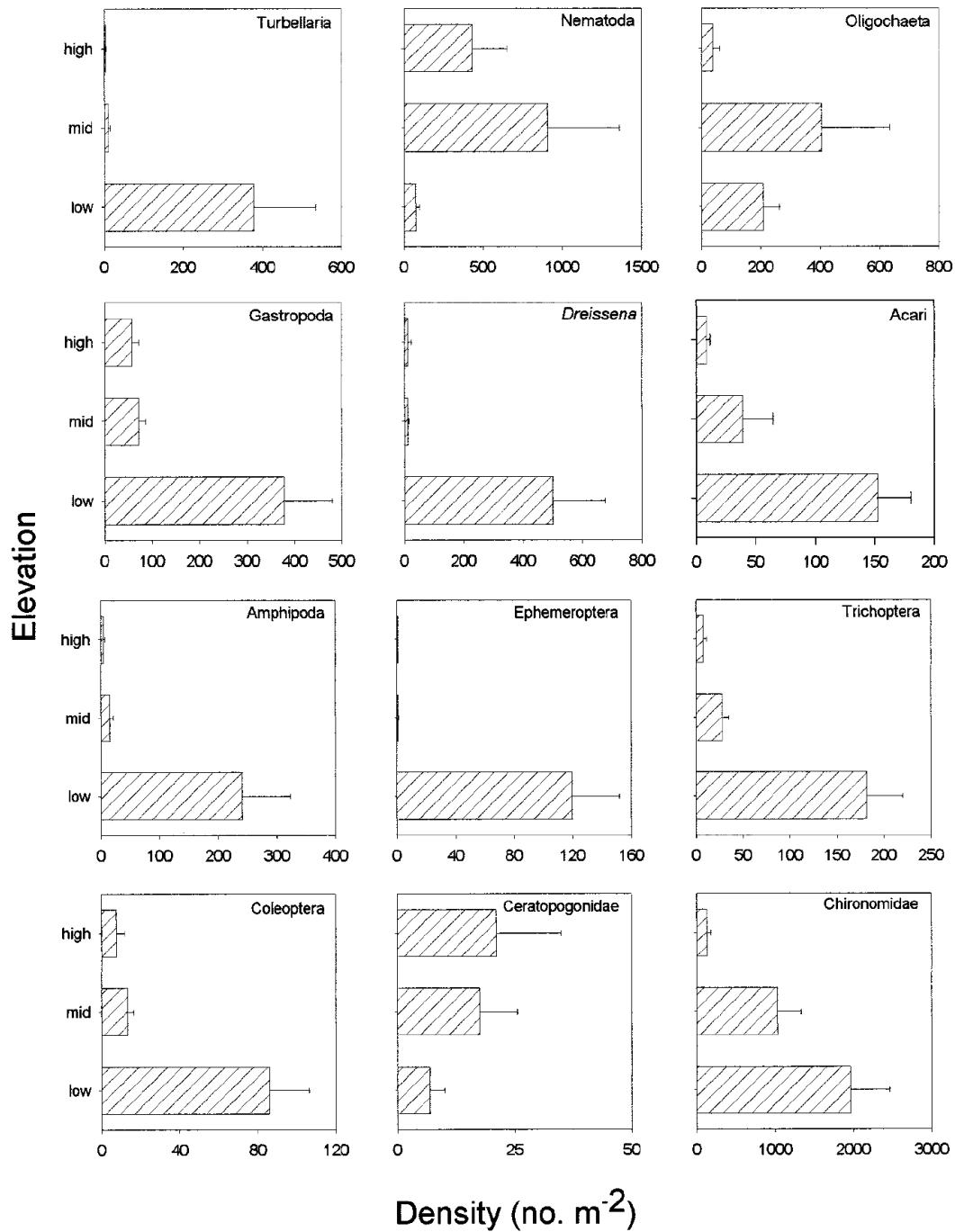


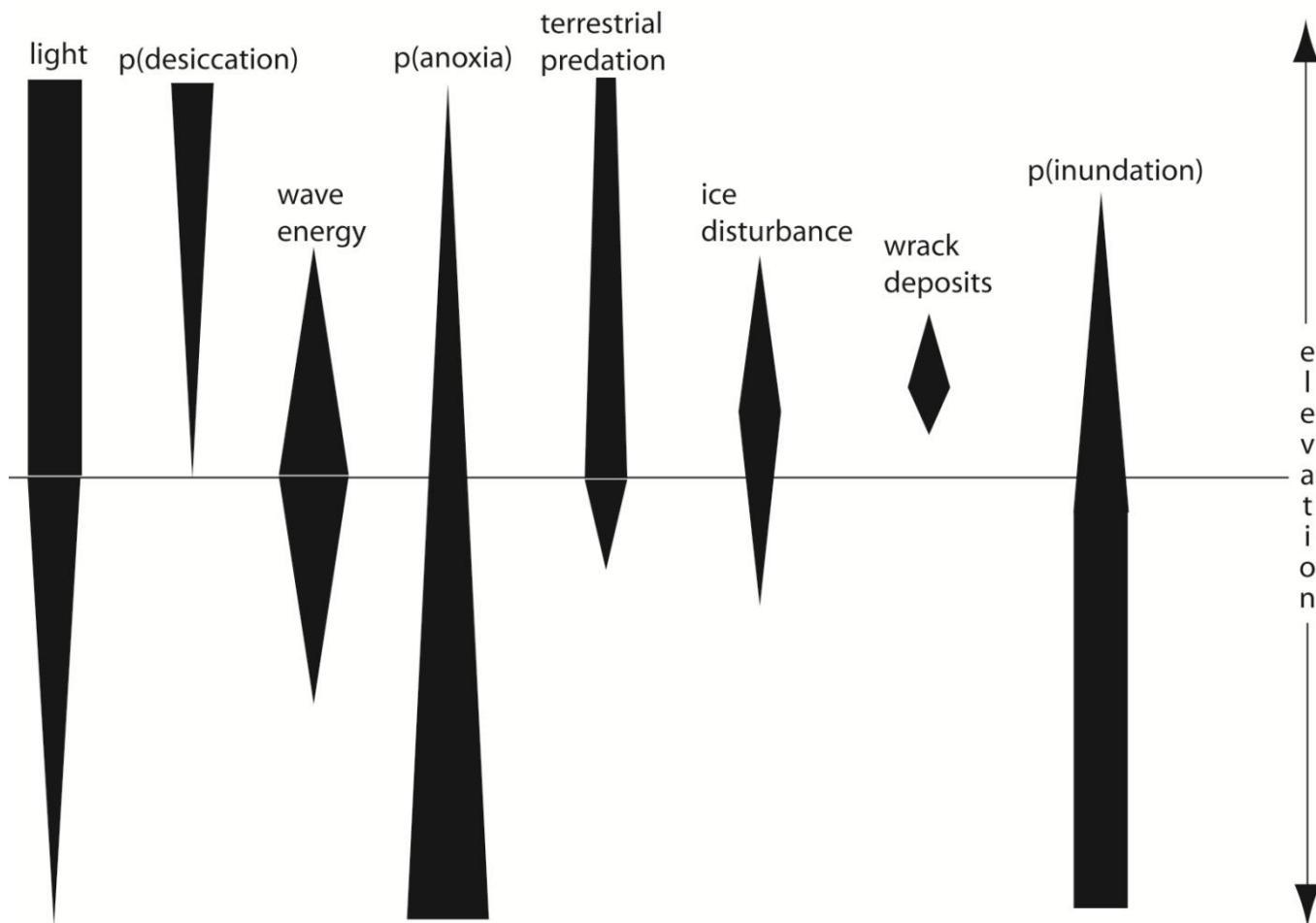


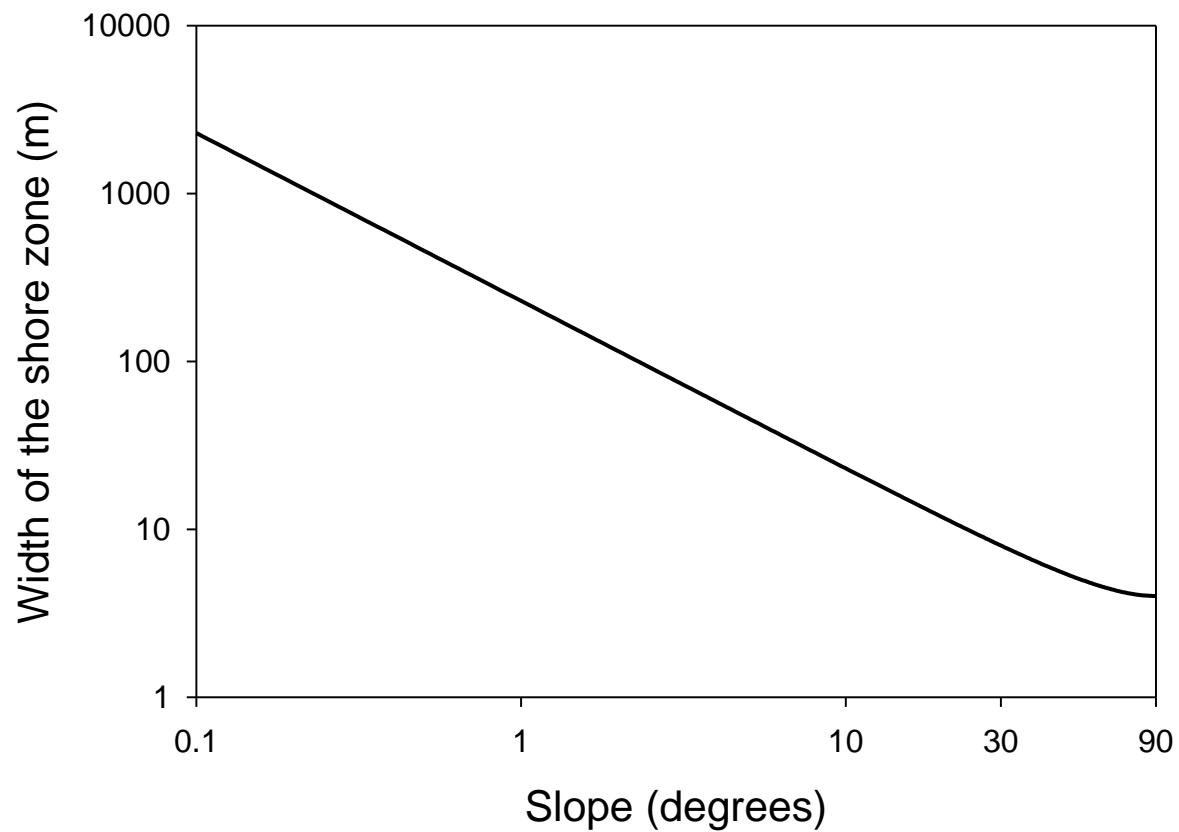


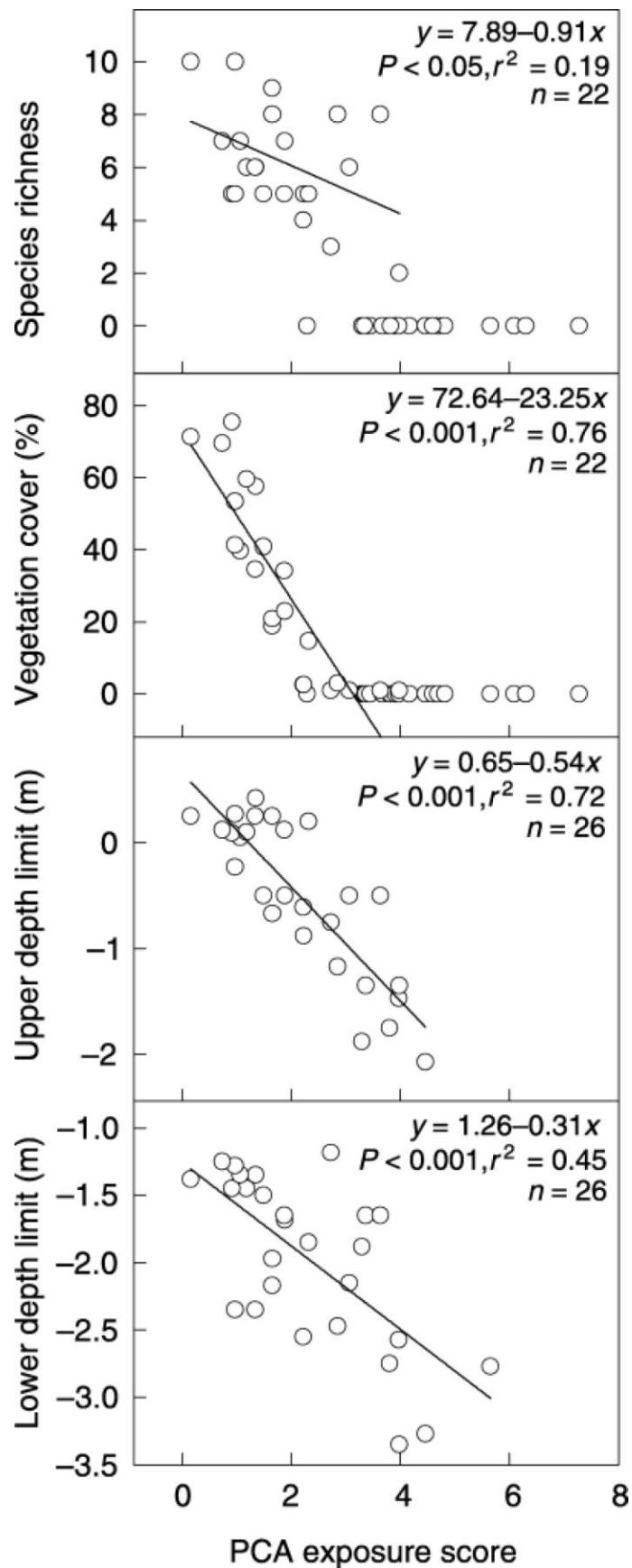








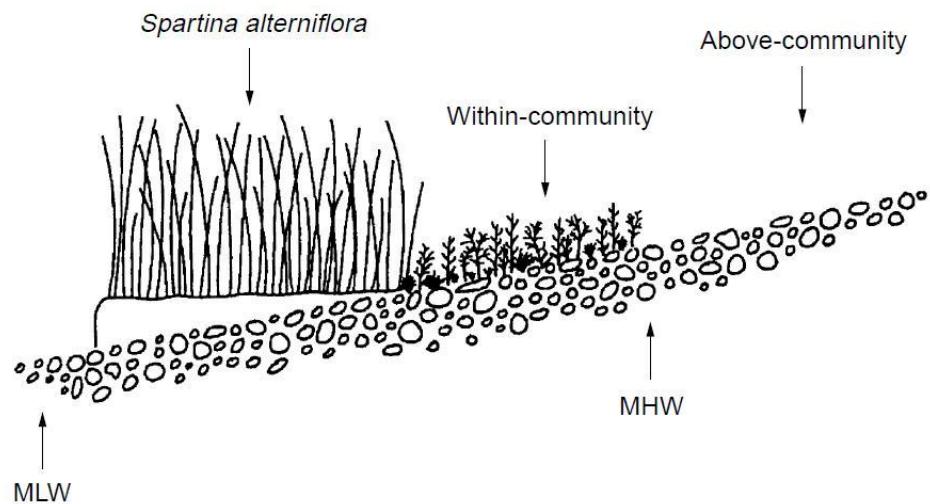


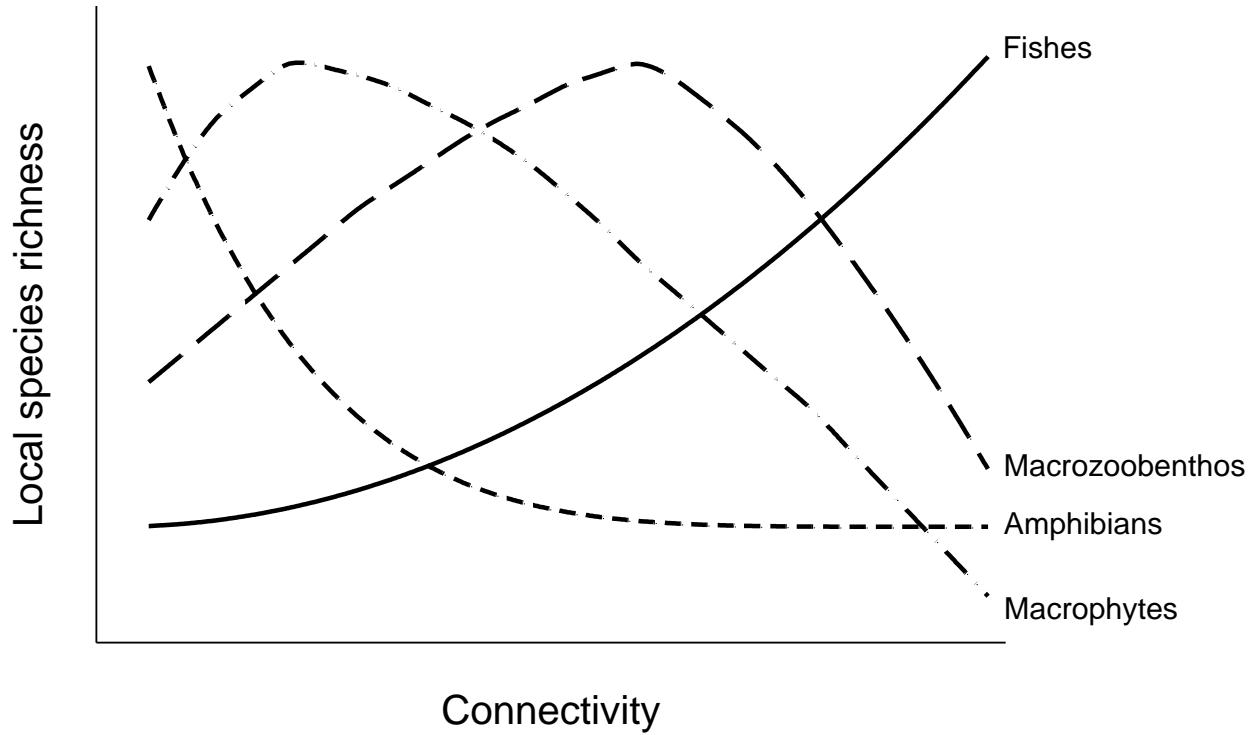


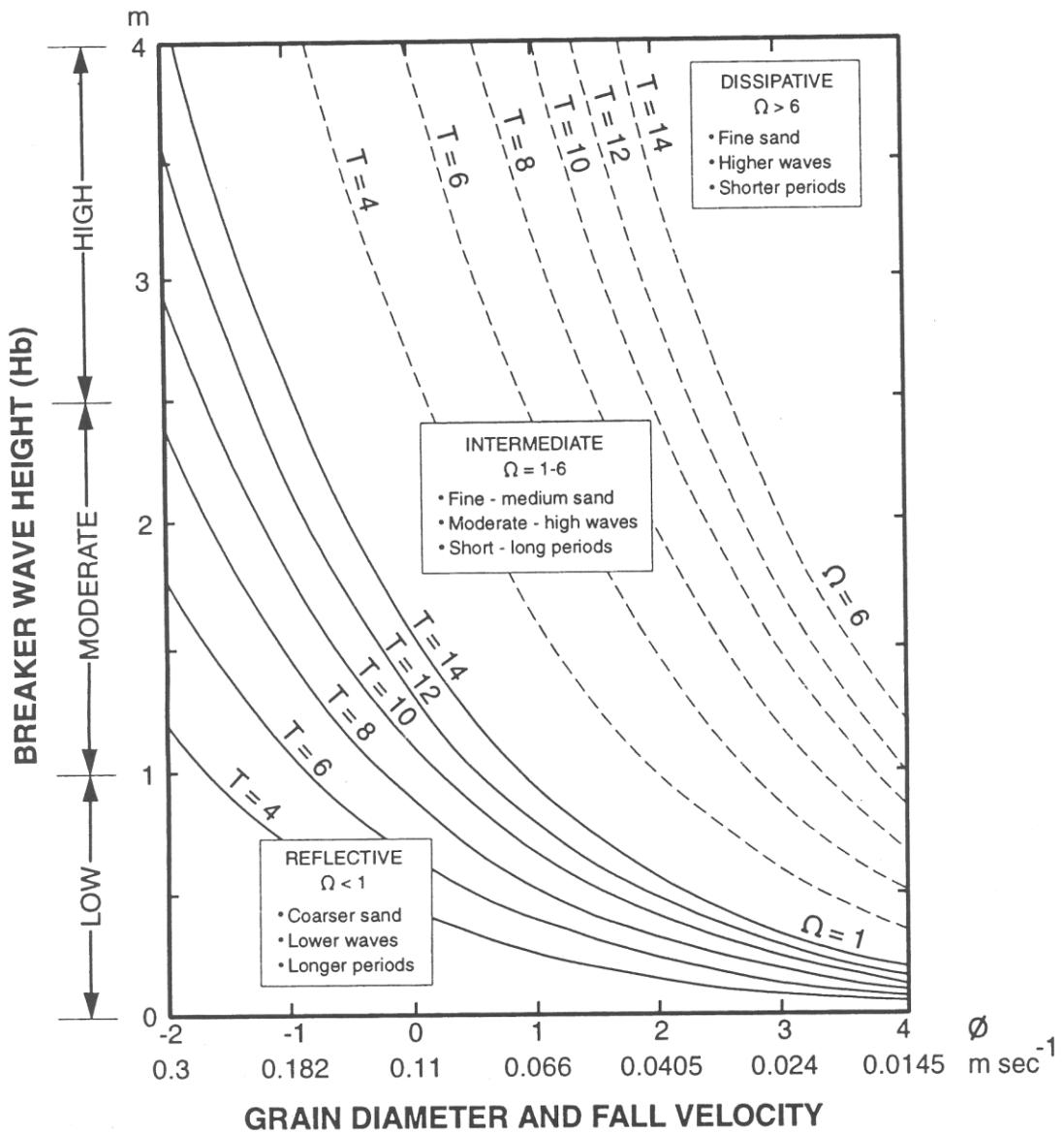
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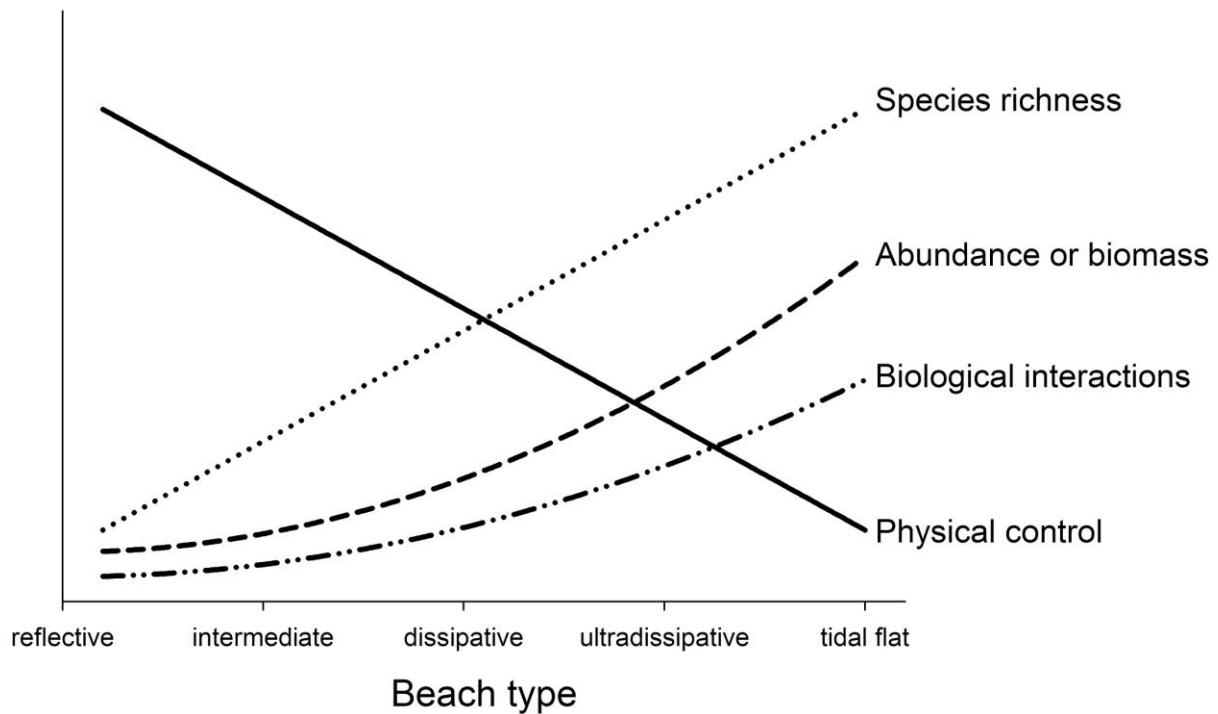


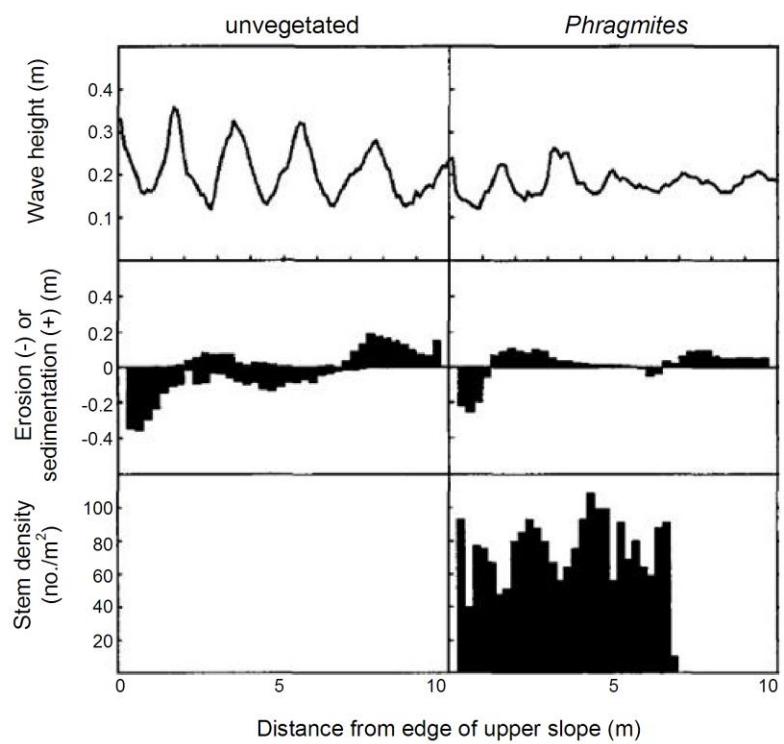
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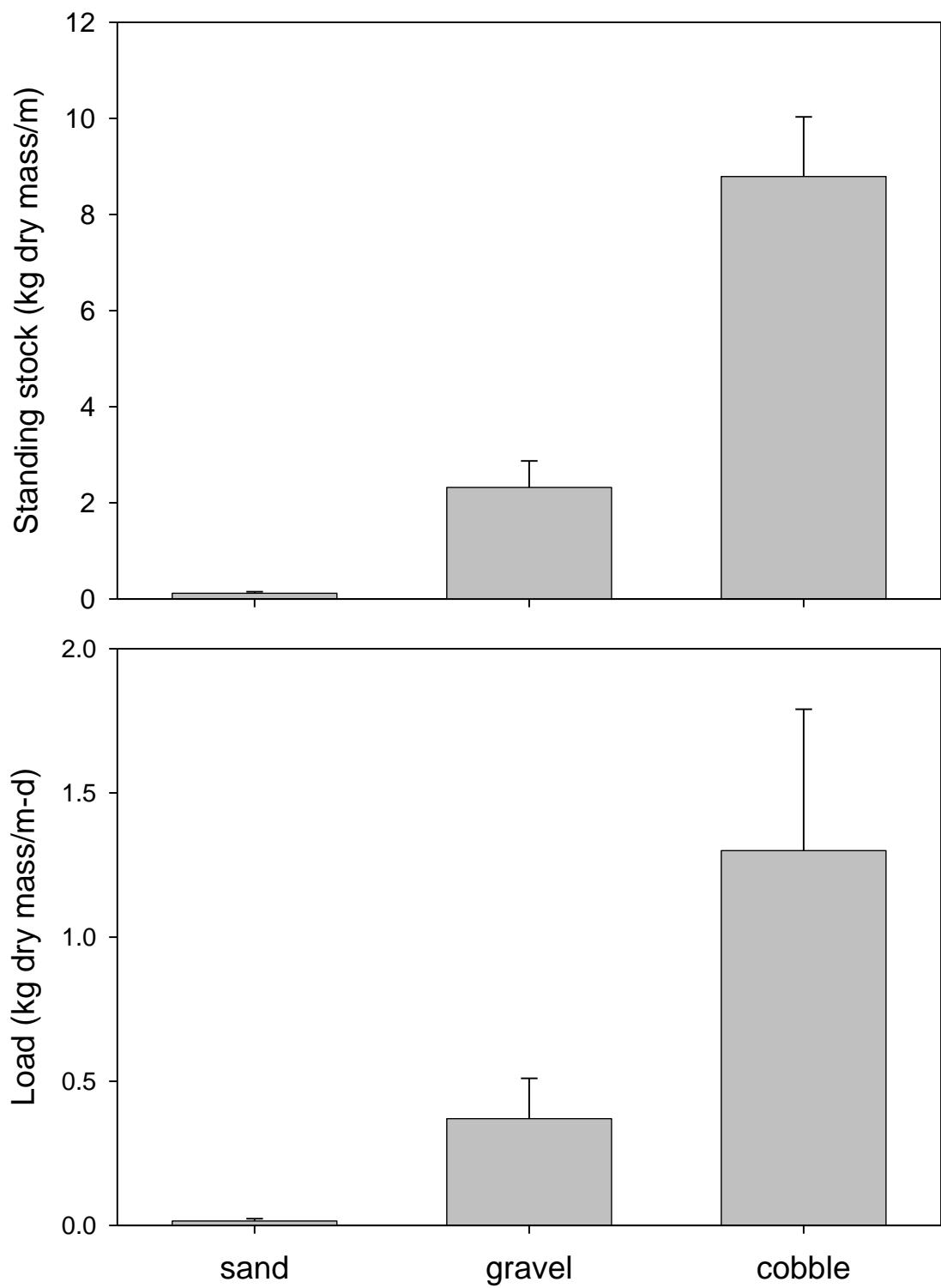


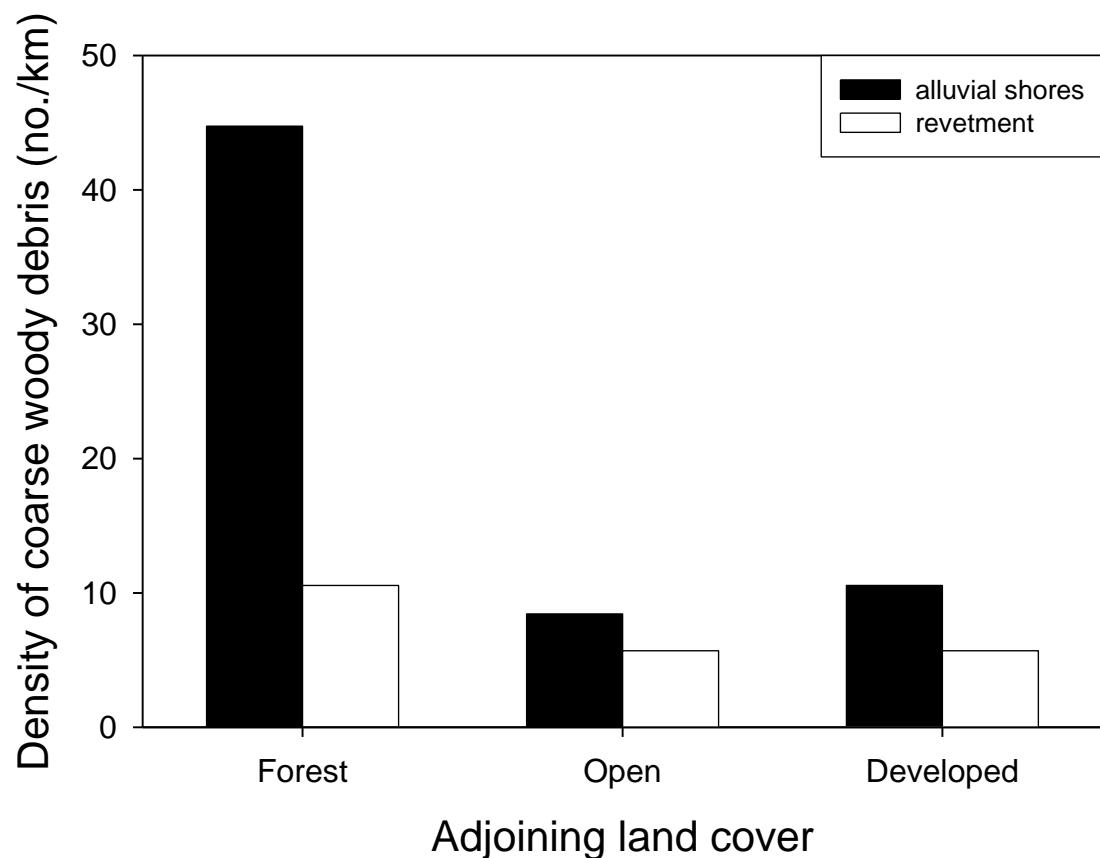


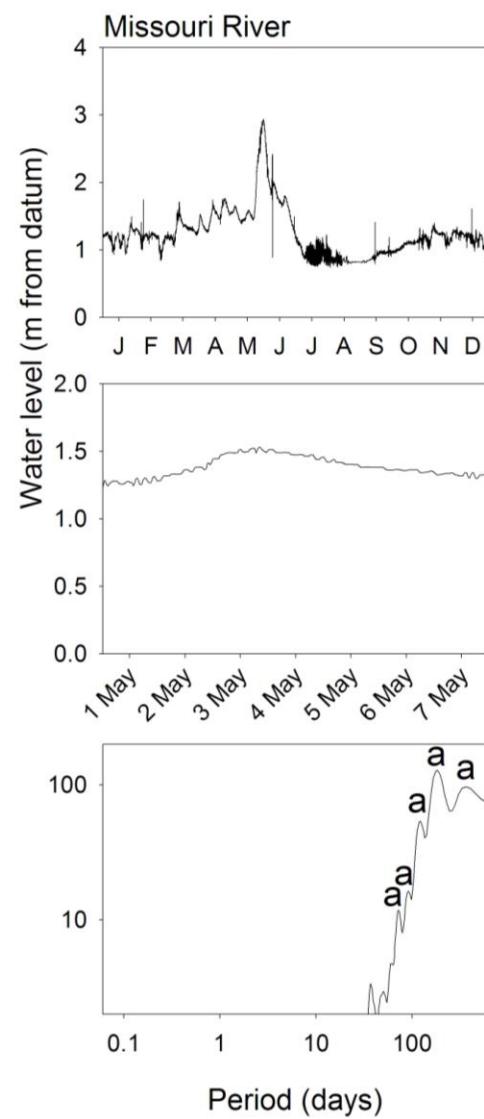
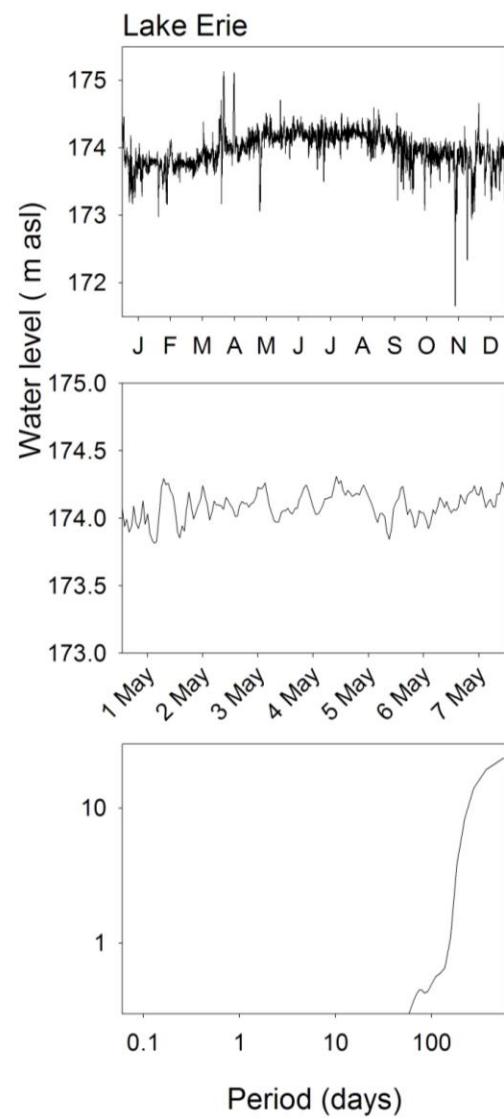
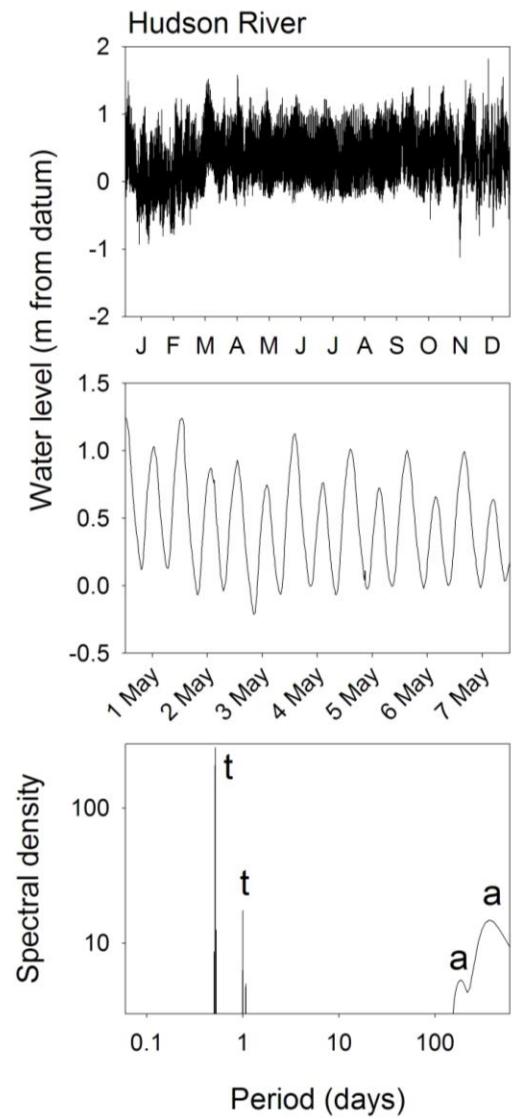


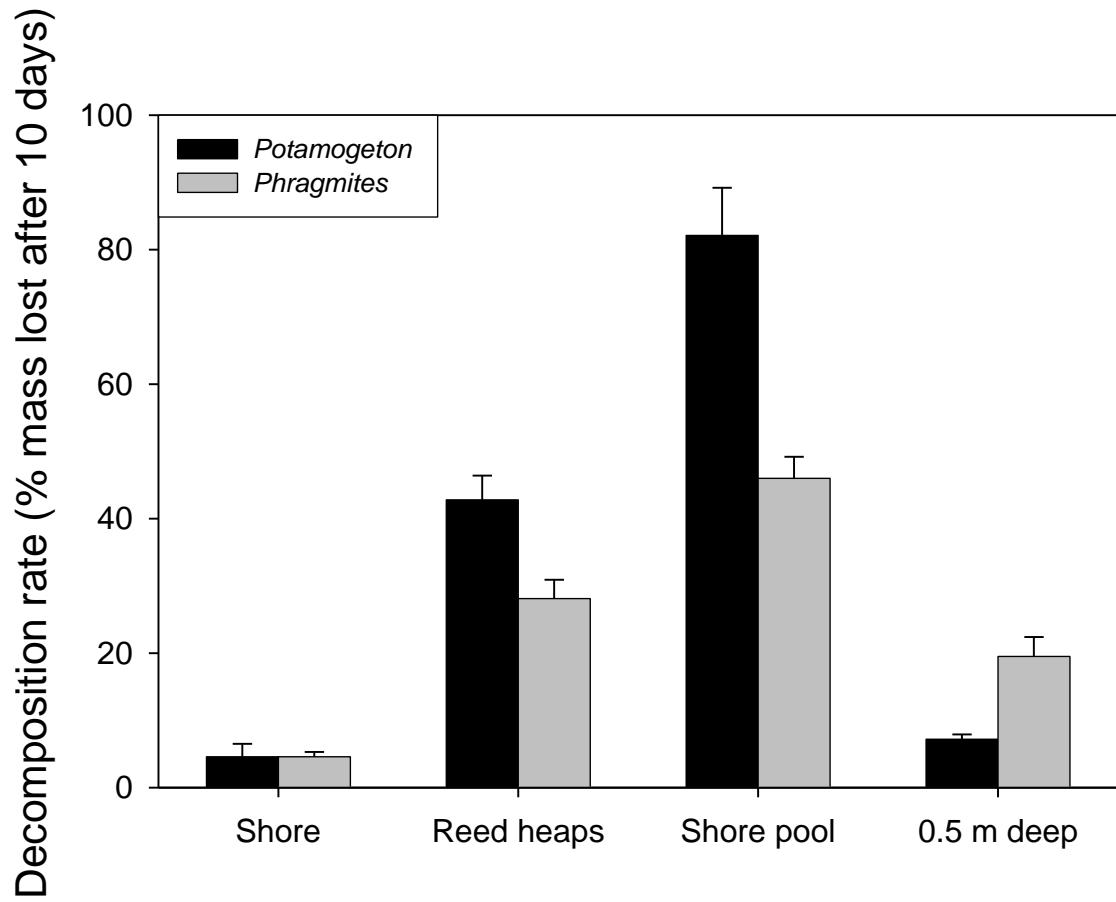


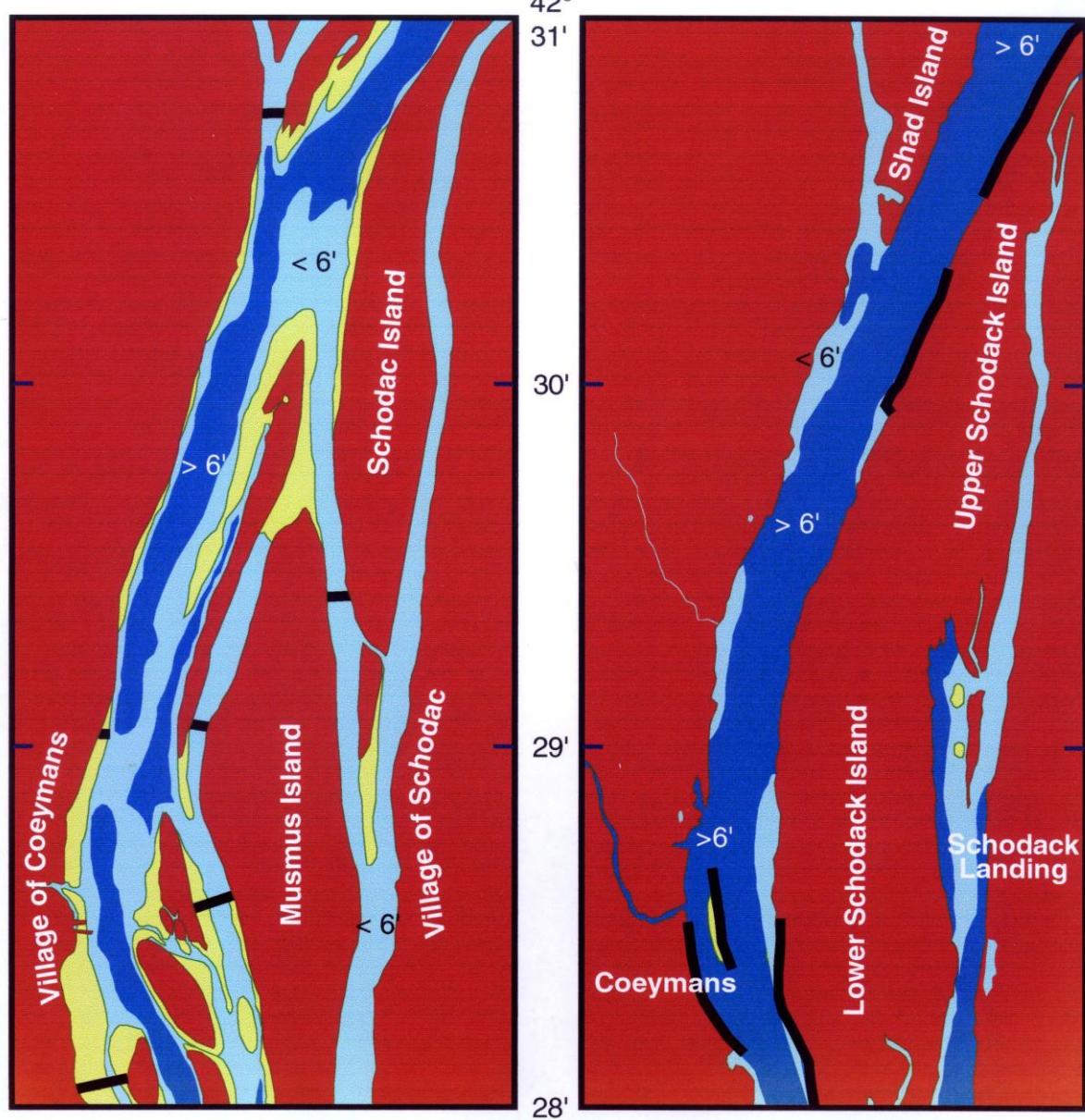


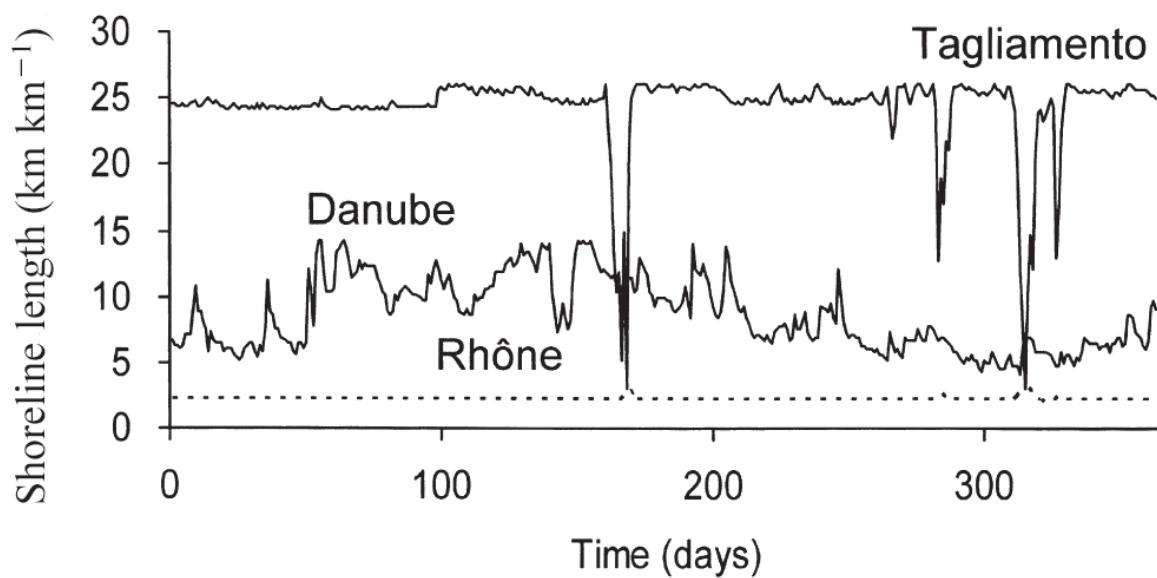


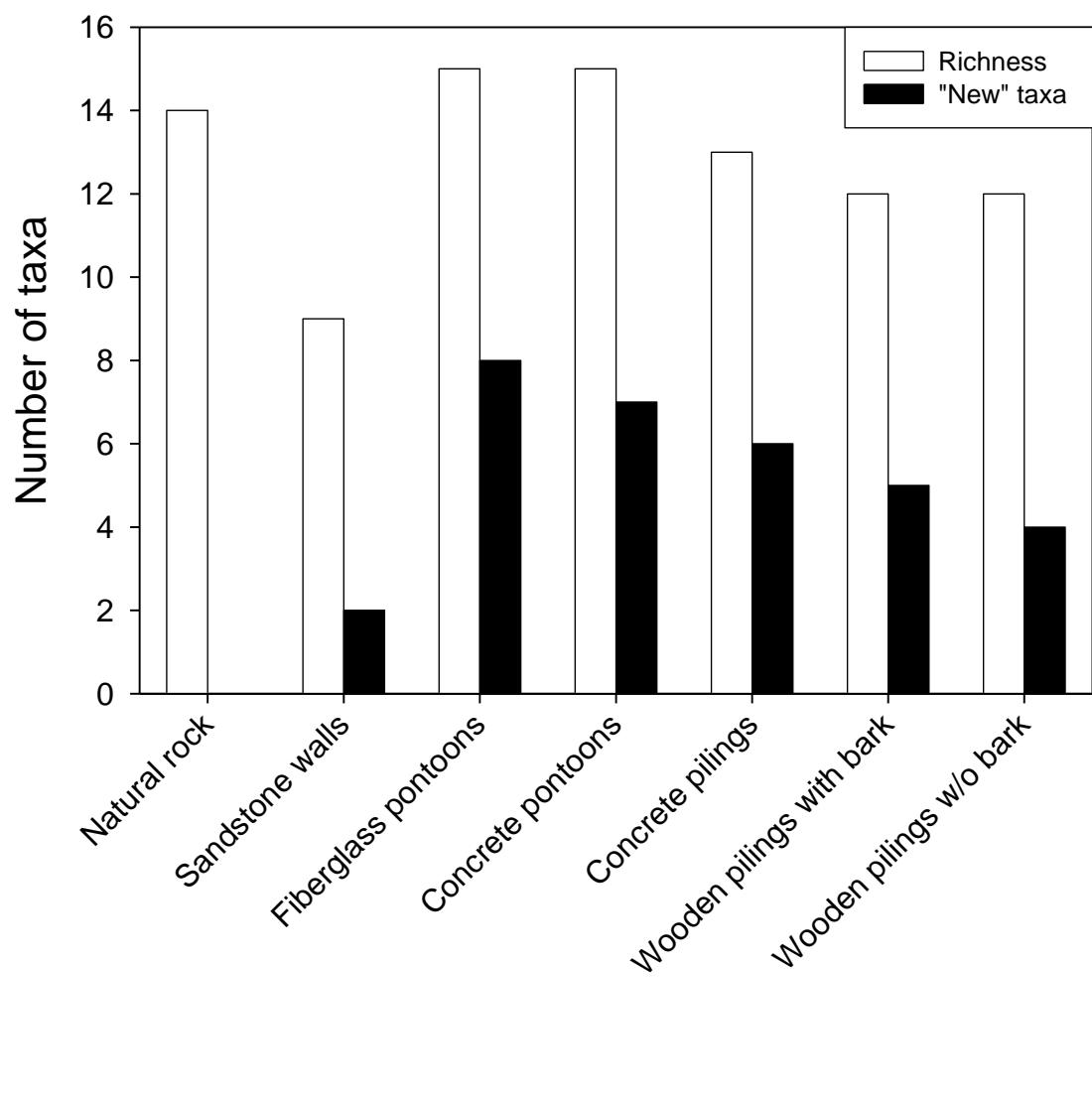












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Chapter 2: Biodiversity in Hudson River shore zones: influence of shoreline type and physical structure

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Abstract

29 The shore zones of the Hudson River, like those of many developed waterways, are
30 highly varied, containing a mix of seminatural and highly engineered shores. Our goal was to
31 document the biodiversity supported by different kinds of shore zones in the Hudson. We chose
32 six common types of shore zones, three of them “natural” (sand, unconsolidated rock, and
33 bedrock), and three of them engineered (riprap, cribbing, and bulkheads). We measured selected
34 physical characteristics (shore zone width, exposure, substrate roughness and grain size,
35 shoreline complexity) of three examples of each of these shore types, and also sampled
36 communities of terrestrial plants, fishes, and aquatic and terrestrial invertebrates. Community
37 composition of most taxa differed across shore types, and frequently differed between wide,
38 sheltered shores and narrow, exposed shores. Alien plant species were especially well
39 represented along engineered shores. Nevertheless, a great deal of variation in biological
40 communities was not explained by our six-class categorization of shore zones or the physical
41 variables that we measured. No single shore type supported the highest values of all kinds of
42 biodiversity, but engineered shore zones (especially cribbing and bulkheads) tended to have less
43 desirable biodiversity characteristics than “natural” shore zones.

44

45 **Key words:** Shorelines, littoral zone, estuary, fish, macroinvertebrates, riparian zone, vegetation
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Introduction

49 The shore zone of aquatic ecosystems (the region adjoining the shoreline in which direct
50 interactions tightly link the terrestrial and aquatic ecosystems) is ecologically important, highly
51 modified and understudied (e.g., Airolidi and Beck 2007; McLachlan and Brown 2006; National
52 Research Council 2007; Strayer and Findlay 2010). As a consequence of the typically high
53 heterogeneity and large inputs of organic matter to the shore zone, both aquatic and terrestrial
54 biodiversity often are high in the shore zone, including many species not found in adjacent
55 habitats (e.g., Ward et al. 1999; Sabo et al. 2005; Strayer and Findlay 2010; Kennedy and Turner
56 2011), and rates of primary production, respiration, and other biogeochemical processes can be
57 very high (e.g., Wetzel 1990; Polis and Hurd 1996; Coupland et al. 2007; Strayer and Findlay
58 2010). However, human activities such as agriculture, urbanization, commercial navigation, and
59 recreation have been focused on shore zones for millennia, so many shore zones have been
60 highly modified (e.g., Tockner and Stanford 2002; Scholten et al. 2005; Strayer and Findlay
61 2010). In particular, many shore zones now contain structures such as walls and revetments
62 designed to protect valuable waterfront property. Consequently, the biodiversity and ecological
63 function of many shore zones has been greatly reduced (e.g., Strayer and Findlay 2010; Kennedy
64 and Turner 2011).

65 Despite their importance and imperiled condition, shore zones may be understudied
66 because they are claimed by neither aquatic nor terrestrial ecologists. Further, the extremely high
67 heterogeneity of the shore zone makes it difficult to design sampling schemes and apparatus that
68 are efficient throughout the full range of conditions encountered. As a result, detailed
69 information on the biodiversity and ecological functioning of shore zones often is lacking,
70 especially along fresh waters.

71 Nevertheless, information about the biodiversity and ecological function of different
72 kinds of shore zones is necessary for wise management of these important ecosystems. A
73 challenge for shore zone management is to preserve human uses of the shore zone while
74 retaining or improving ecological function. To reach this goal, we will have to understand what
75 characteristics of shore zones determine their biodiversity and ecological functioning.

76 An extensive review of the literature led to the conclusion that shore zone biodiversity
77 depends chiefly on the physical energy regime, geologic (or anthropogenic) structure, the
78 hydrologic regime, nutrient inputs, and climate (Strayer and Findlay 2010). If we are thinking of
79 managing a particular site, physical structure often will be the easiest of these factors to
80 manipulate. In particular, high biodiversity often is associated with high physical heterogeneity,
81 so it may be desirable to design sites or manage for high physical heterogeneity.

82 Here, we report on surveys of biodiversity in the shore zone of the freshwater tidal
83 Hudson River. The goals of our study were to (1) describe the biological communities that
84 occupy the shore zones of the freshwater tidal Hudson River; (2) test whether those biological
85 communities differ among different types of shore zones, whether natural and engineered; and
86 (3) test whether the physical characteristics of shore zones (e.g., roughness, slope, exposure) can
87 be used to predict the attributes of their biological communities. Specifically, we hypothesized
88 that high biodiversity would be associated with high physical complexity of shore zones, and that
89 engineered shore zones would be physically simpler and therefore support lower biodiversity
90 than natural shore zones. Instead of focusing on a single taxonomic group, we deliberately chose
91 to study several taxa, both aquatic and terrestrial. We hope that this information will help to
92 better manage shore zones along the Hudson and elsewhere.

93 **Methods**

94 *The study area*

95 The study area is the freshwater tidal portion of the Hudson River (Fig. 1), which extends
96 from RKM 100 (i.e., river kilometer 100 as measured from The Battery at the southern end of
97 Manhattan in New York City) to the head of tide at RKM 248 in Troy. The entire study area is
98 subject to twice-daily tides with an average range of 0.8-1.6m; tidal range does not diminish
99 upriver and is as large at Troy as at Manhattan (Geyer and Chant 2006). Because daily tidal
100 flows are much greater than typical freshwater flows (Geyer and Chant 2006), water levels along
101 the Hudson's shores are determined more by tides than by freshwater flows (Strayer and Findlay
102 2010, Fig. 17), and the Hudson does not have the large, well-defined floodplain characteristic of
103 typical alluvial rivers. The average water depth is ~8m and the average channel width is ~900m.
104 The Hudson is used by ocean-going ships as far as Albany (RKM 226), and smaller commercial
105 ships all the way to Troy, and is heavily used by recreational boaters throughout the study area.
106 Wakes from this traffic probably are important forces on shore zones throughout the study area.

107 The water is moderately hard, turbid, and fertile (typical growing-season values:
108 calcium=25 mg/L, NO₃-N=0.5 mg/L, PO₄-P=28 µg/L, Secchi transparency=1m; Caraco et al.
109 1997; Simpson et al. 2006). Large beds of the macrophytes *Vallisneria americana* (submersed)
110 and *Trapa natans* (floating-leaved) are common (Nieder et al. 2004). The fauna is dominated by
111 species typical of warm fresh waters, although diadromous fishes (e.g., *Alosa* spp.) and several
112 typically brackish-water fishes and invertebrates are common in the freshwater estuary (e.g.,
113 Simpson et al. 1980).

114 We defined the shore zone as the region extending from 1 m vertically below mean low
115 water to 1 m vertically above mean high water. Although admittedly arbitrary, this definition is
116 consistent with previous definitions (reviewed by Strayer and Findlay 2010) that delimit the

117 shore zone as a region of strong interactions between land and water, and was practical to apply
118 in the field. Note that this definition of the shore zone includes areas that are usually under water,
119 areas that are usually exposed to the air, and areas that are intermittently inundated.

120 *Study design*

121 We studied six types of shore zones, three of them engineered (riprap, cribbing, and steel
122 or concrete bulkheads) and three of them without obvious signs of human engineering (bedrock,
123 natural unconsolidated rock, and sand). Even these “natural” shore zones often showed some
124 signs of past human activity. Definition of shore types was based on predominant conditions at
125 and just above the high water mark. Riprap shores are revetments constructed of large stone
126 (typically >50 cm in diameter), cribbing shores consist of wooden pilings (typically ~25 cm
127 diameter) back-filled on the land side with crushed stone 15-25 cm in diameter, and bulkheads
128 are vertical walls or revetments made of steel or concrete. These engineered structures typically
129 extend from well below mean low water to well above mean high water, although some parts of
130 the cribbing are overtopped at mean high water. Designation of shore types and their locations
131 were based on a complete GIS inventory of both shores of RKM 50-248 of the Hudson in 2006
132 (D. Miller, unpublished).

133 We selected one example of each type of shore zone in three reaches of the Hudson (Fig.
134 1): upper (RKM 213-247), middle (RKM 151-213), and lower (RKM 100-151). Blocking by
135 reach was intended to control for north-south differences in biota along the length of the river.
136 We selected a random point in each river reach, then chose the closest example of each shore
137 type to that random point that met the following criteria: it was at least 130 m long (i.e., 100 m of
138 shore to be studied plus at least a 15 m buffer on each end) and was not interrupted by a tributary
139 mouth or any major human structure (e.g., a marina). In two cases where a particular shore type

140 was rare in a section of the river, we had to relax these standards and choose a slightly shorter
141 reach of shore (the shortest reach was 75 m long).

142 *Physical variables*

143 We measured several physical properties of each site: shore zone width, sediment grain
144 size, exposure, substrate roughness, and shoreline complexity. We measured shore zone width as
145 the distance along a line perpendicular to the shoreline from 1 m vertically above the high-water
146 mark to 1 m vertically below the low-water mark. At a few sites with very shallow slopes, we
147 measured the underwater slope only to a point 60 m from the shoreline, where the water was less
148 than 1 m deep and extrapolated the slope from the low water mark to the 1 m depth contour. We
149 repeated this procedure three times at each site: at the upriver end, middle, and downriver end of
150 the site. These estimates were then combined into a single estimate of shore zone width for each
151 site.

152 We used the modified pebble count method of Lazorchak et al. (1998) to estimate
153 sediment grain size in the intertidal zone. Briefly, we laid out a 100-m long tape along the low-
154 water line, the mean-water line, and the high-water line, and categorized the sediment at 1-m
155 intervals along the line as 0 = silt or clay, 1 = sand, 2 = sand to the size of a marble (16 mm), 3 =
156 size of a marble to a tennis ball (64 mm), 4 = size of a tennis ball to a basketball (250 mm), 5 =
157 size of a basketball to 1 m diameter, 6 = 1-4 m diameter, and 7 = larger than 4 m diameter. We
158 averaged these 300 measurements to get a single estimate of average sediment grain size for each
159 site.

160 Sediment grain size of subtidal sediments was estimated from handheld cores (5 cm
161 diameter) taken at depths of 0.33 m and 0.67 m below the low-water mark. Three cores were
162 taken at each depth at each site. We dried each sample, weighed it, than wet-sieved the sample

163 through brass soil sieves of 0.25, 1, and 4 mm mesh, and measured the dry mass of sediment
164 retained on each sieve. We then calculated an index of grain size as [mass retained on 0.25-mm
165 mesh sieve + 2*(mass retained on 1-mm mesh sieve) + 3*(mass retained on 4-mm mesh
166 sieve)]/(total mass of sample). If the sediment was too coarse to core, we assigned it a value of 4.
167 We then calculated a mean value for each site. This index ranged from 0 (if all of the sediment
168 was finer than 0.25 mm) to 4 (if the sediment was too coarse to core).

169 We used three methods to estimate exposure to waves and currents. First, we deployed a
170 modified version (using a weaker spring to accommodate lower wave forces) of the
171 dynamometer of Bell and Denny (1994), which is designed to measure peak wave forces.
172 Second, we set out clod cards (Pettigrew and Kalff 1991) to get a general estimate of the
173 intensity of water movement at each site. Clod cards were ~600 g masses of plaster-of-paris
174 molded in beverage cups and attached to cement blocks. After they were retrieved from the field,
175 they were oven-dried and reweighed to calculate mass loss, which is roughly proportional to
176 water movement. We set out three dynamometers and six clod cards at each site for ~10 days.
177 Because we had only a few dynamometers, we deployed dynamometers and clod cards at the six
178 sites in one reach of river, then later moved on to the other reaches. Third, we assumed that
179 sediment grain size would reflect peak physical forces at a site, and used our estimates of
180 sediment grain size as one measure of exposure. For the sites in each reach of river (the reaches
181 were treated individually because dynamometers and clod cards were deployed at different times
182 in different reaches), we ranked the dynamometer readings from 1 (most exposed) to 6 (least
183 exposed), mass loss of clod cards from 1 to 6, and sediment grain size from 1 to 6. We then
184 summed these three estimates of exposure for each site, and ranked them for all sites in the river
185 from 1 (most exposed site) to 18 (least exposed site).

186 We measured local substratum roughness (rugosity) using the chain technique of Frost et
187 al. (2005). In this method, a 1-m long chain is placed to conform as closely as possible to the
188 contours of the bottom and the distance covered by the chain is measured with a taut tape.
189 Roughness is the ratio of the chain length (1m) to the tape-measured distance. We measured
190 rugosity parallel and perpendicular to the shoreline at nine places using a chain with a 12-mm
191 link (low water, mean water, and high water at upriver end, center, and downriver end of each
192 site).

193 We estimated the complexity of the shoreline in plan view by stepping off the length of
194 the 100-m stretch of shoreline at mean low water level using a pair of 1-m wide calipers.
195 Complexity is estimated as the ratio of shoreline length measured using calipers to that measured
196 using a taut line (i.e., 100m). Values for complexity range from 1 for perfectly straight shorelines
197 to higher values for complex shorelines.

198 In addition, we tested the effect of nearby beds of submersed aquatic vegetation (SAV)
199 (chiefly *Vallisneria americana*). SAV beds could serve as a source of wrack, which is important
200 to shore zone invertebrates and plants (e.g., Backlund 1945; Minchinton 2002), as well as
201 serving directly as a source of fish and invertebrate colonists to nearby shore zones. We
202 constructed an SAV index as the area of the nearest mapped bed of SAV (in m²) divided by the
203 squared distance to the bed (in m), using data described by Nieder et al. (2004).

204 *Biological sampling*

205 We sampled fishes, plants, aquatic invertebrates, terrestrial invertebrates, and snails
206 living in each shore zone site. We sampled fishes by electrofishing using a Smith-Root Type VI-
207 A electrofisher mounted in a 6.4-m long john boat. Sites were continuously shocked until we had
208 covered the length of the study site or 5 minutes total of shocking time had elapsed, whichever

209 occurred first. Sampling occurred within 3 hours of high tide. Fishes were dipped and placed in
210 an onboard live well. After we finished sampling, we identified, measured, and counted fish. If
211 more than 25 individuals of a species were collected at a site, the first 25 individuals were
212 measured. We sampled fish three times: spring, summer, and autumn of 2008.

213 We sampled terrestrial plants using timed searches on 4-20 August 2008. Timed searches
214 are an efficient way to locate rare species (cf. Strayer and Smith 2003). We walked each site for
215 three consecutive 10-minute periods (a total of 30 minutes searching) and recorded as many plant
216 species as possible between the low water mark and 1 m above the mean high water mark. This
217 search was not sufficient to detect all plant species, especially at high-diversity sites. As a result,
218 our data probably underestimate differences between high- and low-diversity sites. Nevertheless,
219 inspection of the species-accumulation curves suggested that this method detected >75% of the
220 vascular plant species at each site.

221 We sampled aquatic invertebrates using two methods. We took kick samples at all sites,
222 using a 0.5-mm mesh D-net for 10 minutes/site, deliberately attempting to sample the full range
223 of available habitats. We also sampled benthic invertebrates using 5-cm diameter hand-held
224 cores. We tried to take samples at the upriver end, middle, and downriver end of each site at
225 depths of 0.33 m and 0.67 m below the low-water mark. Substrata were too coarse to allow such
226 core samples to be taken at all sampling locations. These core samples were sieved in the field
227 through a 0.5-mm mesh sieve. All aquatic invertebrate samples were preserved in the field in
228 10% buffered formalin and sorted in the laboratory under 6X magnification, and identified to the
229 lowest practical taxonomic level (usually classes or orders). We took samples of aquatic
230 invertebrates between 5 May-6 June and again in 4-20 August 2008.

231 We sampled terrestrial invertebrates using a backpack aspirator. We spent 10 minutes at
232 each site taking a sample from the ground and an additional 10 minutes sampling the air and
233 vegetation, again attempting to cover the full range of microhabitats available at each site.
234 Invertebrates were killed in the field using a killing jar with ethyl acetate, then stored in the
235 freezer until they were identified to the lowest practical taxonomic level (usually orders or
236 families). We took samples of terrestrial invertebrates in early June and again in early September
237 2008.

238 We examined land and aquatic gastropod communities in detail, identifying all specimens
239 to genus or species. We sampled aquatic gastropods by taking a 30-second sweep of 1 m² of
240 substrate at a depth of 1 m below the low tide mark with a 1.2-mm mesh D-net. Intertidal
241 gastropods were sampled by handpicking and washing substrate from a 1 m² plot at mid-tide
242 level through a 1.4-mm mesh sieve. Upland gastropods were collected within 10 m (horizontally)
243 inland of the high tide mark, by handpicking and sieving soil through a 1.4-mm mesh sieve. Each
244 type of sample was repeated three times, near the upriver end, middle, and downriver end of each
245 site. We collected gastropods twice at all sites, on 1-3 June and 29 June-2 July 2008. All
246 gastropods collected were preserved in the field in 95% ethanol, and identified in the laboratory
247 using Pilsbry (1939-1948), Burch (1962, 1989) Harman and Berg (1971), Strayer (1990), and
248 Jokinen (1992).

249 *Statistical analyses*

250 We conducted four statistical analyses for most taxonomic groups. First, we used one-
251 way ANOVA (following data transformation, where needed) to test for differences in abundance
252 or diversity across the six types of shore zones. We used Gini diversity as a measure of
253 taxonomic diversity because it is relatively insensitive to sample size (Gotelli and Ellison 2004).

254 Second, we ran two-dimensional nonmetric multidimensional scaling ordinations (NMS, PC-
255 ORD 5.10) to display variation in community composition across sampling sites (McCune and
256 Grace 2002). We transformed the data using a $\log_{10}(X+1)$ transformation and removed taxa
257 present at fewer than three sites prior to ordination. Plant ordinations were based on presence-
258 absence data, because we did not collect data on relative abundance of plants. We then used
259 multi-response permutation procedures (MRPP) to test for significant differences in community
260 composition among shore types. Third, we used multiple regression using Pearson correlations
261 (Table 4) and best subset regression in Statistix 9.0 to identify associations between biodiversity
262 (abundance and species richness of each taxon, scores on ordination axes) and the physical
263 characteristics of the study sites. We transformed shore zone width using a $\log_{10}(X+0.1)$
264 transformation and the SAV index using a log transformation prior to statistical analyses.

265 **Results**

266 *Physical properties of Hudson River shore zones*

267 The shore zones that we studied were highly varied, both within and among shore types
268 (Table 1). Important environmental characteristics differed significantly among shore types, as
269 well as between natural and engineered shores (Table 2). The primary axis of variation in the
270 physical characteristics of shore zones, which accounted for 61% of variance in a principal
271 components analysis (Fig. 2), distinguished flat, sheltered, fine-grained shores (e.g., sand) from
272 steep, exposed, coarse-grained shores (e.g., bulkheads). A secondary axis (accounting for an
273 additional 28% of variance) separated sites with complex shorelines and rough surfaces from
274 those with simple shorelines and smooth surfaces.

275 *Terrestrial plants*

276 We identified 190 taxa of plants in Hudson River shore zones, 46 of which are alien to
277 the region. Plants that were especially frequent (detected at >50% of sites) included bush
278 honeysuckles (*Lonicera* spp.), false indigo (*Amorpha fruticosa*), Virginia creeper
279 (*Parthenocissus quinquefolia*), wild grapes (*Vitis* spp.), dogwoods (*Cornus* spp.), ashes
280 (*Fraxinus* spp.), cottonwood (*Populus deltoides*), goldenrods (*Solidago* spp.), sugar maple (*Acer*
281 *saccharum*), poison ivy (*Toxicodendron radicans*), bedstraw (*Galium* spp.), roses (*Rosa* spp.),
282 and elms (*Ulmus* spp.).

283 Total taxonomic richness of plants did not vary significantly among shore types ($p=0.55$),
284 but was higher along natural than engineered shores (Table 2). Species richness of alien plant
285 species tended to be higher along engineered shores than natural shores (Fig. 3), but this
286 difference was not significant ($p=0.43$). Species richness of native plants differed marginally
287 among shore types (Fig. 3, $p=0.05$), and was higher along natural than engineered shores (Table
288 2). As a consequence of opposing trends in native and alien plant species, the percentage of shore
289 zone plants that are aliens differed significantly among shore types (Fig. 3, $p=0.0003$) and was
290 significantly higher along engineered shores than natural shores (Table 2).

291 The ordination (Fig. 5) showed some clustering by shore type (e.g., the mowed bulkhead
292 sites grouping in the lower left), but with considerable overlap among shore types, so that overall
293 this clustering was not statistically significant ($p=0.18$, MRPP). Axis 2 was significantly
294 ($p<0.05$) correlated with exposure ($r^2=0.45$). Sites near the bottom end of axis 2 were exposed,
295 narrow shore zones with coarse sediments, while sites near the top end of the axis were sheltered,
296 wide, and fine-grained. Typical plants of sites near the lower left of the ordination were lawn
297 weeds such as butter-and-eggs (*Linaria vulgaris*), English plantain (*Plantago lanceolata*),
298 chicory (*Cichorium intybus*), and bedstraw (*Galium* spp.), while shrubs such as willows (*Salix*

299 spp.), witch hazel (*Hamamelis virginiana*), and ninebark (*Physocarpus opulifolius*) were typical
300 of sites near upper right. Axis 1 was not significantly correlated with any of the environmental
301 variables that we measured.

302 Attempts to predict other characteristics of the shore zone plant community from the
303 physical variables we measured were only partly successful. Models to predict native, alien, or
304 total species richness from physical variables had $R^2 < 0.25$. Echoing the differences we saw
305 across shore types, the percentage of shore zone plants that were aliens was strongly ($r^2=0.50$)
306 and positively correlated with exposure (Fig. 4).

307 *Fishes*

308 We collected 1121 individual fishes, representing 24 species. Numerical dominants
309 included spottail shiner (*Notropis hudsonius*, 41%), banded killifish (*Fundulus diaphanus*, 25%),
310 pumpkinseed (*Lepomis gibbosus*, 7%), blueback herring (*Alosa aestivalis*, 5%), white perch
311 (*Morone americana*, 5%), and alewife (*Alosa pseudoharengus*, 4%). The abundance, but not the
312 Gini diversity ($p=0.39$) of fishes varied significantly among shore types (Fig. 3). Natural shore
313 zones had higher numbers of small fishes than did engineered shore zones (Table 2). Sand shores
314 supported dense communities dominated by small fishes such as spottail shiners and banded
315 killifish, whereas riprap and rock shores supported communities of moderately high density.
316 Bulkheads and cribbing supported low numbers of fishes, and especially low numbers of small
317 fishes.

318 The physical properties of shore zones that we measured were significantly correlated
319 with fish communities. Gini diversity was positively related ($R^2=0.43$) to high roughness
320 ($p=0.005$) and low shoreline complexity ($p=0.06$), with roughness having by far the largest
321 influence (Fig. 4, Table 4). Density of small fishes (total length <20 cm) was positively

322 correlated ($R^2=0.63$) with small sediment grain size and high shoreline complexity, or nearly as
323 well ($R^2=0.52$) with wide shore zones (Fig. 4, Table 4). The density of large fishes was
324 somewhat correlated ($R^2=0.37, p=0.013$) with coarse underwater sediments.

325 The ordination (Fig. 5) confirmed the existence of clear differences in fish communities
326 among shore types. The first ordination axis was significantly ($p<0.05$) correlated with sediment
327 grain size (pebble count), exposure, and slope, and separated steep, high-energy shores
328 (bulkheads and cribbing) on the left end of the axis from flat, low-energy shores (sand) on the
329 right end of the axis. The second axis was not significantly correlated with any of the physical
330 variables that we measured, nor did we see any evidence of consistent differences in physical
331 attributes among the different geographic sections of the river.

332 *Aquatic macroinvertebrates*

333 The D-net samples were dominated by oligochaetes (overall mean = 275/sample),
334 chironomids (163/sample), zebra mussels (102/sample), cladocerans (79/sample), amphipods
335 (59/sample), gastropods (53/sample), and mites (44/sample). Neither the overall abundance nor
336 diversity of D-net invertebrates was related to shore type ($p=0.15$ and 0.37, respectively), or
337 differed between natural and engineered shore zones ($p>0.4$). Of the dominant groups just listed,
338 only the abundance of oligochaetes, zebra mussels, and cladocerans was related to shore type
339 (Fig. 3). Oligochaetes tended to be less abundant off of high-energy shorelines (bulkheads and
340 cribbing), zebra mussels were most abundant on coarse-grained shores (bulkheads, bedrock,
341 riprap, and cribbing), and cladocerans were most abundant on bedrock, sand, and riprap.

342 Community structure of D-net invertebrates varied across shore types (Fig. 5). Axis 2
343 was clearly related to site exposure, with highly exposed sites having coarse-grained substrates
344 near the upper end of the axis, and sheltered sites with fine-grained substrates near the lower end

345 of the axis. Axis 1 scores were not closely correlated with any of the environmental variables
346 that we measured.

347 Gini diversity of D-net invertebrates was weakly correlated with shore zone width (i.e.,
348 slope) ($r=-0.47$, $p=0.05$). Generally, abundance of dominant taxa (or of all taxa combined) and
349 diversity of D-net invertebrates were poorly correlated with environmental variables (R^2 of
350 models with the lowest AIC usually were <0.2). Exceptions were models for the abundance of
351 zebra mussels ($R^2=0.66$, positively correlated with pebble count – Fig. 4 – and surprisingly
352 negatively correlated with roughness), oligochaetes ($R^2=0.36$, positively correlated with SAV
353 index and exposure), amphipods ($R^2=0.32$, positively correlated with SAV index and pebble
354 count), and gastropods ($R^2=0.29$, positively correlated with pebble count).

355 We were able to obtain cores at both depths and months at only 10 of the 18 study sites,
356 so the statistical analyses of densities and diversity are based on this subset of 10 sites. Mean
357 invertebrate density was $20,500/m^2$; dominant groups were oligochaetes ($10,400/m^2$),
358 chironomids ($3400/m^2$), nematodes ($1900/m^2$), zebra mussels ($1200/m^2$), amphipods ($660/m^2$),
359 and sphaeriids ($610/m^2$). Neither total macroinvertebrate density nor the density of any of the
360 dominant groups just mentioned varied significantly among shore types or between natural and
361 engineered shores, possibly because of the small, unbalanced data set. Furthermore, density of all
362 macroinvertebrates and most groups taken individually was statistically unrelated to the
363 environmental characteristics that we measured. The exception was oligochaetes, whose density
364 was negatively related to sediment grain size and positively related to the SAV index ($R^2=0.81$,
365 $p=0.003$). Gini diversity of sediment macroinvertebrates in cores did not differ significantly
366 across shore types, but was positively correlated with both shore zone width and site exposure
367 ($R^2=0.67$, $p=0.02$; data not shown).

368 We ordinated samples from each site, depth, and time separately (we had at least one
369 sample from 14 of the 18 sites). Inspection of this ordination showed that samples from the two
370 sampling times (May and August) fell out separately, so we re-analyzed samples from each
371 month separately. There were no clear relationships between shore type and the ordination axes
372 for either month (data not shown), but community structure was clearly related to environmental
373 characteristics, especially sediment grain size. In May, axis 1 was significantly related to
374 exposure, the SAV index, and sediment organic content ($R^2=0.65, p=0.0001$), while axis 2 was
375 related to sediment grain size and organic content ($R^2=0.65, p=0.0001$). In August, axis 2 was
376 unrelated to measured environmental characteristics, but axis 1 was related to sediment grain size
377 and organic content, log(shore zone width), and exposure ($R^2=0.61, p=0.0009$).

378 *Terrestrial invertebrates*

379 Our samples of terrestrial invertebrates were strongly dominated by dipterans (79% of
380 animals collected, on average) and hemipterans (8%). Other taxa that constituted >1% of the
381 catch included gastropods, collembolans, spiders, mites, ants, and beetles. There were no
382 significant differences among shore types, or between natural and engineered shores, in densities
383 of total invertebrates or of any of the taxa just named, except for mites ($p=0.01$), or in Gini
384 diversity of terrestrial invertebrates.

385 Density of terrestrial invertebrates was positively related to the SAV index ($R^2=0.31,$
386 $p=0.02$), perhaps reflecting inputs of wrack from nearby SAV beds. Densities of specific
387 invertebrate groups were related to environmental characteristics as follows (data not shown):
388 mites (complexity[+], logSAV[+], $R^2=0.44, p=0.01$); beetles (log-shore zone width[-], pebble
389 count[-], $R^2=0.48, p=0.008$); collembolans (logSAV[+], $R^2=0.31, p=0.02$); dipterans
390 (logSAV[+], rugosity[-], $R^2=0.45, p=0.01$) . Densities of spiders, ants, gastropods, and

391 hemipterans, and Gini diversity were not significantly correlated with any of the environmental
392 features that we measured.

393 The ordination results separated the sampling sites partly on the basis of environmental
394 characteristics (the two bulkhead sites near the top of Fig. 5 both are mowed lawns) and partly on
395 the basis of geography (note the cluster of upper-river sites in the lower-right corner of the
396 figure). Axis 1 scores were weakly related to log SAV index ($R^2=0.18$, $p=0.08$), whereas axis 2
397 scores were not related to the environmental variables that we measured.

398 *Gastropods*

399 We found 20 species of freshwater and land gastropods along the Hudson's shores. The
400 amphibious *Fossaria* sp. was most abundant, with the freshwater *Physella* sp. and *Littoridinops*
401 *tenuipes* also being common and widespread. Gastropod communities were highly variable
402 across sites, and neither abundance nor diversity (Gini index) differed significantly among shore
403 types for subtidal or intertidal gastropods. There were significant differences across shore types
404 for upland gastropods, however, with higher densities and diversities along sandy and rocky
405 shores (Fig. 3). Ordinations of gastropod communities (not shown) did not clearly distinguish
406 among shore types, although communities of flat slopes were weakly separated from those of
407 steep slopes.

408 Although there were few clear differences in gastropod communities among the pre-
409 defined shore types, high density and diversity of gastropods were consistently associated with
410 high structural complexity of the shore zone. Abundance of subtidal gastropods was significantly
411 correlated ($R^2=0.53$, $p=0.005$) with high shoreline complexity, and abundance of intertidal
412 gastropods was significantly correlated with high roughness ($R^2=0.36$, $p=0.009$). Gini diversity
413 of both subtidal and intertidal gastropods was positively correlated with rugosity ($R^2=0.24$,

414 $p=0.04$; $R^2=0.23$, $p=0.05$, respectively). In the upland zone, gastropod abundance was not
415 significantly correlated with any of the environmental variables that we measured, but Gini
416 diversity was correlated ($R^2=0.53$, $p=0.004$) with pebble count (-) and exposure (+).

417 **Discussion**

418 Hudson River shore zones support rich biological communities. Even in a cursory survey,
419 we found hundreds of taxa of plants and dozens of species of fishes, as well as diverse
420 communities of terrestrial and freshwater invertebrates. The densities of aquatic invertebrates are
421 at least twice as high as those in the rest of the river (Strayer and Smith 2001).

422 The Hudson's shore zones are enormously varied in terms of their physical characteristics
423 (Table 1) and the biodiversity they support (Table 3). Quite a lot of this variation was associated
424 with our classification of shore type, even though this classification was very simple and based
425 only on conditions around the high-water line. Presumably, a more sophisticated classification
426 that considered adjoining land use (e.g., forest, railroad, lawn) and intertidal and subtidal
427 conditions (depth, particle size, submersed vegetation) more thoroughly would be even more
428 successful in explaining variation in biodiversity.

429 As a class, engineered shore zones differed from “natural” shore zones (Tables 1, 2).
430 Engineered shores were narrower (and therefore steeper), coarser-grained, and more exposed
431 than natural shore zones. Engineered sites may have been more exposed prior to human activity
432 (i.e., defenses were built on the most naturally exposed sites, so the engineering is a result of the
433 naturally high exposure) or often because the shoreline was built out into deeper water or more
434 exposed locations (i.e., the high exposure is a result of the engineering activity). Surprisingly,
435 some of the engineered shore zones (riprap and cribbing) were rougher than many natural shores,
436 at the scale of our roughness measurements.

437 Community composition of most taxonomic groups differed across shore types (Fig. 5).
438 For the majority (13/18) of our biological attributes, there was some relationship with a physical
439 variable that we measured (Table 4). Because we identified invertebrates only to a coarse
440 taxonomic level, we probably underestimated the importance of shore type in determining the
441 composition of the invertebrate community. If we had identified all of the invertebrates to
442 species or genus, we might have seen clearer separations among the invertebrate communities of
443 different shore types (e.g., Lenat and Resh 2001; but see Bailey et al. 2001). Overall, we found
444 that shore zone types supported quite different biological communities and often these could be
445 traced to relationships between specific taxa and some physical attribute of the shore zone. For
446 the biodiversity variables that differed significantly across shore types (Table 3), engineered
447 shore zones tended to have less desirable characteristics than natural shore zones: fewer fishes,
448 fewer species of native plants, and a higher percentage of alien plants. It is worth noting that
449 riprapped shore tended to have more desirable values for biodiversity variables than the other
450 engineered shore types, presumably a result of its higher physical complexity and lower wave
451 reflectivity (cf. Pister 2009).

452 Nevertheless, there was a great deal of variation in biodiversity among our study sites
453 that was not related to shore type. Even our relatively small sample (18 sites or 1.8 km out of
454 ~300 km of shoreline) revealed large variation in both shore zone character (several to 100-fold
455 differences) and associated biota. Some of this variation surely arose from unmeasured physical
456 variables and a host of biotic interactions. Moreover, while it may be tempting to view
457 relationships between shore zone attributes and biota as causal the patterns may be driven by
458 indirect interactions or covariation with other factors. Our findings have important implications
459 for management or design of shore zones capable of supporting higher biodiversity but in our

460 desire to encompass as much of the range in shore zone function as possible we could not
461 explore these mechanistic linkages.

462 Not surprisingly, no single shore type provides high values of all ecological functions
463 (Table 3). Wide, sandy, dissipative shores support many small fishes and a high proportion of
464 native plant species, but few large fishes. Thus, no shore zone maximizes all kinds of
465 biodiversity.

466 Our study sites can be broadly arranged according to their physical characteristics along
467 the two axes of exposure and complexity (Fig. 2). Both of these dominant physical axes appear
468 to affect shore zone biodiversity. Community composition varies along the first axis (defined by
469 the related variables of exposure, sediment grain size, shore zone slope, and shore zone width),
470 as shown both by the ordinations and the responses of individual taxa such as small fishes (which
471 avoid highly exposed shores) and zebra mussels (which favor highly exposed shores). The
472 association between alien plants and high exposure and engineered shorelines may result from
473 the ability of alien plants to exploit disturbed sites (e.g., Davis et al. 2000). The second axis of
474 physical complexity (expressed by variables such as substrate roughness or shoreline
475 complexity) may generally favor high biodiversity (Fig. 4; Barwick 2004; Brauns et al. 2007;
476 Paetzold et al. 2008; Pollock et al. 1998; Sass et al. 2006; Strayer and Findlay 2010). We suggest
477 that these two physical axes (exposure and complexity) may generally be useful in explaining
478 variation in predicting the species composition, diversity, and dominant ecological traits of shore
479 zone communities.

480 Although we were able to point to the importance of exposure to shore zone
481 communities, scientists and managers will need to develop faster, easier, more reliable, and more
482 standardized ways of measuring “exposure”, which up to this point has often been treated as a

483 narrative variable or simply assumed to be related to fetch (e.g., Keddy 1982; Brodersen 1995;
484 Ekebom et al. 2003). When we say “exposure”, do we mean average wave force, peak wave
485 force, peak forces of any kind (whether wave or ice-push), or all of the preceding? How do we
486 reliably measure these forces so we can compare across studies?

487 Clearly, our results present only a broad and preliminary assessment of how the
488 biological communities of shore zones vary according to their physical characteristics and human
489 engineering. Nevertheless, even at this early stage in our investigations, we can offer the
490 following suggestions for shore zone management. Because biotic communities consistently vary
491 along the gradient between wide, sheltered, fine-grained shore zones and narrow, exposed,
492 coarse-grained shore zones, it seems important to preserve or restore a mix of shore types all
493 along this gradient, at least to the extent that they occurred naturally. In particular, the common
494 trend to replace wide, sheltered shore zones with narrow, exposed shore zones (Strayer and
495 Findlay 2010) may require special protection for the former to preserve biodiversity in
496 intensively developed waterways. At a finer scale, biodiversity often is enhanced by local
497 roughness and heterogeneity (e.g., Barwick 2004; Brauns et al. 2007; Paetzold et al. 2008;
498 Pollock et al. 1998; Strayer and Findlay 2010). Thus, the common tendency to destroy such local
499 heterogeneity by using uniform building materials, smooth grades, and straight-line designs may
500 have strongly negative consequences for shore zone biodiversity, and should be avoided.

501 We suggest two lines of future research that should be useful in achieving the level of
502 understanding needed to manage shore zone biodiversity well. First, comparative field
503 investigations like our study might be focused more tightly on a particular type of shore zones
504 (e.g., riprapped shores) or a particular taxonomic or functional group. This tighter focus would
505 allow for use of sampling techniques that are especially well-suited to that shoreline type or

506 taxonomic group, sampling designs well-matched to the taxonomic group (e.g., seasonal or
507 diurnal sampling), and finer levels of identification or analysis (e.g., body size or condition).
508 Ultimately, this tighter focus should lead to higher resolution, lower variance, and increased
509 statistical power to detect differences among shore types or along environmental gradients of
510 interest.

511 Second, it would be very valuable to conduct large-scale field experiments to test how
512 factors that we have identified as potentially important might affect shore zone biodiversity. An
513 experimental approach would allow a much stronger test of the effects of characteristics that are
514 especially amenable to management intervention (e.g., size of riprap, slope of revetments,
515 roughness of bulkheads). As others have suggested (e.g., Doyle et al. 2008), it may be possible to
516 include such experiments in the construction of new shore zone defenses or the repair of aging
517 shore zone infrastructure.

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524

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- 630 Wetzel RG (1990) Land-water interfaces: metabolic and limnological regulators.
631 Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte
632 Limnologie 24: 6-24.

633 Table 1. Environmental characteristics (mean, with range in parentheses) of Hudson River shore zones. Variables marked with
 634 asterisks differed significantly (ANOVA, $p<0.05$) among shore types.

Shore type	Shore zone width* (m)	Pebble count*	Diversity of pebble count	Shoreline complexity	Roughness*	Exposure*	Sediment organic matter (%)	Subtidal sediment index
Sand	124 (55-257)	1.0 (0.96-1.1)	0.25 (0.03-0.65)	1.03 (1.00-1.06)	1.06 (1.02-1.10)	16 (14-18)	2.2 (1.5-2.8)	0.47 (0.14-0.79)
Rock	24 (8.9-52)	3.4 (1.6-4.8)	0.68 (0.63-0.76)	1.08 (1.00-1.12)	1.27 (1.12-1.40)	12 (7-17)	3.7 (2.3-5.3)	2.0 (0.06-3.3)
Bedrock	30 (8.3-72)	4.7 (3.6-6.2)	0.66 (0.33-0.85)	1.11 (1.03-1.20)	1.19 (1.17-1.21)	9.8 (4-14)	3.2 (3.0-3.5)	2.4 (1.0-3.4)
Riprap	8.4 (6.2-11)	5.0 (4.5-5.6)	0.59 (0.45-0.73)	1.23 (1.11-1.44)	1.45 (1.30-1.54)	8 (6-10)	2.9 (0.64-4.2)	2.5 (1.2-3.8)
Cribbing	20 (0-52)	4.2 (2.7-5.7)	0.71 (0.65-0.77)	1.06 (1.00-1.11)	1.37 (1.18-1.58)	10 (7-14)	2.7 (2.3-3.2)	1.6 (0.52-2.6)
Bulkhead	0.8 (0-2.4)	6.4 (5.3-7)	0 (0-0.45)	1 (1.00-1.00)	1.15 (1.00-1.24)	2.7 (1-5)	2.7 (2.7-2.7)	1.3 (0.83-1.7)

635

636 Table 2. Differences between natural and engineered shore zones along the Hudson River (n=9 for each kind of shore zone). We show
637 only variables for which significant ($p<0.1$) differences exist between natural and engineered shore zones.

Variable	Natural	Engineered	p
Log (shore zone width) (m)	1.51	0.68	0.006
Exposure	12.6	6.9	0.01
Rugosity	1.17	1.32	0.07
Pebble count	3.1	5.2	0.02
Native plant richness	30.8	14.8	0.0005
Total plant richness	49.7	34.2	0.01
% alien plants	14.9	27.1	0.002
Abundance of small fish (square-root transformed)	8.2	3.4	0.04

638

639

640 Table 3. Summary of differences in major ecological characteristics of different types of shores along the Hudson River. All variables
 641 are scaled to a maximum of 100, based on untransformed data to allow comparisons across variables (note that statistical tests usually
 642 were based on transformed data). For example, a value of 61 means that the mean value of a variable on a particular shore type was
 643 61% of that of the maximum for any shore type. Boldface indicates variables that differed significantly among shore types. Aquatic
 644 invertebrate data are from D-net samples.

	Sand	Rock	Bedrock	Riprap	Cribbing	Bulkhead	<i>p</i>
Fish diversity	77	95	95	100	100	89	0.32
Abundance of large (>20 cm long) fish	6	55	100	61	15	21	0.01
Abundance of small (<20 cm long) fish	100	12	8	17	5	1	0.0003
Species richness of native plants	100	84	90	55	45	32	0.05
Species richness of alien plants	69	67	56	78	53	100	0.64
% of plant species that are not native	42	43	37	68	53	100	0.0003
Aquatic invertebrate diversity	92	74	100	95	100	78	0.40
Aquatic invertebrate abundance	54	32	100	74	24	50	0.22
Terrestrial invertebrate diversity	58	80	40	100	48	87	0.23
Terrestrial invertebrate abundance	44	27	59	53	37	100	0.48

645 Table 4. Summary of simple Pearson correlations between environmental variables and major
 646 aspects of shore zone biodiversity along the Hudson River. Symbols show the direction of the
 647 relationship; the number of symbols indicates statistical significance (+++, $p < 0.01$; ++, $p < 0.05$;
 648 +, $p < 0.1$). NA = not applicable (i.e., the environmental variable was not included in the statistical
 649 model for that biodiversity variable). “Aquatic invertebrate” results are based on D-net samples.

	Exposure	Log (shore zone width)	Pebble count	- Shoreline complexity	Rugosity	Log (SAV index)	Sediment grain size	Sediment organic matter	
Fish diversity				-	++			NA	
Abundance of large fish			+				++	NA	
Abundance of small fish	---	+++	---					NA	
Fish ordination axis 1	---	+++	---					NA	
Fish ordination axis 2								NA	
Native plant richness						NA	NA	NA	
Alien plant richness	+					NA	NA	NA	
% alien plant species	+++	---	+++			NA	NA	NA	
Plant ordination axis 1						NA	NA	NA	
Plant ordination axis 2	---	+++	---			NA	NA	NA	
Aquatic invertebrate diversity							+	--	
Aquatic invertebrate									

abundance									
Aquatic invertebrate ordination axis 1						+			
Aquatic invertebrate ordination axis 2	+++	---	+++						
Terrestrial invertebrate diversity	+	--	+						
Terrestrial invertebrate abundance					-				
Terrestrial invertebrate ordination axis 1									
Terrestrial invertebrate ordination axis 2		-							

650 **Figure legends**

651 **Fig. 1** Location of the study sites (black circles and italic labels) in the freshwater tidal Hudson
652 River in eastern New York, USA. The first letter of the site code gives the section of river
653 (*L*=lower, *M*=middle, *U*=upper), and the last two letters give the shore type (*BH*=bulkhead,
654 *BR*=bedrock, *CR*=cribbing, *RO*=natural rock, *RR*=riprap, *SA*=sand)

655 **Fig. 2** PCA analysis of Hudson Valley shore zones on the basis of physical characteristics (shore
656 zone width, pebble count, shoreline complexity, roughness, and exposure). Axes are scaled
657 according to the % variance explained (these two axes account for 90% of total variance). The
658 first letter of the site code gives the section of river (*L*=lower, *M*=middle, *U*=upper), and the last
659 two letters give the shore type (*BH*=bulkhead, *BR*=bedrock, *CR*=cribbing, *RO*=natural rock,
660 *RR*=riprap, *SA*=sand)

661 **Fig. 3** Summary of differences in biodiversity across types of shore zones in the Hudson River:
662 a) species richness of native and alien plants; b) percentage of plant species found at each site
663 that are alien; c) number of small (<20 cm long) fish caught at each site; d) number of large (>20
664 cm long) fish caught at each site; e) number of oligochaetes caught per D-net sample; f) number
665 of zebra mussels caught per D-net sample; g) number of cladocerans caught per D-net sample; h)
666 Gini diversity of upland gastropods; i) number of upland gastropods collected. Error bars show 1
667 SE; letters in or above bars show differences between shore types according to Tukey's
668 Studentized Range (HSD) test at $p=0.05$; the vertical dashed line separates "natural" shore zones
669 on the left from engineered shore zones on the right. Note the differences in scaling on different
670 y-axes

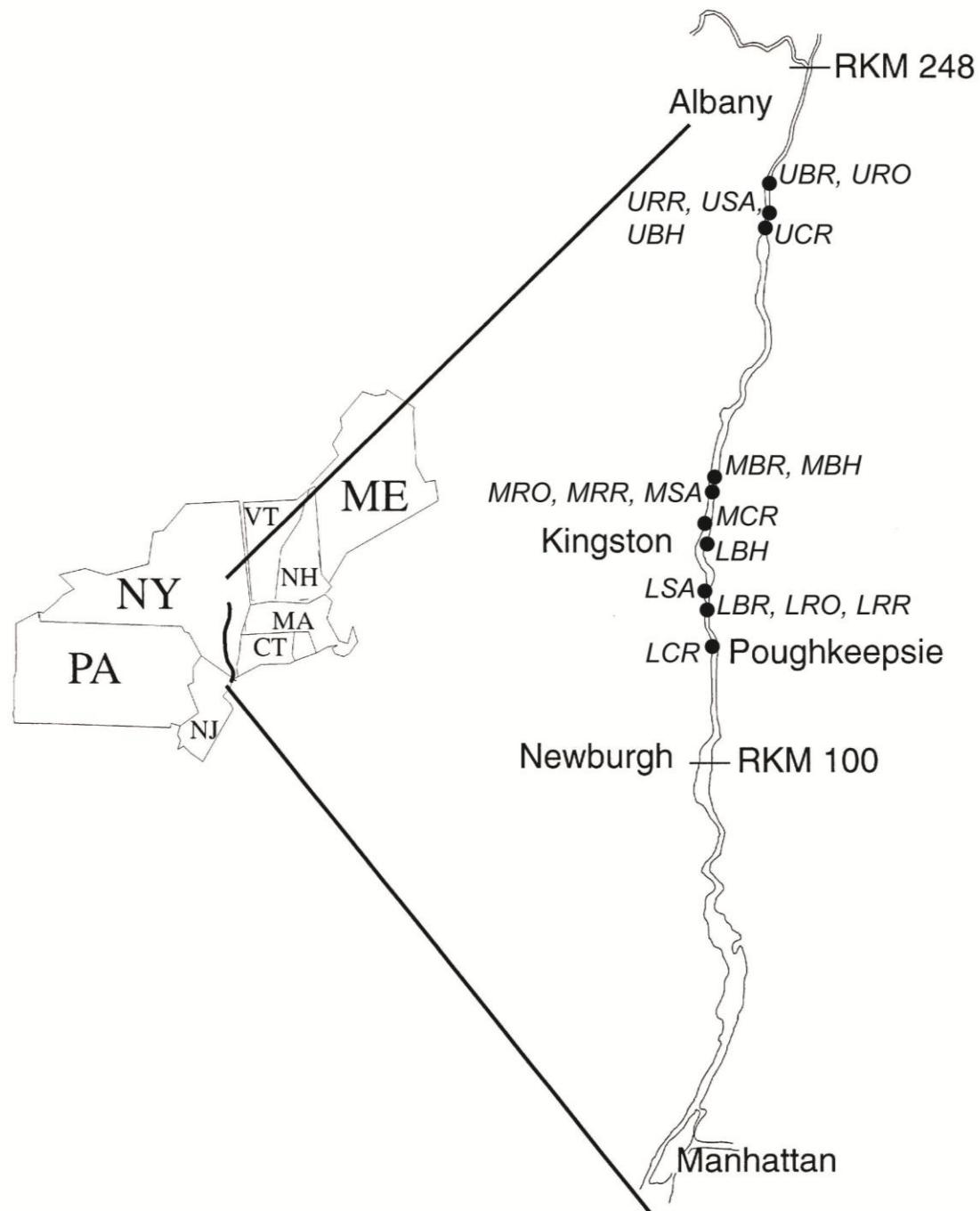
671 **Fig. 4** Examples of relationships between physical characteristics and biodiversity of Hudson
672 River shore zones: a) percentage of plant species found at each site that are alien as a function of

673 site exposure (low values indicate high exposure; $r^2=0.56$, $p<0.001$); b) fish diversity (Gini
674 index) as a function of substrate roughness ($r^2=0.25$, $p=0.03$); c) number of small (<20 cm long)
675 fish caught at each site as a function of shore zone width ($r^2=0.55$, $p<0.001$); d) number of zebra
676 mussels caught per D-net sample as a function of substrate particle size (larger numbers indicate
677 coarser sediments; $r^2=0.56$, $p<0.001$)

678 **Fig. 5** Ordinations of community structure of (a) fishes, (b) plants, (c) aquatic invertebrates (D-
679 net samples), (d) terrestrial invertebrates. The first letter of the site code gives the section of river
680 (L=lower, M=middle, U=upper), and the last two letters give the shore type (BH=bulkhead,
681 BR=bedrock, CR=cribbing, RO=natural rock, RR=riprap, SA=sand). The community structure
682 of different shore types differed significantly (according to MRPP) for fish ($p=0.001$) and aquatic
683 invertebrates ($p=0.008$), but not for plants ($p=0.18$) or terrestrial invertebrates ($p=0.15$)

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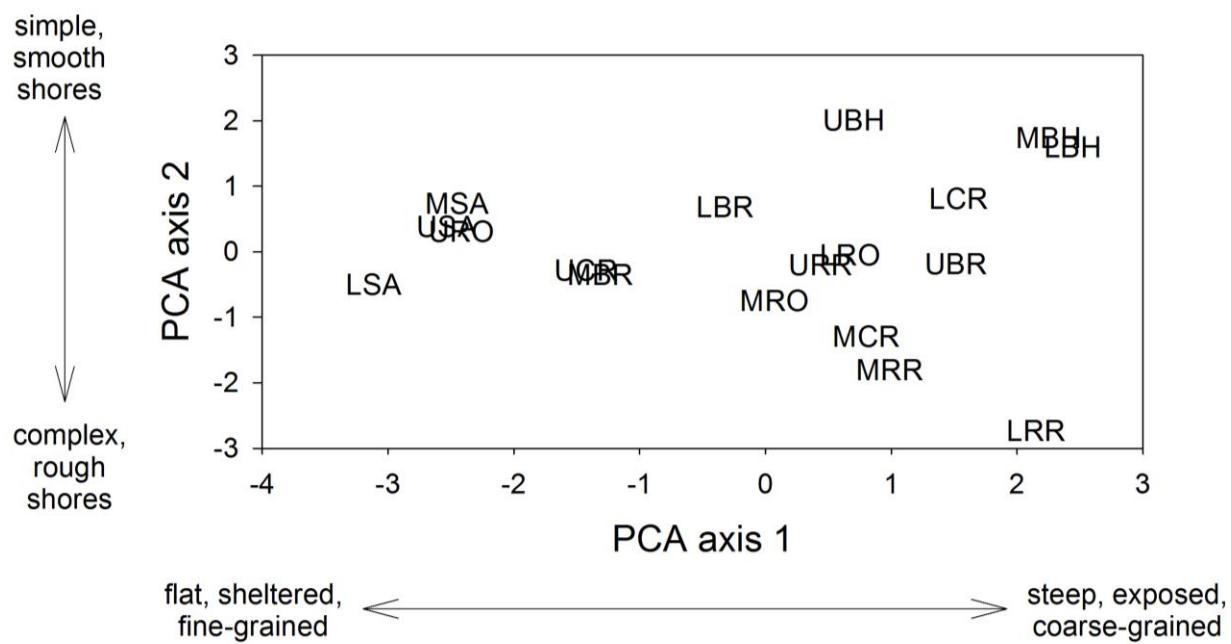


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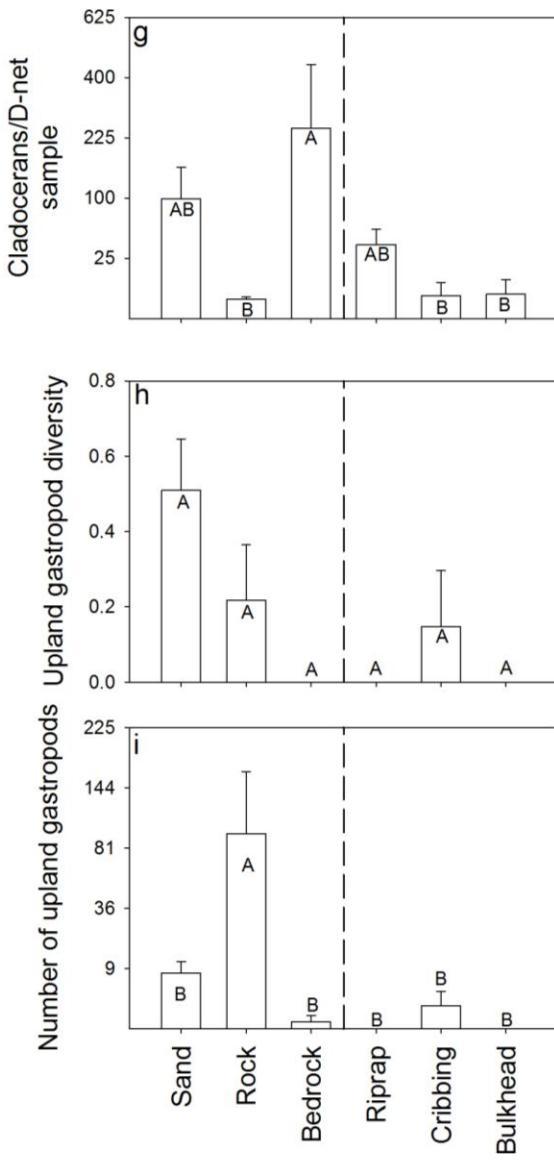
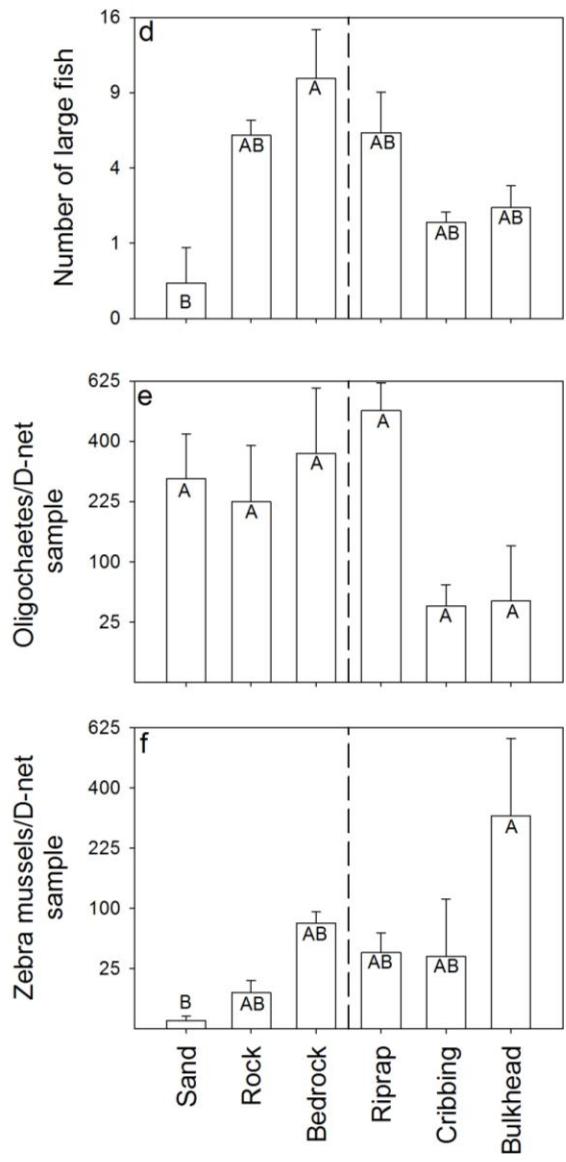
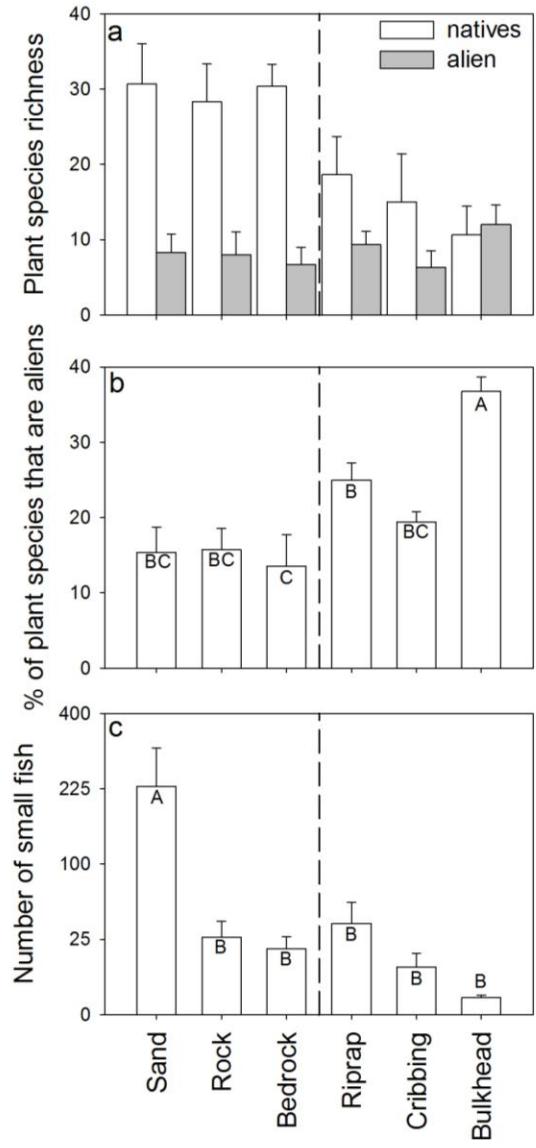
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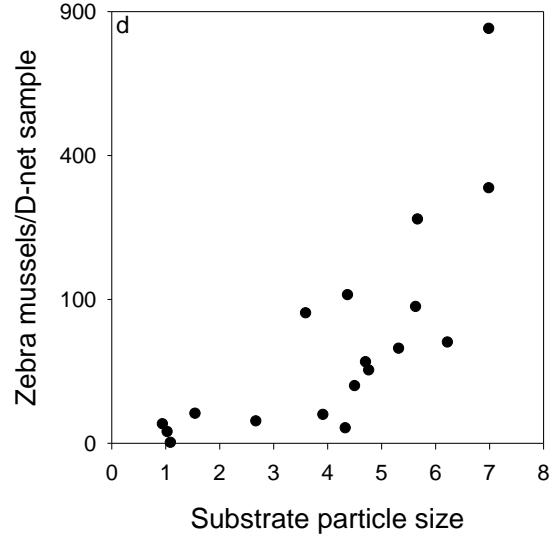
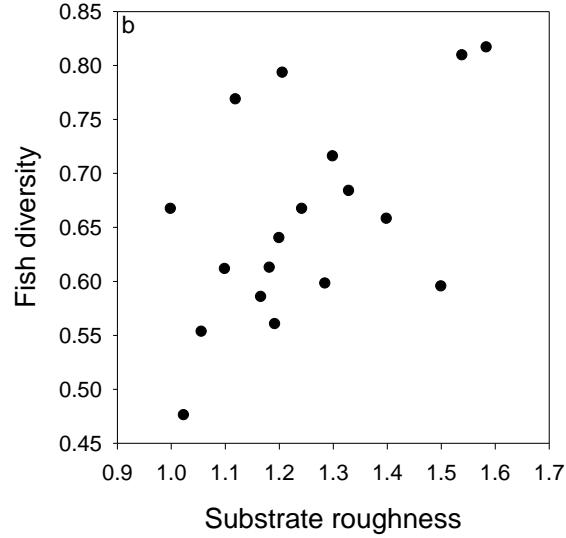
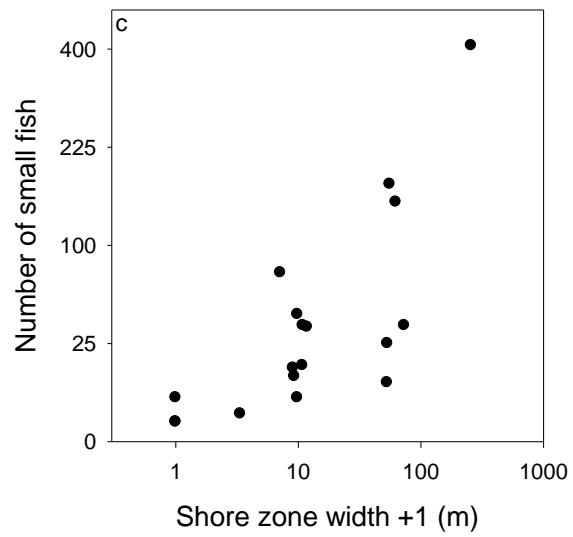
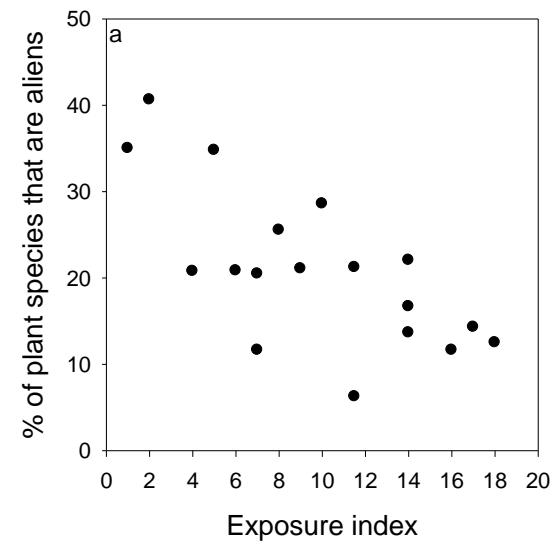


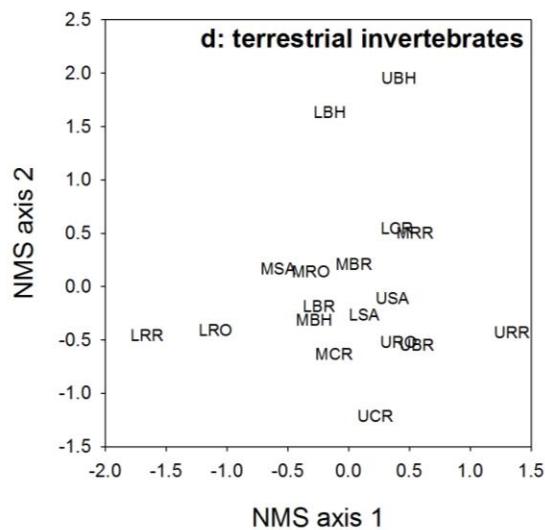
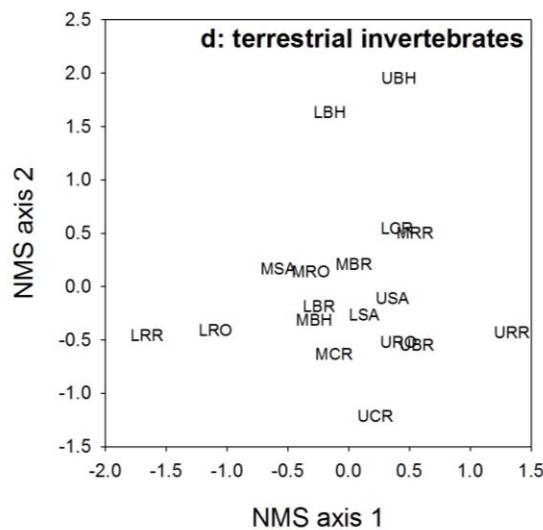
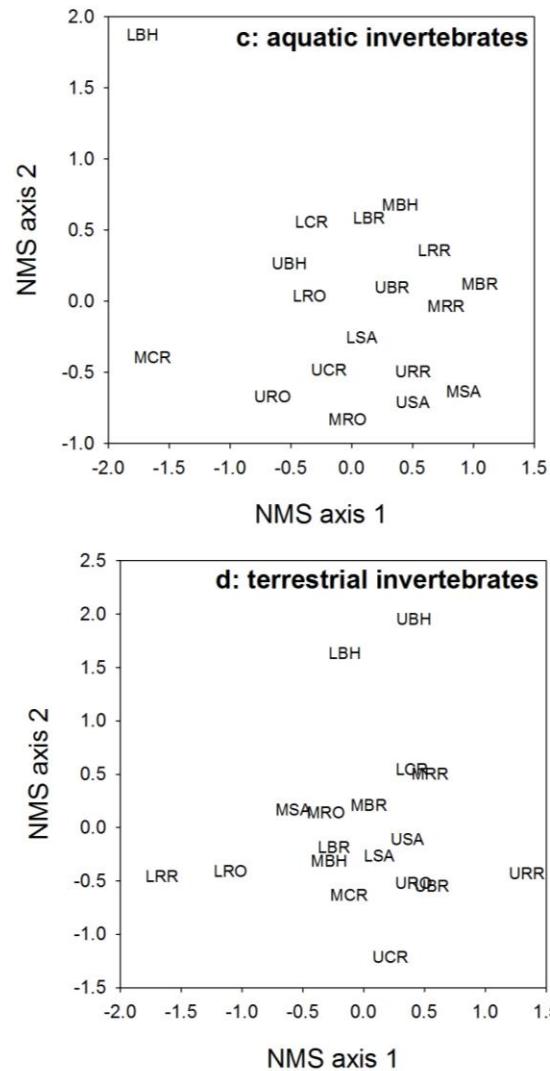
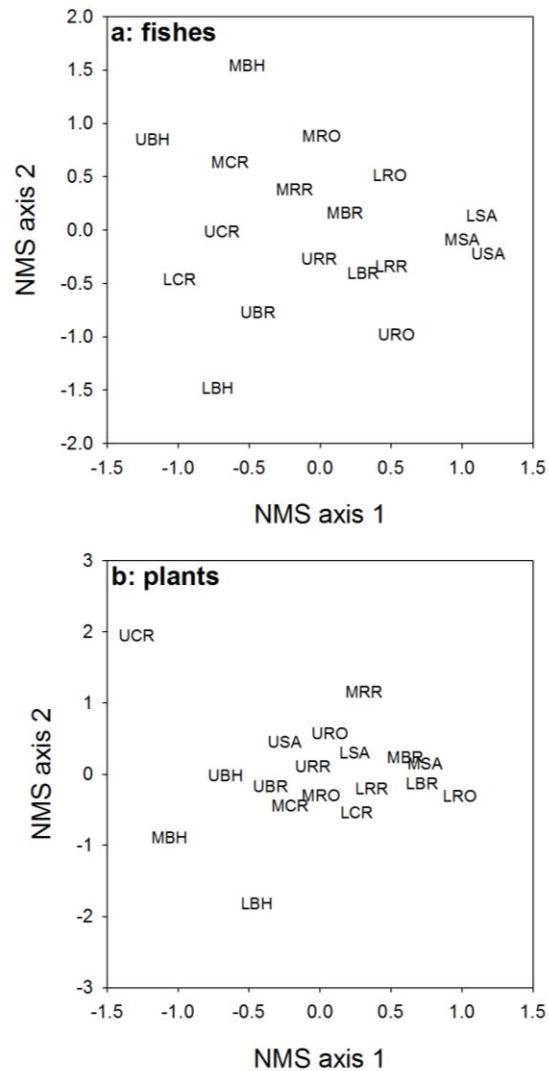
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Chapter 3: The Ecology of Freshwater Wrack along Natural and Engineered Hudson River

Shorelines

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ABSTRACT

Organic matter that is washed onto shore, or “wrack,” is an important component of shoreline ecosystems, providing habitat for invertebrates and organic matter and nutrients to both the upland terrestrial communities and aquatic ecosystems. While marine wrack has been studied extensively, wrack along freshwater shorelines has received less attention. Here, we report on the standing stocks, mobility, decomposition rates, and invertebrate communities of wrack (chiefly *Vallisneria americana*) on different types of Hudson River shorelines, both natural and engineered. Standing stocks of wrack sometimes exceeded 1 kg dry mass /m², and were highest on shorelines having flat slopes. Engineered shorelines such as bulkheads accumulated little or no wrack. Wrack was primarily composed of dead *Vallisneria americana* with lesser amounts of debris from *Trapa natans* and small branches. Artificial wrack (hay) placed below the high tide mark was rarely retained for more than a few tidal cycles, particularly on highly exposed shores. Wrack on cribbing shorelines decayed significantly faster than on other shoreline types with 50% mass loss occurring within 14 days. Invertebrate abundance in wrack was significantly different among shoreline types, with the lowest abundance found on cribbing. Invertebrate diversity was significantly higher on sandy, rocky, and riprap shorelines than on cribbing. Cribbing and other steep, reflective shorelines capture little wrack and provide poor habitat for wrack-dwelling invertebrates. As managers seek to restore shorelines and protect infrastructure from future sea level rise, it is likely structures such as cribbing, bulkheads, and riprap will be used. Because such hard shorelines minimize the ecological functions associated with wrack, they may be inferior to non-structural solutions such as relocating or elevating critical infrastructure, or building shorelines with “soft” engineering.

Keywords: freshwater, wrack, engineered, decomposition, invertebrate diversity, invertebrate density

INTRODUCTION

Organic matter that is washed onto shore, or “wrack,” is an important component of shoreline ecosystems, providing habitat for invertebrates, attracting birds and other predators, and providing organic matter and nutrients to the upland terrestrial communities (e.g., Backlund 1945; Thompson et al. 2002; Dugan et al. 2003; Polis et al. 2004; Strayer and Findlay 2010). Marine wrack has been studied extensively (e.g., Backlund 1945; Brown and McLachlan 2002; Polis et al. 2004; Jedrzejczak 2002a), but freshwater wrack has received much less attention (Strayer and Findlay 2010). Defining the role of wrack in various kinds of freshwater ecosystems is important both for managing wrack itself, and for designing more effective shoreline restoration, conservation and management.

Marine shore zones vary widely in their ability to accumulate and retain wrack. Factors such as the availability of nearby sources of organic matter, shore zone roughness and slope, and the energy regime affect the amount of wrack that reaches a shoreline and is retained (e.g., Backlund 1945; Orr et al. 2005). In addition, human management of the shore zone may affect wrack accumulation. Wrack is often removed because it is deemed unsightly, or it may not be able to accumulate along highly engineered shorelines such as bulkheads or cribbing, because they are too steep or smooth (e.g., Llewellyn and Shackley 1996; Malm et al. 2004; Strayer and Findlay 2010).

Large numbers of invertebrates live in marine and estuarine wrack (e.g., Backlund 1945; Llewellyn and Shackley 1996; Romanuk and Levings 2003). Polis and Hurd (1996) found that high production from the ocean subsidized arthropod communities living on the shoreline, which in turn supported communities of birds and mammals (Llewellyn and Shackley 1996; Romanuk

and Leving 2003). The invertebrate community changes over successional time, although studies differ on the importance of these changes to the structure and decomposition of wrack (Griffiths and Stenton-Dozey 1981; Bedford and Moore 1984; Jedrzejczak 2002b).

Based on findings from marine and estuarine shore zones, we would expect wrack to be important along many freshwater shorelines, and to vary widely in amount and decay/export across different kinds of freshwater shore zones. The goals of our studies were to 1) measure the amount of wrack accumulated; (2) measure the mobility of wrack; (3) compare the decomposition of wrack; and (4) document the use of wrack by invertebrates on different kinds of natural and engineered shorelines along the freshwater tidal Hudson River.

METHODS

The Study Area

The study site is the freshwater tidal Hudson River in eastern New York, where tides are present from the mouth of the river to the Federal Dam at Troy, NY at RKM (river kilometer) 248. The Hudson River experiences tidal fluctuations of 1-1.5 m, accompanied by high variability in exposure to wind waves. The tidal currents are generally stronger than the velocity of the freshwater outflow, and usually reverse the direction of water flow every 6 hours (Geyer and Chant 2006).

The Hudson River's shoreline is physically heterogeneous, with sandy and rocky beaches and various types of constructed, hardened shorelines (Fig. 1). Just over half (53%) of the shoreline is engineered, with unconsolidated rock, which includes riprap, making up the majority of the structures (Miller 2005). This simplification and hardening of the Hudson River shoreline (sheetpile, bulkheads, or cribbing) eliminates the natural complexity that helps maintain the

biodiversity of these areas, and may decrease the amount of wrack that is able to accumulate (Chapman and Bulleri 2003; Moschella et al. 2005).

We measured slope, roughness, and substratum particle size at 0.6m, 1.2m, and 1.5 m above mean low tide, at three locations along each shoreline type. Slope was measured along each shoreline using a line level and tape measure. To measure roughness, a 100 cm length of chain (link size of 1cm) was laid first parallel and then perpendicular to the water line, following the contours of the substrate as closely as possible (USEPA 2004). The resulting straight-line length between the ends of the chain was measured with a meter stick, and the ratio of chain length to tape length provided a measure of roughness. Particle size description (“pebble counts”) was done at three points along 100 m transects. The particle size class descriptions were used in accordance with USEPA (2004), identifying boulders (250 - 4000 mm), cobbles (64 - 250 mm), coarse gravel (16 - 64 mm), fine gravel (2 - 16 mm), and sand (0.06 - 2 mm).

Sampling took place in August and October of 2009.

The main source of wrack in the Hudson River is from submerged aquatic vegetation (mainly *Vallisneria americana*), which when alive provides habitat for macroinvertebrates, with densities 4-5 times higher than in unvegetated areas (Strayer and Malcom 2007). Floating aquatic vegetation, including the invasive water chestnut (*Trapa natans*), also provides habitat for a diverse community of invertebrates (Strayer et al. 2003; Kornijow et al. 2010). While *V. americana* is more prevalent, both species are very common components of wrack along Hudson River shorelines.

Standing stock of wrack on different kinds of shorelines

We measured the amount of wrack that had accumulated on three examples of each of six types (sand, rock, bedrock, riprap, cribbing, and bulkhead) of shorelines throughout the freshwater tidal Hudson (see Strayer et al. 2012 for details of study design). Each 100-m long site was visited once, during 20 September-14 November 2007. We estimated the amount of wrack in two ways. We ran transect lines at the middle, upriver end, and downriver end of each site, extending from the low-water line to 1 m vertically above the high-water line. We recorded the width of the wrack line crossing each transect and collected a sample where the wrack was thickest along each transect using a 50x50 cm quadrat. Material collected in the quadrats was rinsed in the laboratory to remove sand, then dried to constant mass at 60°C and weighed.

Mobility of wrack on different kinds of shorelines

To determine how mobile wrack is at different elevations and on different types of shorelines, we placed an easily identified wrack analogue (hay) onto different locations on Hudson River shorelines and observed whether it remained in place. We placed 40g of oven-dried hay in a 0.25 m² patch at the mid-tide level, the mean high tide level, and 0.3 m vertically above the mean high tide level on sandy, rocky, and riprapped shores at Cruger Island (a highly exposed site at RKM 159) and Beacon (a sheltered site at RKM 98) during 24 June-28 July 2009. We revisited these sites 1 and 7 days later, collected any hay remaining in the original area, dried it to constant mass at 60°C and weighed it.

Decomposition rates of wrack on different kinds of shorelines

We studied decomposition rates of wrack placed onto four different types of shoreline (sandy, rocky, riprap, cribbing) along the freshwater tidal portions of the Hudson River. “Sandy”

shoreline contained small gravel or sandy substrate, “rocky” shoreline consisted mainly of cobbles and some boulders, and “riprap” was composed of large boulders placed along shorelines for stabilization. “Cribbing” is used to refer to the vertical wooden pilings connected by horizontal timbers retaining crushed stone. We studied two examples of each shoreline types except cribbing, which was unreplicated.

At each site, 15 litterbags of plastic mesh (28x46cm; mesh size 1 mm) were staked, tied, or anchored 1-3 m apart on the shoreline at the +1.2 m elevation line. Many bags at high-energy sites were lost or suffered severe damage. On the sandy shorelines, bags were tied with fishing line to buried bricks. During the second sampling interval (October), litterbags were enclosed in plastic deer fencing (1.9 cm mesh polypropylene) to protect them from wind and wave abrasion. Each bag was wrapped twice with the deer fencing, creating a litterbag within an envelope of plastic mesh.

Each litterbag was filled with 60 grams of oven-dried *Vallisneria americana*, the predominant vegetation found in wrack along Hudson River shorelines. *Vallisneria americana* wrack collected during the summer of 2008 was used for the first sampling period since fresh wrack was not available on the shorelines until late summer. Fresh wrack was then collected in August 2009 for the second sampling period. Random bags were collected from the rocky, riprap, and sandy shorelines at 7, 14, 21, and 28 days after placement. The same timeline was anticipated on the cribbing shoreline, but due to poor weather, collection of the bags was delayed for two weeks, so final retrieval took place at 42 rather than 28 days. All bags were placed in individual sealed plastic bags and transported to the Cary Institute of Ecosystem Studies.

After collection, the contents of the litterbags were dried for three days at 60°C in pre-weighed aluminum pans. Many of the samples had small pebbles embedded in the wrack, so the

organic material was combusted in a muffle furnace at 400°C, weighed, and then rinsed through a 0.5mm sieve. The weight of the coarse inorganic material was subtracted from the weight of the dried samples to obtain the pebble-free dry weight of material remaining in each litterbag.

Invertebrate communities of wrack

We also studied invertebrate communities that developed in the litter bags set out to study wrack decomposition. Invertebrates were collected from bags that were retrieved after 14, 28, and 42 days (the latter for cribbing only). The bags were stored in the refrigerator (5°C) after collection for no more than 48 hours, and then the contents were emptied into a tub of warm water. After agitating the wrack in the water for 1 minute, the mixture was poured onto a coarse-mesh sieve (4.75mm mesh), which was stacked on top of a fine-mesh sieve (0.5mm mesh). The material that remained on the fine-mesh sieve was rinsed into a jar with a 70% ethanol solution for counting and identification under a dissecting microscope. If live organisms were visible on the organic material in the coarse-mesh sieve, a second or third rinse was conducted. All individuals were counted, identified to class, and where possible, to order.

Statistical analysis

Decomposition data were expressed as the amount of dry weight remaining and \log_{10} -transformed, then analyzed with an analysis of covariance (ANCOVA, SAS 9.2) to determine the effect of shoreline type and time. The ANCOVA results were analyzed with a post-hoc Tukey test to see whether differences between decay rates (k) on different shoreline types were significant. Decay rate constants were calculated for each shoreline type using the following single-exponent equation (Weider and Lang 1982):

$$k = -\frac{\left(\ln\left(\frac{M_t}{M_0}\right)\right)}{t} + c$$

where M_t is mass at time t , M_0 is initial mass, k is the decay constant estimated from regression of \ln (proportion mass remaining) against time, c is a constant and t is time in days.

For invertebrate abundance, the data were \log_{10} -transformed and then a 2-way ANOVA was calculated (SAS 9.2). Time was classified into two categories, depending on whether the invertebrates were collected after two weeks or four/six weeks. A post-hoc Tukey test was used to evaluate the significance of the differences between shoreline types.

Invertebrate diversity was evaluated by calculating the Gini index (Gotelli and Graves 1996),

$$= 1 - \sum_{i=1} n * p_i^2$$

where p_i is the proportion of individuals belonging to a taxon out of the total number of individuals in that sample, n . This is a measure of impurity; if all members of the sample are of the same taxonomic group the index would be 0. The closer the index is to 1, the more diverse the sample. The Gini index was chosen because it is relatively insensitive to sample size (Gotelli and Graves 1996). A 2-way ANOVA was calculated to determine the effect of shoreline type and time on invertebrate diversity.

Non-metric multidimensional scaling (PC-ORD 5.10) was used to analyze the community structure of macroinvertebrates among shoreline types, between sampling time periods (August and October), as well as the relationship between invertebrate groups across shoreline types. Non-metric multidimensional scaling (NMDS) calculates a distance matrix based on the number of samples and attributes in the data, and identifies the configuration that minimizes the both stress of the number and the way the axes are arranged (McCune and Grace

2002). The \log_{10} -transformed data had the rare taxa removed prior to ordination, i.e., taxa found in fewer than three samples. Stress values were evaluated using Clarke's rules of thumb, with 2-5 indicating an excellent ordination, 5-10 indicating a good ordination, 10-20 a fair ordination, and over 20 a poor ordination (McCune and Grace 2002).

Multi-response permutation procedures (MRPP) were calculated for each ordination to test for the differences between shoreline types, using the same Sorenson distance as was used for the NMDS. Calculating the chance-corrected within group agreement (A) shows the effect size, with $A=0$ describing a scenario where all items are identical within groups. According to McCune and Grace (2002), values for A are generally low in community ecology, with $A=0.3$ identifying a fairly high value.

RESULTS

Standing stock of wrack on different kinds of shorelines

The amount of wrack along Hudson River shorelines varied widely, with wrackline widths of 0-3.1 m, and maximum wrack standing stocks of 0-1.2 kg DM/m². Wrackline width did not differ significantly among the six shore types ($p=0.20$), but $\log_{10}(\text{maximum wrack mass})$ was marginally different among shore types ($p=0.08$). The greatest amount of wrack was found on sandy shorelines (wrackline width = 2.1m, maximum wrack mass = 517 g DM/m²), whereas no wrack was found along the bulkheads. When all shore zone types were considered together, the amount of wrack accumulated on the Hudson's shores was clearly related to shore zone slope (or more precisely, its reciprocal, shore zone width, Fig. 2).

Mobility of wrack on different kinds of shorelines

Elevation, incubation time, and site exposure all had highly significant effects on the retention of experimentally added “wrack” by Hudson River shorelines (Fig. 3). Essentially all wrack placed in the intertidal zone was swept away within a day, regardless of site characteristics, whereas at least some of the “wrack” placed at and above the high tide line was retained, especially at sheltered sites. Shoreline type had a small, marginally significant effect on wrack retention ($p=0.051$).

Decomposition rates of wrack on different kinds of shorelines

The *Vallisneria americana* wrack decomposed rapidly, and more than 50% of the original mass was lost within each four-week experimental period on all shoreline types (Fig. 4). Shoreline type ($p<0.0001$, $F=39.32$) and time ($p<0.0001$, $F=46.61$) both significantly affected the mass remaining of *Vallisneria americana* (overall ANCOVA, $F=50.76$, $N=112$, $DF=107$ $p<0.0001$, $r^2=0.655$). Decomposition rates were higher on engineered shorelines, with cribbing experiencing the fastest decay rates (Fig. 4). After 28 days in the field, less than 10% of the *V. americana* remained in the litter bags on cribbing shorelines. Decay constants (k) were calculated for each shoreline type along with an overall decay rate of 3% per day. Average daily decay rates for riprap (3.4%), rocky (1.7%), and sandy (2.7%) were significantly different from decay rates on cribbing (4.8%), according to post-hoc Tukey tests which showed significant differences between all shoreline pairs except rip rap and rocky shorelines (Tukey $\alpha=0.05$, $N=112$, $DF=107$).

Invertebrate communities of wrack

We found representatives of 21 different taxa during the course of this study. Across all sites, the most abundant order was Isopoda, followed closely by Diptera and Collembola. The abundance of invertebrates varied a great deal among shoreline types and between the two

sampling periods (Fig. 5). The largest numbers of organisms were collected on the sandy shoreline in August, while the fewest organisms were collected at the cribbing site (in both August and October). More invertebrates were collected at all sampling locations in August, regardless of shoreline type. On riprap, the most common invertebrate orders were Gastropoda and Diptera in August, and Diptera in October. On rocky shorelines, dipterans (excluding Chironomidae) dominated both August and October samples. Isopods were the most common order found on the sandy shorelines in August, but the samples were dominated by Collembola in October. The family Chironomidae (midges, order Diptera) was the most common invertebrate group found on cribbing shorelines in August (Fig. 5).

Invertebrate abundance was significantly different among shoreline types (ANOVA, $p=0.001$; $N=59$, $DF=51$). There was no significant main effect of time ($p=0.5268$) or interaction between time and shoreline type ($p=0.8605$). Tukey post-hoc analysis indicated that cribbing had significantly lower invertebrate abundance than the other three shoreline types (Tukey $\alpha=0.05$, $N=59$, $DF=51$).

Invertebrate diversity (using the Gini index) was significantly different among shorelines (ANOVA, $DF=49$, $N=57$, $p=0.0031$, Fig. 6). There was no significant interaction of time with shoreline type ($p=0.3957$) or main effect of time ($p=0.1629$). The Gini diversity value of the cribbing shoreline was significantly different from that on all other shoreline types, according to post-hoc Tukey tests (Tukey $\alpha=0.05$, $DF=49$, $N=57$).

Invertebrate community structure among shoreline types, with both sampling periods combined, was expressed by NMDS ordination, with a 3-dimensional solution and a stress level of 14, indicating a fairly good ordination. The cribbing sites were clearly separated into a cluster distinct from the other three shoreline types (Fig. 7) on Axis 1. A Multi-Response Permutation

Procedure showed an overall within-group agreement of A=0.1036, which rejects the null hypothesis that all groups are the same. The pairwise comparisons showed the highest A-values were for rocky vs cribbing and cribbing vs sandy shorelines (Table 1).

DISCUSSION

The amount, mobility, decomposition rate, and invertebrate communities of wrack varied widely across natural and engineered shorelines of the freshwater tidal Hudson River. The engineered shorelines (riprap, cribbing, and bulkheads) tended to accumulate little wrack, have high loss rates of wrack, and poor invertebrate communities. Therefore, as a group these shore types lost the ecological functions provided by wrack. Natural shorelines, especially sandy shores of low slope, tended to accumulate large amounts of wrack and supported distinct invertebrate communities.

Standing stock of wrack on different kinds of shorelines

Wrack accumulation along the Hudson during the autumn (probably the season of highest wrack accumulation) varied from zero along steep shorelines such as bulkheads to wracklines >1m wide and >1 kg DM/m² along shorelines of low slope. The human tendency to replace natural shore zones of low slope with steep or vertical engineered shorelines has greatly reduced the ability of the Hudson's shore zone to retain wrack. This tendency to build wrack-shedding shorelines probably has affected many large lakes and rivers, and may have substantially reduced the ecological role of wrack in many fresh waters. Our estimates of wrack accumulation are far lower than what has been reported along some marine shorelines, especially shore zones of low slope with high wave energy that are close to large sources of organic matter such as kelp beds, which reach values as high as 2920 kg wet mass per meter of shoreline per year (Backlund 1945;

Polis and Hurd 1996; Colombini and Chelazzi; 2003, Orr et al. 2005). It seems likely that standing crops of wrack much higher than those along the Hudson will be found in large, shallow lakes where fetch is large and there are abundant plant beds.

Mobility of wrack on different kinds of shorelines

Very little artificial wrack (hay) was retained below the high-water line in the Hudson. The Hudson's intertidal zone contains few structures capable of retaining wrack (e.g., woody vegetation, driftwood), probably because waves and ice scour and remove such structures. On the other hand, wrack placed at or above the high-water mark was held in place for at least a week, probably long enough to allow colonization by invertebrates. Thus, in the Hudson, wrack probably moves with the wind, currents, and tides until at least some is carried well above the high-water line by spring high tides or large waves. In more sheltered fresh waters, and even at the high-water level at our sheltered site along the Hudson, retentive structures may be sufficient to retain wrack at lower elevations, where it is permanently or intermittently wetted. Presumably, the decomposition rates and invertebrate communities of such "semaquatic" wrack may be different than those of the litter bags that we studied, which were placed at the high-water level.

Decomposition rates of wrack on different kinds of shorelines

The average decay rate across all sites of 3%/d is similar to that found for *Vallisneria americana* by Bianchi and Findlay (1991), who measured a daily decay rate of 3.34% in the lab. Decay rates varied among shore types, with wrack on the rocky shoreline decaying the most slowly (1.7%)/d and wrack on the cribbing site decaying the fastest (4.8%/d). Despite the higher slope of the riprap (21°) as opposed to the more gradual slopes of the rocky (7°) and sandy (9 °) shoreline, decomposition was not significantly different among the three types. The roughness of the shoreline also did not correlate to decomposition rates (data not shown).

Cribbing is essentially a vertical wall highly exposed to tidal currents, waves, and wakes, and the majority of litterbags deployed at the cribbing site were lost or damaged. Disturbance likely contributed a great deal to the loss of organic matter, as the wrack could have been broken into small pieces and washed out of the litterbags. However, bags at other sites also sustained damage, including 9 of the 60 bags on rocky shorelines, and 4 out of 60 bags on the riprap shoreline. Consequently, although disturbance was probably a factor in the rapid loss of organic matter on the cribbing shoreline, it is likely that photodegradation and decomposition by other consumers not sampled in this study played a role.

Although this study demonstrated the relatively high rate at which organic material decomposed on cribbing, this shoreline type is not expected to be a major site of wrack decomposition due to low wrack accumulation (cf. Fig. 2). In nature, most wrack that encounters a wall of cribbing would likely be swept away to a site with lower slopes, or be retained behind the wall without direct contact to the water. Some wrack may become stuck between slats of the wood piling, but the likelihood of high disturbance remains due to exposure to physical stress.

Invertebrate communities of wrack

Cribbing had the lowest numbers of invertebrates and the lowest diversity of invertebrates in litterbags, while the other engineered shoreline, riprap, did not have significantly lower numbers of invertebrates or less diversity when compared to the natural shorelines (Figs. 5, 6). Although riprap had a slope almost three times steeper, on average, than the rocky and sandy shorelines, and a rougher shoreline, this did not affect the abundance or diversity of invertebrates in wrack on the riprap.

As the seasons began to change, and with it water temperature, vegetation, and light, the invertebrate community changed as well (Fig. 5). Both Gastropoda and Collembola became less numerous on riprap from August to October, with Diptera increasing in number. On the sandy shoreline, Isopoda dominated the August samples, while Collembola dominated the October samples. Due to the small numbers of invertebrates found at the cribbing site, it is difficult to describe the change over time. There was no large difference in invertebrate groups using wrack on the rocky shorelines between August and October.

The high abundance and diversity of invertebrates on riprap may have been a result of the great physical heterogeneity of this habitat; previous work has found that structural complexity encourages high densities (Way et al. 1995; Lewin et al. 2004) and species richness of aquatic invertebrates (Chapman and Blockley 2009).

Implications for shoreline development and restoration

More than 50% of the Hudson River shoreline has been modified or hardened in some way, with many additional development projects currently taking place or planned (Squires 1992; Miller 2005). Such modifications are common on rivers, lakes, estuaries, and coastal waters around the world (e.g., Bänziger 1995; Moreira et al. 2006; Strayer and Findlay 2010). The most common engineered shoreline type on the Hudson is riprap, making up 52% of engineered shoreline (roughly 25% of total shoreline length) (Miller 2005; Fig. 1), and future shoreline modifications will likely include a mix of riprap, cribbing or bulkheads. The sea level at New York City has increased about 40cm since 1850, and is expected to continue to rise, with estimates ranging between 11-20 cm and 45-77cm by the end of the century (New York State Sea Level Rise Task Force Report 2010). As the climate warms and the sea level rises, coastal

shorelines (including the Hudson River) will likely experience more erosion and more frequent flooding of adjacent properties. Landowners and businesses near the shore are apt to seek the easiest and cheapest methods for protecting their investments without concern for ecological function unless viable alternatives, incentives or legal restrictions are put into place.

Adaptation strategies for sea level rise range from “hard” engineering solutions such as riprap revetments or bulkheads to “soft” engineering solutions or living shoreline techniques that incorporate natural elements along with protective structures such as breakwaters (Klein et al. 2001; National Research Council 2007). Whenever possible, soft engineering or living shoreline techniques should be attempted to maintain as many of the ecosystem services as possible (New York State Sea Level Rise Task Force 2010; Strayer and Findlay 2010). These techniques offer benefits beyond shoreline stabilization, providing better habitat, food production, wave attenuation, nutrient processing, and aesthetic value than hard shorelines (Klein et al. 2001; Strayer and Findlay 2010). Local governments may also establish areas for migration of shorelines as well as large buffers between new development and the shoreline, and “incentivize the use of non-structural shoreline protection measures” (New York State Sea Level Rise Task Force Report 2010).

Of the engineered shorelines that we studied, riprap offered the most ecological value in terms of wrack retention and invertebrate communities. It is possible that riprap could be used to restore shorelines that were previously rocky. When constructing a riprap shoreline, adding complexity in the form of varying slope and roughness might create refugia for organisms (Way et al. 1995; Lewin et al. 2004; Chapman and Blockley 2009). Maintaining adjoining upland habitat of good quality is likely also of high importance (Harding et al. 1998; Petersen et al. 2004; Sawyer et al. 2004; Morgan and Cushman 2005; Strayer 2006). Providing upland

vegetation or vegetation interspersed in the boulders could provide habitat for terrestrial invertebrates, as it would likely mimic the natural shoreline more closely.

Sandy shorelines may be unique, and cannot be replaced by riprap or bulkhead without some negative ecological consequences. Wrack accumulation was greater, decomposition rates were different, and the invertebrate community composition on sandy shorelines was significantly different from the other shoreline types.

As society begins to consider adaptation strategies for rising sea levels, those with vested economic interests will likely advocate for what they perceive to be the most secure and durable forms of protection, namely dikes or bulkheads. Creating these types of structures to stabilize shorelines will negatively affect the ecological functioning of shore zones. Our findings support the implementation of non-structural solutions such as elevating or relocating important infrastructure, or building shorelines with “soft” engineering to improve the overall ecological health of shorelines along the Hudson River and elsewhere.

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Table 1: Multi-response permutation procedure for macroinvertebrate ordination in Fig. 7; all shoreline type comparisons are significant.

Shoreline Types Compared	A value	p value
Riprap vs rocky	0.01733	0.033
Riprap vs cribbing	0.09244	<0.001
Riprap vs sandy	0.05315	<0.001
Rocky vs cribbing	0.11785	<0.001
Rocky vs sandy	0.05139	<0.001
Cribbing vs sandy	0.18177	<0.001

Figure legends

Fig. 1: Types of engineered shoreline along the Hudson River estuary, after Miller (2005).

Unconsolidated rock includes riprap.

Fig. 2: Wrack accumulation along Hudson River shorelines as a function of the width of the shore zone (horizontal distance between 1m below the mean low water line and 1m above the high water line): a. width of the wrackline ($r^2=0.38, p=0.008$); b. maximum mass [need to change figure Y-axis to mass] of the wrackline ($r^2=0.21, p=0.06$).

Fig. 3: Amount of added “wrack” (i.e., hay) remaining after 1 day (open symbols) and 7 days (closed symbols) at a sheltered site (circles) and an exposed site (triangles) along the Hudson River. Bars show 1 SE. Exposure, elevation , and incubation time all are significant at $p<0.001$ (ANOVA).[Can slightly offset “low” so all the symbols show up? Can put legend in box on Figure?]

Fig. 4: Changes in ash-free dry weight of *Vallisneria americana* in litterbags placed on four different Hudson River shoreline types. Data points are means of 2-3 bags on each shoreline type.

Fig. 5: Relative abundance of invertebrates organized by shoreline type; the most abundant 7 groups on each shoreline type are shown, with other taxa lumped into the category “other.” Abundance is proportional to the area of the circles.

Fig. 6: Gini diversity index for invertebrates on different Hudson River shorelines. Diversity on the cribbing shoreline was significantly different from the other shoreline types.

Fig. 7: NMDS plots illustrating macroinvertebrate community structure on the four shoreline types in both sampling periods; the cribbing samples are enclosed by the oval, illustrating the cluster.

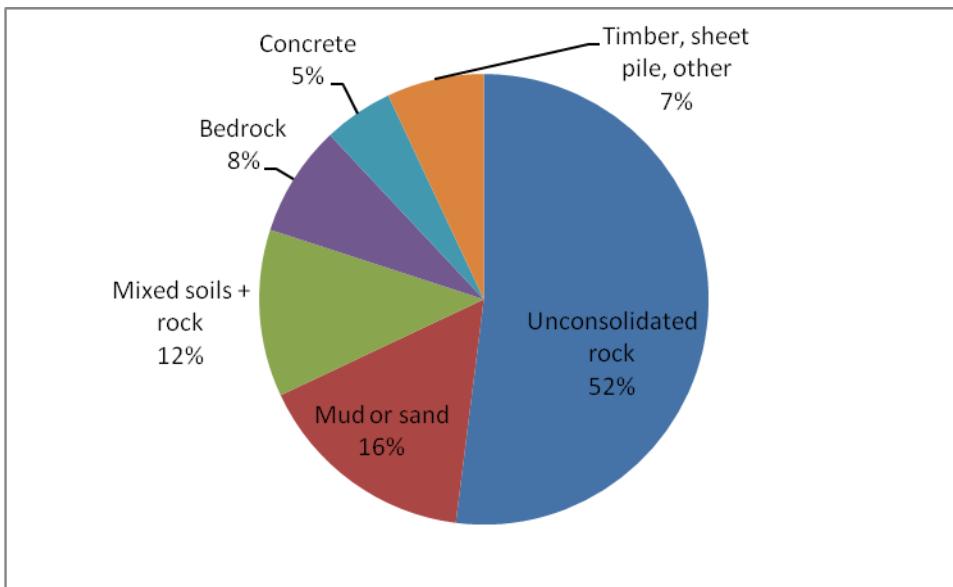


Fig. 1

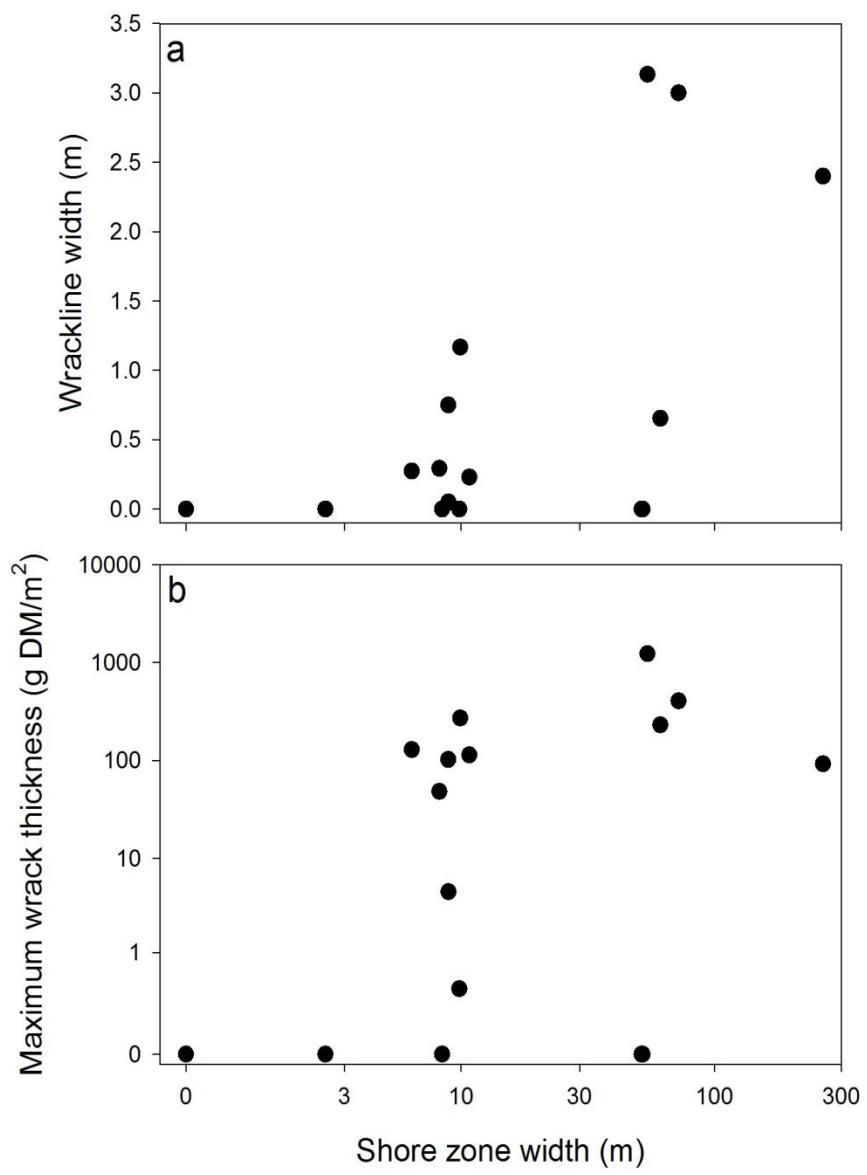


Fig. 2

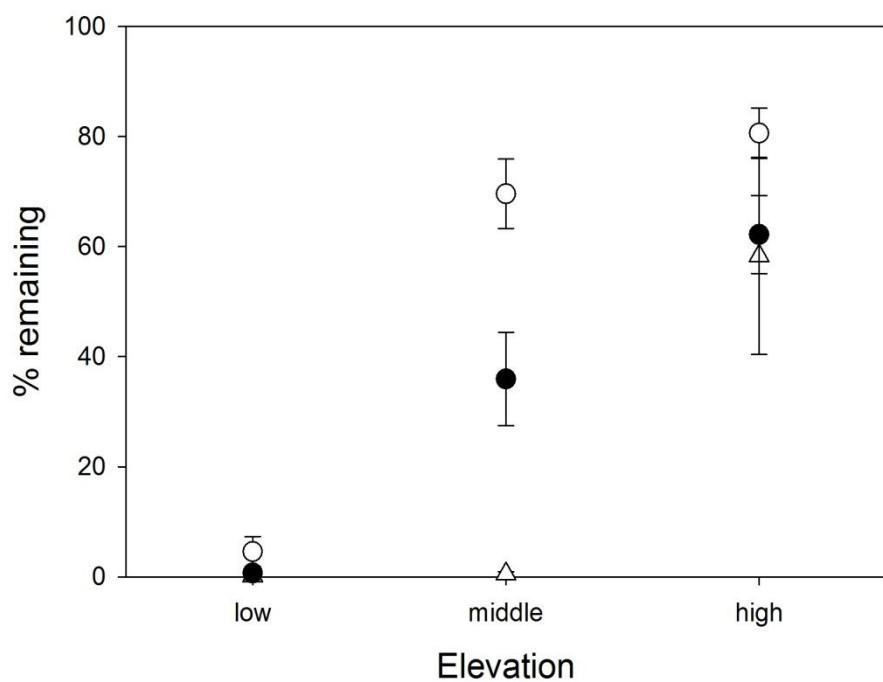


Fig. 3

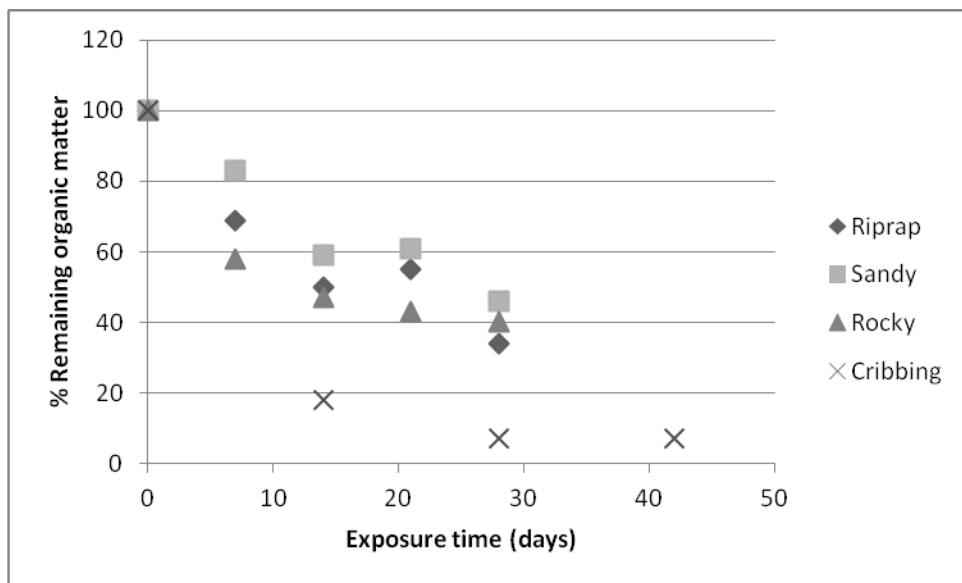


Fig. 4

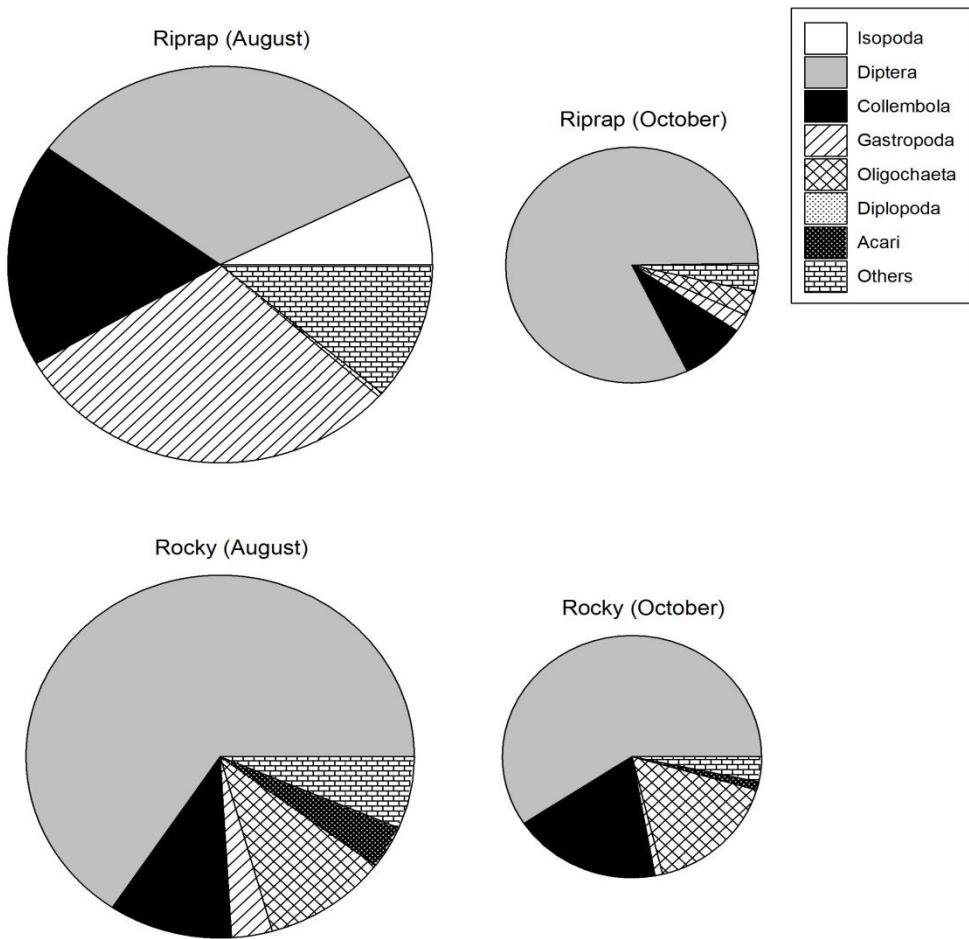
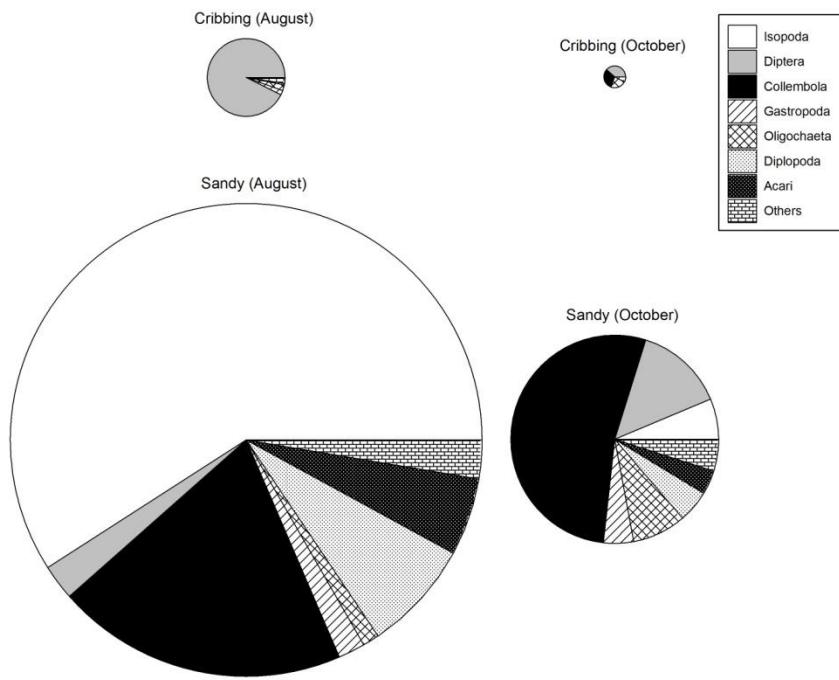


Fig. 5



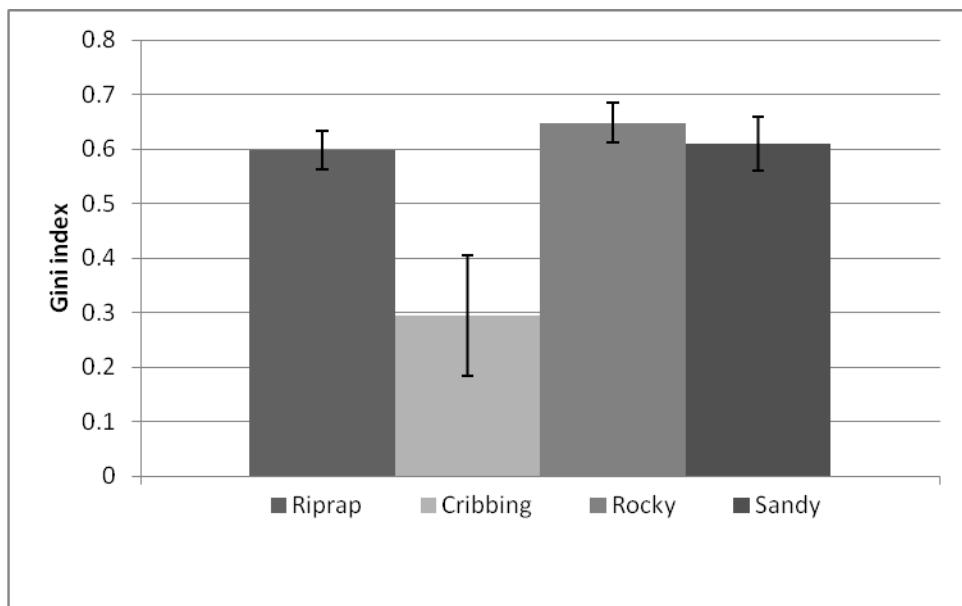


Fig. 6

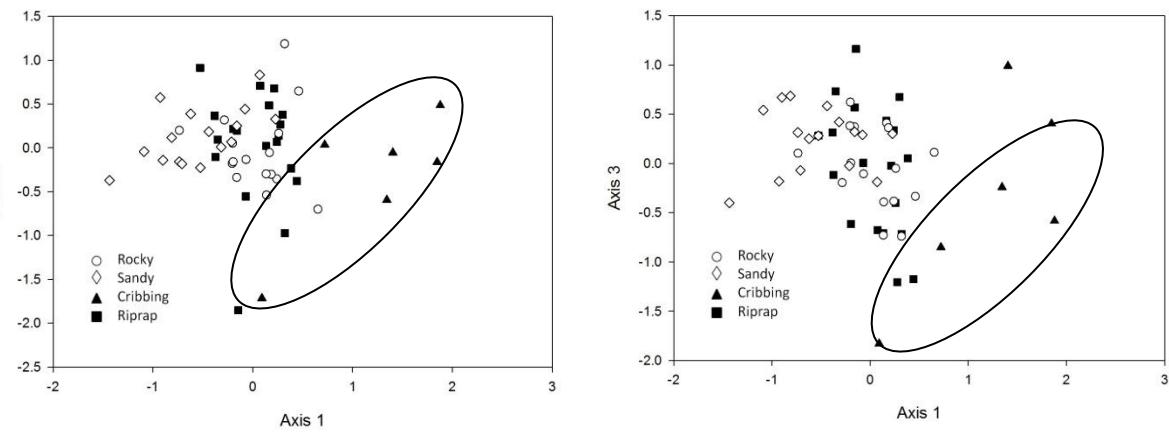


Fig. 7