

# Introduction

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This book is an attempt to encourage comparative studies on the ecology of sedimentary shores. Most research on muddy and sandy shores has been local or regional, analyzing small to meso-scale patterns and the underlying processes. Comparisons between distant shores, across latitudinal gradients or between separate biogeographic provinces, have rarely been carried out, and such comparisons are often hampered by methodological differences in quantifying coastal biota. Field experiments may not provide comparable results when the spatio-temporal scales are different and, usually, little is known about how representative an analyzed process or pattern is across an entire region. Between different coasts, several important variables are likely to differ at the same time. When particular aspects are compared, either data from a large number of sites or a choice of carefully selected sites is required and researchers must be cautious in the interpretation of such data.

Zonation of organisms perpendicular to the shoreline is less distinct in sediments than on rock (Peterson 1991), and the ability of many species to transform habitat structure and the mobility of species in soft sediments contribute to dynamic and heterogeneous patterns over many spatial scales. Not many soft-sediment comparisons have been conducted within regions along gradients from exposed to sheltered, from atidal to macrotidal, from onshore to offshore currents, from brackish to marine, from oligotrophic to eutrophic, from small to large organic supplies originating from the sea or the land, and with respect to other similar variables. Even fewer comparisons are available between latitudes and between biogeographical provinces. Most of these are confined to surf beaches (Dahl 1952; McLachlan et al. 1993).

Nevertheless, the authors of this volume feel that the comparative ecology of sedimentary shores is a ripe area for a global view of patterns and processes studied at selected sites. This is necessary for both the development of conceptual theory, and for providing insights for effective coastal management. It is acknowledged that this volume cannot provide definitive answers to all these issues; its aim is to raise awareness of the need for a comparative perspective on the sedimentary shores of the world. Finding similarities and

convergent biotic traits among biogeographic provinces in response to physical forcing constitutes the necessary basis for general models. Conversely, similar species with small differences in their life-history traits may ultimately lead to divergent flows of energy and matter in coastal ecosystems. In such cases, a similar physical regime and environment may generate quite different biotic effects. The global comparisons advocated here are required to examine and apply the generalities which are claimed to date and to separate these from peculiarities and unique phenomena, some of which may in themselves be noteworthy and deserve special appreciation.

Biotic assemblages of sedimentary shores are strongly dominated by a small set of species. This may ease comparative analyses. However, the question remains: what is the ecological role (if any) of the remaining species? Species richness recorded from intertidal surveys generally yield <100 species of benthic macrofauna in temperate zones and >100 in the tropics, often two to three times more than in temperate regions (i.e., Reise 1991; Pepping et al. 1999; Wijnnsma et al. 1999). The biodiversity of the sedimentary shores of the world in terms of forms of life, species, ecological assemblages and habitats has never been compiled and brought into perspective.

Sedimentary shores may be evaluated across latitudes from the perspectives of migrant birds looking for food and roosting sites (Piersma et al. 1993). Global patterns of zoomass in marine intertidal communities not only show divergent trends of trophic groups (Ricciardi and Bourget 1999), but also reveal that studies comparable in terms of methodology and scale are few, and that the global distribution of such studies is very uneven. Blackburn and Gaston (1998) raised a number of methodological issues that need to be taken into account when individual data sets are assembled to detect trends over large geographical distances. In this volume, primarily pairwise comparisons are conducted with contrasting aspects between geographically distant shores.

Roughly two-thirds of the world's coastline consists of sedimentary shores, in long continuous stretches or in bays interspersed between rocky headlands (Fig. 1). Yet ecological perspectives and theory derived from sandy beaches and mudflats have remained in the shadow of the ecology of rocky shores. The reason is obvious. Most of the organisms of the rocky shore are showy and conspicuous, and are readily accessible to non-destructive quantification and experimentation. Patterns of zonation have been compared worldwide (Stephenson and Stephenson 1972) and the rocky shore served as a model system for the development of community theory (Connell 1975; Dayton 1975; Paine 1994).

Sedimentary shores, though an early focus of geologists (see Davis 1985), are more resistant to progress in ecological research. Most organisms are small, cryptic and difficult to extract from the sediment, and field experiments in this environment may suffer more than on rocky shores from



**Fig. 1.** Exposed sandy beaches, sheltered tidal flats and sand dunes on the barrier island of Sylt in the North Sea (*top*), and sedimentary coves and an estuary between rocky headlands of the Seno de Reloncavi, southern Chile (*bottom*)

experimental artefacts. As a consequence, knowledge has advanced much more slowly. However, apart from their spatial extent and being subjected to many human impacts, sedimentary shores have a number of distinct features that deserve study, and it should not be regarded as the Cinderella to a rocky sister, the rugged beauty. Both shore types rely on food supplies from the sea, and suspension feeders are often prominent. Light allows benthic plants to develop in both shore types: kelp forms extensive stands on rocky coasts and seagrasses are common on sedimentary shores. Rocks basically provide a two-dimensional substrate, while sediments offer a third dimension in which to live. In this third dimension organic material can be stored and is available to deposit feeders. The third dimension also offers a buffer against the physical harshness of the intertidal environment. The slope of sedimentary shores tends to be gentler than that of rocky shores, so that the former has a much wider areal extent, and thus provides more food to visiting shrimps, fish and birds.

There are two key variables for the broad-scale comparison of biotic richness of sedimentary shores. Firstly, the external supplies of nutrients and organic material, mostly from the sea, but in estuaries also from the land. Secondly, the morphodynamics of the shore, determined by wave energy, the tidal regime and the sediment particles available. The broad-scale composition of shore biota further depends on salinity, the temperature regime and the biogeographic province.

Except for salinity, intermediate states of the above factors and their combinations seem to be the most favorable for the biota of the sedimentary shores. Too great an external food supply may result in anoxia, and too little will exclude the suspension feeders. Strong hydrodynamic forces and a coarse sediment grain render a sedimentary environment very unstable and only a few species are capable of coping with this combination. In embayments and the shallow subtidal these forces are often appreciably ameliorated by biogenic sediment stabilization. Shallow stagnant waters also require specialized adaptations. Without flow there may be little buffer against the high physical fluctuations of the surrounding terrestrial environment. Species richness of the shore increases from high to low latitudes, and is highest in the Indo-West Pacific province. On the other hand, benthic zoomass seems to be highest at mid-latitudes, presumably because under conditions of pronounced seasonality more phytoplankton escapes the pelagic algivores and is left as food for the zoobenthos (Ricciardi and Bourget 1999).

The ecological patterns and processes of almost all shores have been modified by humans. The past and present imprint of human activities on the shore biota not only has to be kept in mind when global comparisons are conducted, but in itself deserves comparative evaluation. On a global scale, the physical changes resulting from land-use practices, planned and unplanned coastal engineering have the most important effects. Often there is a habitat

loss or truncation at the upper or inner shore because of embankments for agriculture and aquaculture, industry, airports, residents, and as coastal protection measures, whilst dredging and dumping activities, particularly in estuaries, hard coastal defence structures and replenished beach sand on open coasts and fishery operations, may all create strong physical disturbance.

The widespread introduction of species across biogeographic barriers from coast to coast is irreversible. This trans-oceanic exchange of species occurs unintentionally with shipping, either fouling or in ballast water, and with aquaculture (Carlton and Geller 1993). Only a few of the introduced species have turned into massive invaders transforming the dynamics and structure of the recipient ecosystem. The cumulative effect is to bring about a sameness between distant coasts which previously had no species in common, except for humans.

The exploitation of living resources on sedimentary shores affected primarily the upper trophic levels: mammals, birds and fish (Wolff 2000a,b). Gray whales have been exterminated from the coastal lagoons of the North Atlantic, and a re-introduction would require whales from the Pacific population. Dugongs and manatees have likewise become rare in parts of their former range and hunting has reduced populations of seals and birds. The latter suffered particularly from harvesting of eggs, a similar problem for sea turtles. More recently, nature conservation has allowed for a partial recovery of coastal bird populations. Overfishing and partly habitat degradations at coasts and rivers lead to declines in a variety of large anadromic fish. Some species of rays with a late and low reproductive output ended as by-catch in the fisheries and became rare and functionally extinct on the coast. Oysters became overexploited (i.e., Rothschild et al. 1994). It seems likely that on the intensively harvested tidal flats of the East-Asian coasts, the entire size-spectrum of benthic invertebrates became truncated at its upper range.

Particularly in densely populated areas around embayments and semi-enclosed seas, eutrophication and toxic pollutants have changed coastal ecosystems. Eutrophication primarily increased primary production (Schramm and Nienhuis 1996), but seagrasses have adapted to oligotrophic waters. These rooted plants give way to fast-growing algae when nutrient levels increase. Mats of green algae cover intertidal sediments enriched with nitrogen, with detrimental effects on the benthic fauna underneath. There is also evidence that eutrophication has increased benthic zoomass in estuaries (Beukema 1991). Toxic pollutants often occur at the same sites where nutrient levels have increased, and the opposite effects of these two components may mask one another. Global warming and the concomitant sea-level rise will interact with most of the factors mentioned above. Whilst anthropogenic effects on the biota of sedimentary shores is not a main focus of this Volume, the widespread occurrence of such effects means that they become an integral part of the comparisons; nowhere can the footprint of human activity be ignored.

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