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THE EFFECTS OF SEDIMENTATION ON ROCKY COAST ASSEMBLAGES

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Abstract Sedimentation is a widespread and increasing process on most rocky coasts. The literature on its effects is reviewed and support is found for the general conclusion that sedimentation is an important ecological factor for hard bottom organisms. Sediments deeply affect the composition, structure and dynamics of rocky coast assemblages, and increased sediment load as a consequence of anthropogenic activities can be a threat to their diversity and functioning. Sediments that accumulate on rocky substrata are important agents of stress and disturbance. They can cause burial, scour and profound modifications to the characteristics of the bottom surface, and interact with other important physical and biological processes. The effects of sedimentation are complex, because they involve both direct outcomes on settlement, recruitment, growth or survival of individual species and indirect outcomes through mediation of competitive and/or predator–prey interactions. Not all species and assemblages are equally affected by sedimentation and responses vary over space and time, depending on the characteristics of the depositional environment, life histories of species and the stage of development of individuals and assemblages, and in relation to variable physical factors, including hydrodynamics, light intensity and bottom topography. Recent studies have much improved our ability to detect and understand the effects of sedimentation on rocky coast assemblages. However, little is still known about the underlying mechanisms. Overall, our present ability to make generalisations and predictions is limited by a paucity of quantitative and experimental research, and by the scant attention devoted to measuring the regime of perturbation by sediments and responses of organisms at relevant spatial and temporal scales. Predicting the magnitude of the effects that different sedimentation regimes have on rocky coast organisms and the critical levels above which detrimental effects become manifest remains a key issue for the ecology of rocky coasts and a challenge for future studies.

Introduction

Context and aim of the study

Over the past few decades, there have been increases in water turbidity and sediment deposition in coastal areas. Sedimentation has occurred at unprecedented rates all over the world as a consequence of anthropogenic activities, such as deforestation, dredging, industrial and domestic discharges, construction activities and land reclamation. Such increase of sediment loads has been recognised as a major threat to marine biodiversity at a global scale (United Nations Environmental Programme 1995). Changes in sedimentation have been dramatic for some coral reefs, where accelerated deposition caused by unsustainable land practices and dredging resulted in rapid shifts in species composition and abundance, and eventually in irreversible deterioration and loss of coral reefs and associated fishery resources (e.g. Johannes 1975, Amesbury 1982, Cortés & Risk 1985, van Katwijk et al. 1993, Hunter & Evans 1995, Chou 1996, McClanahan & Obura 1997, White et al. 2000; but see Larcombe & Woolfe 1999). The increasing concern about degradation of coastal habitats as a result of anthropogenic increase of sediment loads is reflected in the amount of research that has been directed in recent years towards these problems in both temperate and tropical regions. Several reviews have appeared that discuss the effects of sedimentation in different habitats, including coral reefs (Dodge & Szmant-Froelich 1985, Rogers 1990, Richmond 1993), mangroves (Ellison 1998), seagrasses (Vermaat et al. 1997), freshwater systems (Barko et al. 1991, Henley et al. 2000), and estuaries (Ryan 1991). As the development of many human activities is likely to result in the release of suspended sediments in coastal areas and/or in changes to the regime of sedimentation, understanding the effects of sediments on coastal assemblages and predicting threshold levels of impact for different habitats are fundamental to identifying sustainable management strategies.

Rocky coasts are amongst the habitats potentially most sensitive to increased sediment loads, as excessive deposition of sediments may cause dramatic alterations in the characteristics of the benthos. Nevertheless, the impact of sediment loads on rocky coast assemblages has rarely been examined directly. Despite the scarcity of direct observations and experiments, there is an extensive body of literature that indicates the ecological role of sediments in rocky coasts is of major importance. The purpose of this review is to assimilate much of this literature, and attempt to address a number of questions: How does sedimentation affect rocky coast organisms? How do individual species and assemblages on rocky coasts respond to changes in the characteristics of the regime of sedimentation? Are there physiological and morphological adaptations that enhance tolerance of species in rocky coasts to disturbance by sediment? Are there critical levels of change in the regime of sedimentation that will irreversibly damage the biodiversity and/or functioning of rocky coast assemblages?

The review

The review is organised into three major sections. In the first, the variability and major sources of sediments to rocky coasts are described, the different mechanisms by which sedimentation can affect rocky coast assemblages discussed, and problems in measurement and comparison of sedimentation rates outlined. This section is not meant to be inclusive, as it is a vast subject that would require a dedicated review; rather it is intended to provide the reader with a few examples that highlight the complexity of the effects that sediments can have on rocky coast assemblages, the importance of quantifying the spatial and temporal scales of disturbance by sediments, and the necessity of improving comparison of sedimentation rates across different habitats and regions.

In the second section, the available information concerning the effects of sedimentation on biota of rocky coasts at the levels of individuals species and assemblages is critically documented. It is anticipated that, although sedimentation is invoked as an important factor for rocky coast organisms in many papers, direct research to quantify these effects and the underlying mechanisms is relatively scarce, and much of the available information is scattered, fragmental and often incidental. It is not the purpose of this section to cover all sources that mention sediments as a potentially important ecological factor for rocky coast organisms. Rather an attempt is made to cover the pertinent literature that is most frequently cited in international journals, with particular attention to the direct experimental evidence that supports or refutes the hypothesis that sediment accumulation influences the structure of rocky coast assemblages. Much of this literature deals with assemblages on rocky coasts that are naturally subject to the presence of sediments and, in the absence of suitable data, examples have also been drawn from other habitats. The information has been synthesised in tables, which are an essential part of this section. Some observations are also available from assemblages subjected to enhanced sediments loads as a consequence of human activities. However, a thorough coverage of this literature has not been attempted because in most cases discharge of sediments was one of many stresses undergone by the assemblage, and effects due to sedimentation were not separated from effects caused by potentially toxic organic and/or chemical pollutants.

In the last section, information is used to discuss: (a) the knowledge of the role of sedimentation in influencing the structure and functioning of rocky coast assemblages, including direct and indirect effects; (b) the present limited abilities to understand mechanisms of response of individual species and assemblages and to predict critical levels of disturbance by sediments; (c) which factors most hinder generalisations and predictions, including insufficient description of the regime of perturbation by sediments and scarce consideration of the spatial and temporal context; and (d) which questions need to be addressed by future studies.

Organic particulate matter may constitute an important source of food for suspension and detritus feeding benthic animals. On rocky coasts, however, there is a general consensus that high loads of suspended and settling inorganic particles represent a factor of stress and disturbance for both hard-bottom algae and animals. This review focuses on the physical effects of burial and scour by settled inert inorganic particles, because sediments that accumulate to the bottom, as a consequence of either natural or anthropogenic processes, are generally mostly inorganic. Related effects due to the presence of suspended organic and inorganic particles or to the presence of pollutants are touched upon only lightly, in view of the availability of other reviews related to these topics (e.g. Kinne 1971, Moore 1977, Pearson & Rosenberg 1978, Capuzzo et al. 1985, Wotton 1990, Walker & Kendrick 1998). Sediments accumulated on rocky substrata, or trapped within mats of algae, mussels or other invertebrates, will affect the composition and diversity of assemblages on rocky coasts also in terms of providing habitat to a variety of soft-bottom organisms (e.g. macroinfauna and meiofauna). Although the importance of this factor is recognised, effects of sediments on soft-bottom species have not been covered, as this would deserve a review of its own.

The review devotes particular attention to assemblages dominated by macroalgae, reflecting the author’s background experience and the extensive nature and global distribution of these habitats. Nomenclature of macroalgae was updated following Guiry & Dhonncha (2002). Coverage of “grey literature” has been kept to a minimum, to ensure the review is of accessible literature. Reference to work before the 1970s is limited, and readers are directed to the extensive coverage of Moore (1977).

Sediment load to rocky coasts

Some sediments occur on most rocky coasts, to the point that some authors have recently recognised the artificiality of the traditional separation between rocky and sandy shores (Bally et al. 1984, Jørgensen & Gulliksen 2001). Sediments are added to rocky coasts by many natural and human-related processes (Fig. 1), and are redistributed as a function mainly of sediment characteristics, hydrodynamic conditions, bottom profile, and biological factors (Moore 1972, 1973a, Hiscock 1983). These factors operate over a range of scales. Thus, while sediment deposition can be relatively predictable at large spatial and temporal scales, depending on the source and magnitude of sediment loads, at small scales, relevant to individual organisms, patterns may be highly heterogeneous and unpredictable (Trowbridge 1996, Airoldi & Virgilio 1998). This section, does not attempt to give detailed information on these topics, but rather to provide some baseline information relevant to understanding the possible effects of sedimentation on rocky coast organisms, and to analyse problems related to the measurement and comparison of sedimentation rates across different habitats.

Sources

Natural processes

Sediments on rocky coasts (in the forms of clay, silt, detritus, or more frequently sand) derive from a variety of natural processes. The principal sources include discharges by rivers, erosion of cliffs, and resuspension and transport of sediments. In some coastal areas, detritus from benthic and pelagic organisms and atmospheric transport can also be important

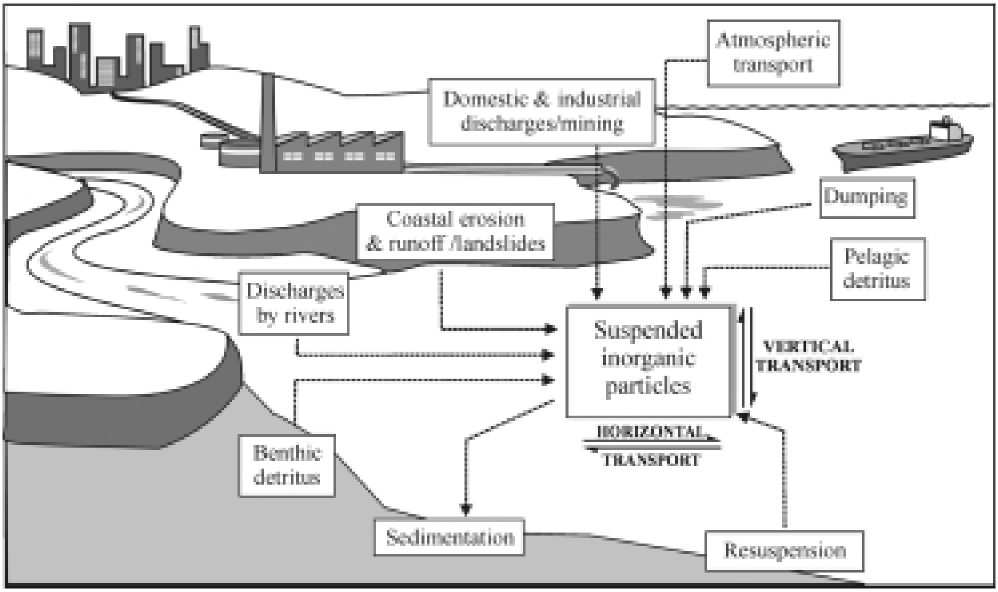

Figure 1 Schematic diagram of inputs and transport of inorganic particles to rocky coasts.

sources of sediments (e.g. Moore 1977 and references therein, Fornos et al. 1992), but there do not appear to be specific examples relative to rocky coasts.

River catchment of land-derived materials from natural soil erosion and runoff is a major input of sediments to coastal areas (Moore 1973a, French 1997). The rate at which terrestrial sediments are washed into rivers is a function of many environmental factors, such as intensity of rainfall, type of soil, and cover by vegetation. The major supplies of river-derived sediments to rocky coasts occur during floods associated with storms; as a consequence, for short time periods (hours to several days) sediment loads can be orders of magnitude higher than normal. Branch et al. (1990), for example, reported that, during a massive flood that occurred for several days in March 1988, the South African Orange River transported up to $55\,\mathrm{t\,silt\,s^{-1}}$ out of the mouth to the surrounding rocky coastal areas. The sediment did not deposit immediately on the rocky shore but was slowly trapped by algae, and after 2 months amounts of silt as high as over $1000\,\mathrm{g\,m^{-2}}$ were accumulated at midshore levels.

While sediment inundations by flooding may be considered extreme and rare events, erosion and runoff of cliffs by rain, wind, ocean waves and ice are relatively frequent local sources of sediments to rocky coasts (French 1997). Vogt & Schramm (1991), for example, reported that in Kiel Bay (Germany) each year about $75\,000\,\mathrm{m^3}$ of rock were eroded by wave action and washed into the bay from about 35 km out of 90 km of cliff; about 35% to 40% of such material, in particular coarse sand, gravel and stones, were deposited near the shore line at the base of the cliff, resulting in the formation of sandy floors and sandbanks which in some places have significantly reduced the amount of rocky substrata available for settlement of rocky coast organisms. Sediment traps placed along vertical cliffs have allowed some quantification and analysis of the composition of detritus rolling down the cliffs (Evans et al. 1980, Gulliksen 1982, Bavestrello et al. 1995). Along rocky cliffs in the Ligurian Sea (Italy), for example, fluxes of sediment were closely related to wave action and rain, with peaks up to more than $100\,\mathrm{g\,m^{-2}\,day^{-1}}$ during the spring and autumn (Bavestrello et al. 1991). Sediments were mainly composed of inorganic particles from the cliff but debris from animals and plants was also present.

In some areas, such as the Pacific coasts of North America, or the coasts of New Zealand, landslides are a relatively common natural phenomenon that can cause local inundation of rocky shores by sediments. Examples of the extent and impact of landslides are discussed by Shaffer & Parks (1994), Konar & Roberts (1996), Slattery & Bockus (1997), and Smith & Witman (1999). The contribution of sediments from these events, however, although locally important and persistent, has been considered small when compared with the annual contribution of sediments from other sources (Shaffer & Parks 1994).

The most frequent natural source of sediments to rocky coasts is re-suspension and transport of sediments from nearby soft-bottom areas (Storlazzi & Field 2000). Periodical inundations of sand by coastal currents or the action of storms are a very common feature of rocky coasts throughout the world, including California (Littler et al. 1983, Stewart 1983), Oregon (Markham 1973, D’Antonio 1986, Menge et al. 1994, Trowbridge 1996), New Hampshire (Daly & Mathieson 1977), Maine (Moring 1996), North Carolina (Renaud et al. 1996, 1997), British Columbia (Mathieson 1982), Mexico (Pineda & Escofet 1989), Ireland (Cotton 1912), Egypt (Aleem 1993), Morocco (Birje et al. 1996), Ghana (Towsend & Lawson 1972, Evans et al. 1993), Namibia (Engledow & Bolton 1994), and South Africa (Stephenson 1943). The degree of inundation by sand can be extremely variable, and Bally et al. (1984) have proposed a scheme of classification of “mixed shores” in relation to the spectrum of relative abundances of rock and sediments.

Human-related processes

There are many reports of major increases of water turbidity and sediment load that occur in rocky reefs as a consequence of human activities. Sediments may originate directly from industrial and domestic discharges (Boney 1978, Eagle et al. 1979, Schroeter et al. 1993, Gorostiaga & Díez 1996, Raimondi et al. 1997, Kim et al. 1998), mining activities (Castilla & Nealler 1978, Ellis 1988, Bernier et al. 1997, Hyslop et al. 1997, Fariña & Castilla 2001, Pulfrich et al., in press), construction of roads, bridges, tunnels, harbours and residential developments (Meinesz et al. 1991, Bach et al. 1993, Iannuzzi et al. 1996, MacDonald et al. 1997, Turner et al. 1997), dredging operations (Eagle et al. 1979), replenishment of beaches (Guidetti 2001), and aquaculture (Holmer et al. 2001). Most often, however, man's activities affect supply of sediments to rocky coasts in indirect ways, such as by accelerating natural soil erosion, by modifying the coastline and river catchments thus changing hydrodynamic and bottom characteristics, or by altering the abundance of important species that control the distribution of sediments (Seapy & Littler 1982, Meinesz et al. 1991, French 1997, Saiz-Salinas & Urkiaga-Alberdi 1999, Gillanders & Kingsford 2002). Paucity of long-term quantitative data sometimes makes it difficult to quantify the trends, and unequivocally attribute the causes to human activities (Lumb 1990). However, there are many lines of evidence that acceleration of natural soil erosion in relation to changes in land use both inland and along the coast is one of the most likely causes of enhanced inputs of sediments to coastal areas in both tropical and temperate regions (Cortés & Risk 1985, Rogers 1990, van Katwijk et al. 1993, McClanahan & Obura 1997, MacDonald et al. 1997). The greatest impacts are felt when forests are cleared for timber, agriculture, or urban developments. Deforestation increases soil erosion, water runoff, and occurrence of landslides, with dramatic results for the amount of sediments washed into rivers and brought downstream to the coast. It has been estimated that, in tropical woodlands, forest clearance and cultivation have increased natural losses of soil from $3\,\mathrm{t\,ha^{-1}\,yr^{-1}}$ up to $54–334\,\mathrm{t\,ha^{-1}\,yr^{-1}}$ (French 1997). Similarly, MacDonald et al. (1997) estimated that erosion from urban land uses and development of roads caused at least a 4-fold increase in sediment yields and unprecedented sedimentation rates in coastal areas around St John, US Virgin Islands. Pronounced increase of water turbidity and sediment loads in rocky coasts have also been observed in relation to fires of coastal vegetation (Airoldi et al. 1996), which in some regions are most often accidentally or deliberately started by humans.

Sediments deriving from these different activities may vary in chemical composition and grain size, may contain various organic and inorganic pollutants, and may range from slurries with a high water content to highly compacted sediments (e.g. Eagle et al. 1979). Sometimes the discharges occur over limited space and/or timescales, and sediments are dispersed relatively quickly by natural processes. However, more often the discharges are long lasting, resulting in persistent accumulations of sediments. Along the coasts of England, for example, considerable discharges of sediments from mining and industrial activities occurred continuously at some sites for about 95 yr (Eagle et al. 1979): although in the 1990s dumping had been substantially reduced, colliery waste was still washed up on to rocky shores near former dumping sites (Hyslop et al. 1997). Similarly, asbestos excavations at Canari Mine (Corsica, France) from 1948–65 greatly modified the natural rock escarpments, ultimately determining the appearance of artificial shores up to 300 m in width at the bottom of existing steep cliffs over a distance of more than 5 km (Bernier et al. 1997). Schroeter et al. (1993) reported important increase of sediment fluxes and water turbidity as far as 1.4 km from the diffusers of a coastal nuclear power plant in southern California: muddy sediments accumulated on the bottom and became armoured with coarser materials, accreting over time up to covers above 40%.

In recent years, at a few locations there has been reported a decrease of sediment load, which has been attributed to a recession of industries and mining activities and to better treatment of domestic discharges (Gorostiaga & Díez 1996, Hyslop et al. 1997). Although this is still a limited process, and although available data do not allow us to draw any conclusions about the possible timings for recovery of rocky coast assemblages, this seems an auspicious trend.

Spatial and temporal variability of sediment deposition

Identifying the main pathways of dispersal and accumulation of sediments is important for predicting the impact of discharges from natural and human-related processes. Overall, the distribution of sediments on rocky coasts is influenced by the characteristics of the sediments themselves and hydrodynamic conditions (Hiscock 1983). Whereas larger particles tend to settle quickly (e.g. close to the source points), the very fine particles can be kept in suspension for long periods by water turbulence, and thereby be transported over long distances by prevailing currents (Moore 1972, Capuzzo et al. 1985, Bach et al. 1993). In a report on the effects of the disposal of solid wastes off the northeast coast of England, for example, Eagle et al. (1979) showed how the area of impact of sediments released by different industrial developments extended far away from the dumping sites: sediments were transported and redistributed as a function of particle characteristics (i.e. composition, size, shape and density), tidal and wave-induced currents, and bottom characteristics.

Patterns of deposition and movements of sediments can be variable over space and time (Airoldi & Cinelli 1996a). For example, accumulation of sediments, especially the finest fractions, is in general most pronounced at sheltered locations (Lilly et al. 1953, Mathieson 1982, Hiscock 1983, D'Antonio 1986), whereas at exposed locations, sediments, if any, tend to be coarser, and generally persist accumulated in small crevices and depressions or trapped by local assemblages (Gotelli 1988, Airoldi & Virgilio 1998). Movements of sediments have greater effects in terms of abrasion at exposed than sheltered sites (Mathieson 1982, Hiscock 1983, Engledow & Bolton 1994), also due to the larger size of particles at the former sites. Sedimentation is generally greatest following strong rainfall and storms, due to increased runoff and resuspension of sediments (Bavestrello et al. 1995, Airoldi et al. 1996). Similarly, on some rocky shores, inundations by sand can assume seasonal, neap-spring tide, or even daily cycles (e.g. Daly & Mathieson 1977, Littler et al. 1983, Stewart 1983, D'Antonio 1986). Along the coasts of British Columbia, for example, Mathieson (1982) and Markham & Newroth (1972) recorded seasonal fluctuations of the levels of sand of 1 m to 1.5 m: generally the largest deposition occurred in late spring, and the sand persisted until the first autumn storms, which then removed the sand completely, sometimes in less than 24 h.

Superimposed on these large-scale, relatively predictable patterns, sediments may be redistributed within each shore contingent on the microtopography of the bottom and local profiles of flow speed. This process can result in highly heterogeneous spatial and temporal patterns of distribution of sediments within each shore. Sediments, for example, tend to be more abundant on horizontal than sloping surfaces (Whorff et al. 1995, Jørgensen & Gulliksen 2001). Trowbridge (1996) observed that on intertidal shores in Oregon, patterns of

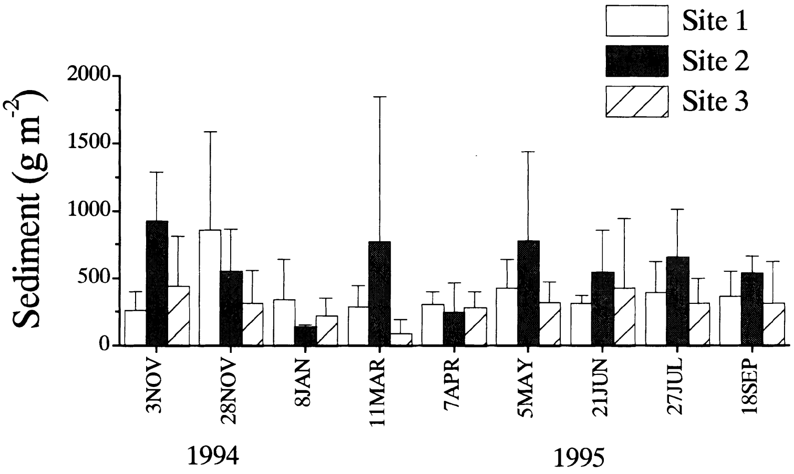

Figure 2 Example of heterogeneous spatial and temporal patterns of distribution of sediments on rocky coasts (modified from Airoldi & Virgilio 1998, published with permission). Data are average (+1 SD) dry weights of sediment (total amount, including coarse and fine fractions) deposited above and trapped into filamentous turf-forming algae at three nearby sites (about 100 m apart) on subtidal reefs south of Livorno, Italy.

accumulation of sand were more regular on planar benches than on heterogeneous substrata with surge channels. Furthermore, at a local scale, relevant to individual algal thalli or invertebrates, patterns of sand burial (frequency, duration, depth) were unpredictable, and shores that appeared to be buried for long periods were actually locally uncovered for short periods, affecting the extent of sand burial as well as conditions during burial. Similar observations were reported for subtidal rocky reefs in the Mediterranean Sea (Airoldi & Virgilio 1998): accumulation of sediments significantly differed among nearby sites 100 m apart, and was highly patchy at a scale of metres within each site (Fig. 2).

The importance of sediments as a major source of spatial and temporal heterogeneity for rocky coast organisms has been fully recognised only recently (Daly & Mathieson 1977, Littler et al. 1983, McQuaid & Dower 1990, Trowbridge 1996, Airoldi 1998). In particular, Airoldi & Virgilio (1998) and Airoldi (2000b) have shown how the responses of rocky coast assemblages to stress and disturbance by sediments may vary with changes in spatial and temporal scales. Thus the perception of the effects of sediments on rocky coast assemblages may be influenced by the spatial and temporal extent of the study. So far, however, little work has been undertaken to identify the relevant spatial and temporal scales of interactions between sedimentation and rocky coast assemblages.

Control by biological factors

Biological factors may control the distribution of sediments on rocky coasts. For example, several authors (e.g. Scoffin 1970, Stewart 1983, Airoldi & Virgilio 1998) have shown how turf-forming algal assemblages can bind and stabilise sediments even on exposed coasts, main-

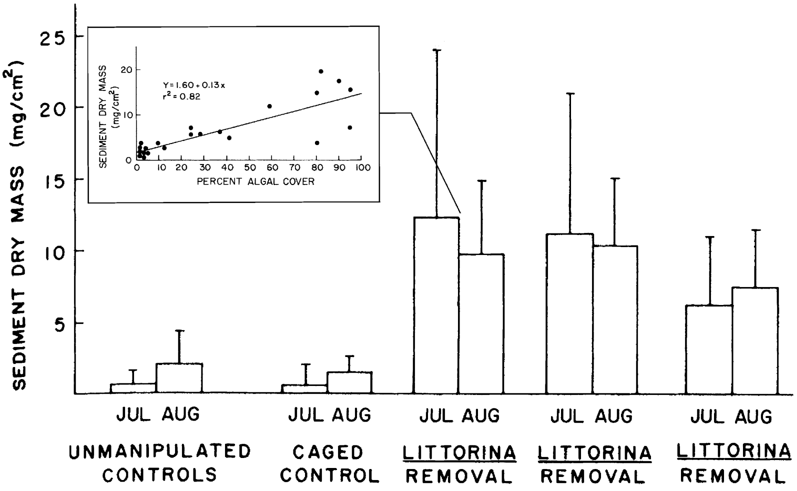

Figure 3 Example of biological control of the distribution of sediments on rocky shores (redrawn from Bertness 1984, published with permission). The experimental removal of the snail *Littorina littorea* from a sheltered New England rocky beach resulted in rapid accumulation of sediments, and the development of foliose algae, which further accelerated sedimentation. Data are average sediment dry weights (+1 SD) measured at two different times in each of unmanipulated controls, caged controls, and three *L. littorea* removal treatments. The box insert shows the relationship between weight of accumulated sediment and per cent cover of foliose algae (*Enteromorpha intestinalis* and *Ulva lactuca*) measured in one *Littorina littorea* removal treatment.

taining relatively constant accumulations of sediments despite marked temporal variations in sediment load (see p. 187). In some areas, kelp canopies have been reported to accelerate sediment deposition and prevent sediments being washed away (e.g. Moore 1972, 1973a, Eckman et al. 1989), while in others there have been reports of little to no accumulation of sediments under kelp canopies because of whiplash by fronds (e.g. Kennelly 1989, Melville & Connell 2001). In both cases, kelps have been shown to exert an important control on sediment dynamics and Estes & Palmisano (1974) have suggested that, by controlling the abundance of kelps, sea urchins may indirectly control the sedimentation regime of many subtidal habitats. Branch et al. (1990) observed that accumulation of sediments transported to rocky shores following the Orange River floods was not immediate but started only after the disappearance of patellid limpets and the consequent development of algal beds that trapped silt. Bertness (1984) showed that some herbivorous snails may prevent accumulations of sediments either directly, by bulldozing surfaces, or indirectly by removing algal films that trap sediments (Fig. 3). Bertness speculated that biological factors can mediate sedimentation rate and sediment binding sufficiently to dictate whether a habitat is primarily soft- or hard-bottomed. Although the effects of biological activity in controlling sediment transport, deposition and accrual rates have long been recognised as an important phenomenon in soft-bottom marine and lentic environments (e.g. Scoffin 1970, Fonseca & Fisher 1986, Power 1990, Pringle & Blake 1994, French 1997, Gacia & Duarte 2001), the role of biological factors in influencing the presence and distribution of sediments on rocky coasts has been so far largely neglected.

Mechanisms by which sediments affect organisms on rocky coasts

Because of the variety of possible sources, and of the synergistic effects of environmental and biological processes in controlling the distribution and dynamics of sediment particles, the nature and amount of sediments that are present on rocky coasts is highly variable in space and time. Sediments can be clay, silt, sand or detritus, may have variable composition and grain size distributions, and may or may not include pollutants. They may occur as a thin stratum, or form deposits centimetres to tens of centimetres thick, and may or may not turn into compact, impermeable layers. They may accumulate locally or be resuspended and transported above the substrata, depending on local hydrodynamic and topographic conditions. Furthermore, high rates of sedimentation are generally accompanied by high levels of turbidity from suspended sediments, and may often be associated with elevated inputs of nutrients or lower levels of salinity, as in the case of river floods (Gillanders & Kingsford 2002). This heterogeneity results in a variety of possible effects on rocky coast organisms, which are often difficult to separate from each other or from the concomitant effects of other environmental factors. Indeed, while in recent years there has been an increasing number of studies aimed at testing experimentally the effects of sediments on rocky coast organisms and assemblages, very few attempts have been made to try to clarify and separate the mechanisms of action of sediments (but see Devinny & Volse 1978, Marshall & McQuaid 1989, Kendrick 1991, Airoldi 1998, Chapman & Fletcher 2002), and identify the relevant spatial and temporal scales of impact of these different and interacting processes (Airoldi & Virgilio 1998).

With these problems in mind, and leaving out the possible interacting effects related to other environmental factors often covarying with sediments (e.g. hydrodynamics, turbidity, salinity, organic and inorganic pollutants), at least three major mechanisms by which inert inorganic sediments may directly affect rocky coast organisms have been postulated by a number of authors (e.g. Lilly et al. 1953, Daly & Mathieson 1977, Devinny & Volse 1978, Littler et al. 1983, Turner 1985, D'Antonio 1986, Kendrick 1991, Airoldi et al. 1996, Airoldi 1998, Chapman & Fletcher 2002). Namely,

(1) Burial/smothering, which may involve reduced availability of light, oxygen, nutrients, or accumulation of hydrogen sulphide and metabolic waste products, thus resulting in major changes in the characteristics of the chemical microenvironment.
(2) Scour/abrasion by moving sediments, that may damage and remove whole organisms or their parts.
(3) Changes in the physical characteristics of the bottom surface, which occur as a consequence of the replacement of stable hard substrata with unstable particles, and can result in a loss of habitat suitable for settlement.

Probably these mechanisms often occur together. For example, on exposed rocky coasts, sediment burial and scour are often combined, owing to high turbulent flow near the bottom (Devinny & Volse 1978, Mathieson 1982, Airoldi et al. 1996) but the effects they have on benthic communities are different and should be distinguished (Taylor & Littler 1982, D'Antonio 1986, Kendrick 1991, Airoldi 1998). Overall, the characteristics of sediment particles (e.g. grain size, shape, density, mineral and chemical composition), the extent, degree, location, frequency and duration of sediment burial, and the strength of water motion all contribute to determine the regime of perturbation by sediments, which can range from a large-scale, sub-lethal, chronicle stress, to an abrupt severe disturbance that locally disrupts the assemblage by removing organisms (Airoldi et al. 1996, Airoldi 1998). In this context, "stress" and "disturbance" are defined as in Grime (1977): stress refers to mechanisms that preclude or limit the growth of the assemblage, whereas disturbance refers to mechanisms causing the partial or total removal of the assemblage. Given that, with notable exceptions, ecologists have frequently referred to the effects of "sedimentation" (or analogous terms) ambiguously, in the absence of data on the regime of perturbation by sediments (see next section), and without explicit distinction of the mechanisms involved, the term "perturbation" is used here to refer to the complex range of effects related to presence of sediments, and more specific definitions (e.g. burial, scour, stress, disturbance) are used whenever explicit information is available.

Problems in measurement and comparison of sedimentation

It is often difficult to interpret and compare results from studies on the effects of sedimentation on rocky coast assemblages because either no or very limited information is given about the magnitude, characteristics and spatial and temporal variability of sedimentation regime, or different methods are used to quantify sedimentation, sometimes without an explicit consideration of which aspect of "sedimentation" is measured (i.e. sediment deposition, accumulation or movement, scour, or turbidity). This difficulty makes it rather arbitrary to identify which levels of sedimentation should be considered as "high" or "low" for rocky coast organisms or, just as importantly, which effects of sedimentation should be considered as "stressful" or "non stressful".

The majority of the field studies included in a later section of the review (p. 174) reported no or limited information on sediment abundance or reported qualitative subjective visual estimates (e.g. "little", "moderate", "heavy", "very heavy") without any reference to actual levels of sediments (Fig. 4). Less than 50% of the papers reported quantitative estimates of sediment abundance, either measured directly or through reference to previously published work. Unexpectedly, sometimes information on abundance of sediments was lacking even from experimental work in the laboratory, where no information was given about the type of sediment treatment applied (see "Laboratory experiments", p. 196), and lack of quantitative information on the effectiveness of manipulations of sediment is a major shortcoming of most field experiments (see "Field experiments", p. 207). Less than 10% of the papers reported data on sediment characteristics (e.g. type, size or composition of sediment particles). Even less information was available on temporal variability of sedimentation, and only very few papers reported quantitative information on spatial variability of sediment deposition or acknowledged the potential importance of this factor.

Measurement of sediment deposition and accumulation

Methods used to quantify sedimentation to rocky coasts have been very variable. The use of different methods is, in part, related to the characteristics of the habitat where researchers operate. Trowbridge (1996), for example, suggested that in areas where sand fluctuations are greater than 1 m, and the underlying rocks have high topographic relief, quantifying

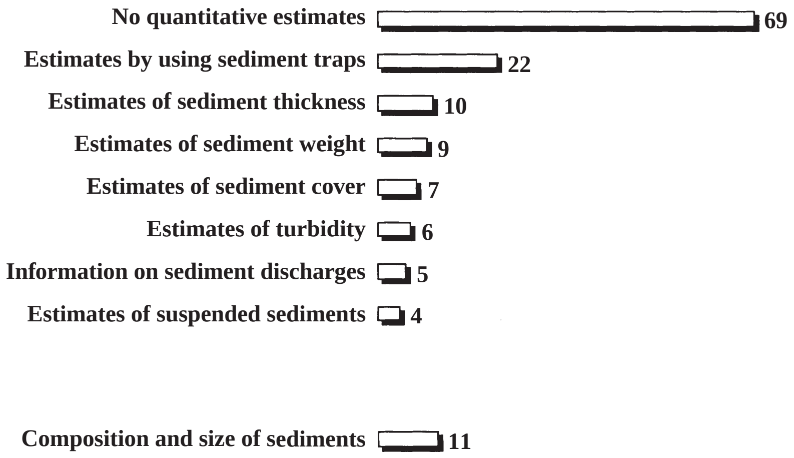

Figure 4 Estimates of sediment load reported in selected studies on the effects of sedimentation on rocky coast assemblages. Bars represent number of studies.

sediment cover, depth or mass may be difficult to apply or not informative. As an alternative, she used qualitative estimates of the degree of burial of the surveyed algae (i.e. thalli not buried, some thalli uncovered and some buried, or thalli totally buried). However, sometimes, the choice seems dictated more by personal preference rather than by objective constraints.

Rocky intertidal habitats In rocky intertidal habitats sedimentation is generally estimated in terms of accumulated sediments. The principal methods used include:

(1) estimates of distribution and per cent surface cover of sediments by using visual, photographic or video techniques (e.g. Stewart 1982, Littler et al. 1983, Renaud et al. 1996),
(2) estimates of sediment depth by direct measurements or by using reference marks (e.g. Markham 1973, Daly & Mathieson 1977, Mathieson 1982, Moring 1996, Renaud et al. 1996),
(3) estimates of sediment mass per unit area (e.g. Emerson & Zedler 1978, Stewart 1983, Branch et al. 1990, Engledow & Bolton 1994, Whorff et al. 1995), and
(4) estimates of sediments accumulated over time on panels or trapping surfaces (Bertness 1984). Sometimes sedimentation has also been estimated indirectly by using
(5) measurements of sediment suspended in waters close to the shore, by filtering known volumes of water (e.g. Little & Smith 1980, Hyslop et al. 1997, Fariña & Castilla 2001), and
(6) estimates of water turbidity (Mettam 1994, Iannuzzi et al. 1996). It should be noted, however, that high levels of suspended sediments do not necessarily result in high levels of sediment accumulation on the bottom.

Rocky subtidal habitats The principal methodologies used to quantify sedimentation in rocky subtidal habitats include:

(1) the estimation of sediment deposition by using sediment traps, which collect settling sediments over a given time (e.g. Moore 1972, Gulliksen 1982, Deysher & Dean 1986, Bavestrello et al. 1991, 1995, Kendrick 1991, Schroeter et al. 1993, Airoldi et al. 1996, Airoldi & Virgilio 1998, Maughan 2001),

(2) measurement of sediment cover and/or thickness, or mapping of sediments (e.g. Kennelly 1983, Gotelli 1988, Renaud et al. 1997, Slattery & Bockus 1997), and

(3) measurements of suspended solids or water turbidity (Saiz-Salinas & Urkiaga-Alberdi 1999).

Sediment traps can have variable designs, which can affect the performance of estimates of sedimentation rates in moving waters (Bloesch & Burns 1980). In recent years, laboratory and *in situ* experiments have shown that stable, vertically suspended, smooth cylinders, with an inner diameter of >45 mm and an aspect ratio of >3 give the most reliable results (Blomqvist & Håkanson 1981, Butman et al. 1986), which has lead to a major uniformity in the design of traps used. However, there is still variability in the way traps are positioned and in the methods used to quantify sediment trapped. In some cases, due to experimental or habitat constraints, traps have been replaced by panels or other small trapping structures, which have been generally used for relative comparisons of sedimentation rates rather than to estimate absolute fluxes of sediments (e.g. Eckman et al. 1989, Airoldi & Cinelli 1997).

Sediment traps are invaluable as research tools for documenting gross sediment inputs to rocky coasts. Caution has been recommended, however, as results are greatly affected by resuspension and movement of sediments, particularly in highly energetic habitats (Moore 1972, Blomqvist & Håkanson 1981, Gulliksen 1982, Bavestrello et al. 1995, Airoldi et al. 1996, Lund-Hansen et al. 1997). Thus, the downward flux of particles does not necessarily equal the rate of accumulation of sediments to the bottom and the sessile biota (Gardner 1980). Ideally, studies should incorporate direct sampling of sediments accumulated on rocky substrata and organisms (Purcell 1996) but, probably due to the constraints of working underwater, estimates of sediment mass per unit area have been scarce in subtidal rocky habitats (Kendrick 1991, Herrnkind et al. 1988, Airoldi & Virgilio 1998).

Measurement of scour

In highly energetic habitats, movement of sediments, particularly the coarse fractions, can have important effects on organisms in terms of scour. The intensity of scour by sediments, however, has generally been inferred indirectly from observations on either movements of sediments and/or damage to and removal of organisms (e.g. Daly & Mathieson 1977, Robles 1982, Littler et al. 1983, D'Antonio 1986, McGuinness 1987a, Menge et al. 1994, Airoldi et al. 1996, Trowbridge 1996, Airoldi 1998, Underwood 1998). Craik (1980) proposed a method for measuring scour in intertidal areas based on the rate of dissolution of cement blocks anchored to the substratum; this method, however, could not separate the scour due to movement of blocks over the substratum by wave action from scour due to abrasion from suspended sediments. Estimates of scour have also been obtained by using tiles painted with a thin coat of colour that is removed by contact with particles (Thompson et al., unpubl. data), similar to those used to measure scour by kelp fronds on understorey species in kelp forests (e.g. Kennelly 1989).

Effects of sedimentation

Historically, studies on the effects of sedimentation on rocky coast organisms have focused on reports of lists of species from areas naturally affected by sediments, or more rarely on examinations of life histories and structural adaptations of single species or groups of species. A consistent body of literature has reported observations on species that tend to bind and trap sediments but quantitative data have been scarce. In the last two decades quantitative observations on responses of individual species or assemblages to sedimentation have become relatively more frequent, probably in response to the increasing concern for the trend of enhanced sediment loads to coastal areas. These studies have sometimes been supported by laboratory experiments. However, it is only recently that systematic attempts have been made to investigate experimentally, both in the field and in the laboratory, the causal mechanisms by which sediments may affect rocky coast organisms. In this review an attempt is made to summarise the major findings from this considerable body of literature, and analyse whether observations stimulating the hypothesis that sediments have an important ecological role on rocky coasts are supported by experimental evidence.

Most of the papers that are included in the present section of the review have been published in international journals indexed in *Current Contents*. Many represent papers that reported qualitative, and sometimes fortuitous, observations (Fig. 5). This information included records of species that appeared to be more frequent or less frequent in habitats characterised by high levels of sediments, or observations done during studies not specifically aimed at analysing the effects of sedimentation on rocky coast organism. In most cases, these papers invoked sedimentation as a possible explanation for patterns observed in the assemblage, but provided little or no supporting data. About 35% of the papers reported quantitative observations of changes in the abundance of rocky coast organisms that were attributed to variations in the regime of sedimentation. The reliability of these studies was variable, and the papers that reported rigorous observations repeated over time or with an adequate level of spatial replication were few. In many cases, effects of sediments were difficult to separate from the possible influence of other environmental factors covarying with

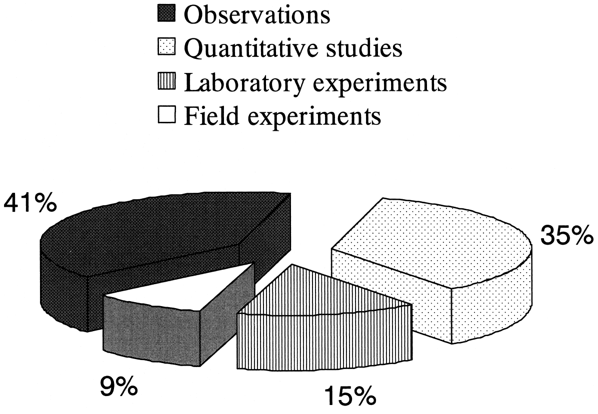

Figure 5 Percentage of qualitative and quantitative observations and/or laboratory and field experiments in studies on the effects of sedimentation on rocky coast assemblages.

sediments (e.g. variations in the hydrodynamic regime, changes in bottom topography and depth, natural seasonal patterns) or from factors often associated with high sediment loads (e.g. turbidity, presence of organic or chemical pollutants). In this group, also included are "natural experiments", in which sediments were not manipulated directly, but effects were studied by repeating experiments or transplanting organisms across habitats "impacted" or "non-impacted" by sediments. Papers reporting results from experiments in which sedimentation was directly manipulated were in a minority: most work was done in the laboratory, while experiments in the field made up $<10\%$ of studies.

Qualitative and quantitative observations

The effects most frequently attributed to the presence of sediments on rocky coasts are summarised in Figure 6. Effects were most generally based on comparisons among areas with "low" and "high" sediment load, or on changes observed over time and presumably related to variations in sediment load. Interpretation of results as responses to "high" or "low" levels of sedimentation, however, was limited in many studies by lack of quantitative information on the characteristics and variability of the regime of sedimentation (see p. 171), by scarce consideration of spatial and temporal issues, and by confounding effects because the distribution of sediments on rocky coasts generally covaries with other important physical and biological factors (see pp. 167 and 168). Furthermore, it is important to note that identifying relationships between the distribution of sediments and species on rocky coasts, while important for the formulation of predictive hypotheses, cannot be considered an evidence of causality.

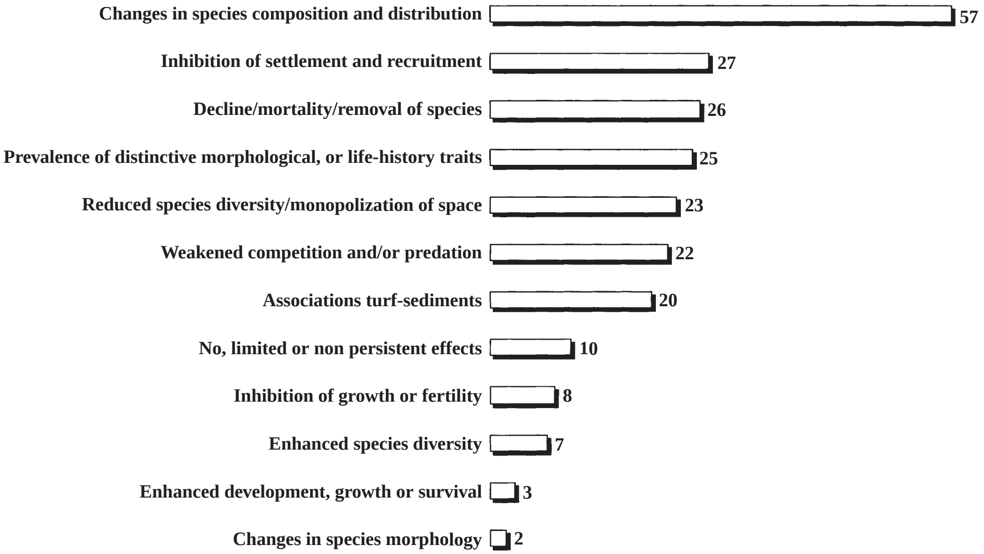

Figure 6 Effects or lack of effects most frequently attributed to the presence of sediments on rocky coast organisms and/or assemblages. More than one effect was often attributed to sediments in any study. Bars represent number of studies.

Changes in species composition and abundance

Early indication that sediments are an important factor influencing the composition of rocky coast assemblages can be found in past taxonomic accounts of the species occurring in rocky coast habitats naturally affected by sediments (e.g. Cotton 1912, Hoyt 1920, Kitching et al. 1934, Rees 1935, Doty 1947a,b, Mathieson & Fralick 1972, Mathieson 1979, Mathieson 1982). These habitats appeared to be peculiar systems, characterised by distinctive assemblages of plants and animals; taxonomic records included species that appeared to be restricted to sediment affected areas, species that seemed to occur at both sediment affected and unaffected areas, and species that occurred more frequently at unaffected areas but were occasionally present also in areas with sediments.

More recent quantitative works on assemblages from sediment impacted rocky coasts have confirmed the observation that the composition and distribution of species often seems to be closely related to spatial and/or temporal changes in sediment load. Daly & Mathieson (1977), for example, reported that the composition, abundance and distribution of intertidal species in New Hampshire were related to fluctuations of sand levels: assemblages at shores most affected by sediments were characterised by the dominance of opportunistic species (e.g. *Enteromorpha* spp. and *Ulva lactuca*), and perennial “psammophytic” species (e.g. *Ahnfeltia plicata* and *Sphacelaria radicans*), and by the notable absence of species common on nearby rocky shores and considered intolerant to sediments (e.g. *Ascophyllum nodosum*). Furthermore, the lower limits of distribution of some species (e.g. *Mytilus edulis*, *Semibalanus balanoides* (as *Balanus balanoides*), and *Porphyra umbilicalis*) appeared to be related to the historical sequences of sand inundations in the area, as they approximated the zone of highest summer elevations of sand. Littler et al. (1983) described how patterns of species abundance on intertidal rocky shores in southern California were related to the relative degree of sand stress on different portions of the study site: opportunistic macrophytes (e.g. *Chaetomorpha linum*, *Cladophora columbiana*, *Ulva lobata* and *Enteromorpha intestinalis*) and highly reproductive macroinvertebrates (e.g. *Tetraclita rubescens*, *Chthamalus fissus/dalli* and *Phragmatopoma californica*) dominated areas routinely buried by sand; long-lived species (e.g. *Mytilus californianus*, *Haliotis cracherodii* and *Lottia gigantea*) dominated areas where rock contours provided a refuge from sand deposition, and sand tolerant species (e.g. *Anthopleura elegantissima* and *Phyllospadix scouleri*) dominated areas with greatest sediment deposition. Gorostiaga et al. (1998) reported that sedimentation, probably related to wave exposure, was the environmental factor that best matched the gradient in the distribution of sublittoral benthic algae along the eastern Basque coast. Along a gradient of increasing levels of sediments (characterised by using a semi-quantitative scale of cover), they observed changes in the relative abundance of some species; for example, the abundance of *Gelidium corneum* (as *G. sesquipedale*) and *Mesophyllum lichenoides* was negatively related to sediments, whereas *Halopitys incurvus* and *Chondracanthus acicularis* were most abundant in areas with high cover of sediments. The general pattern was a decrease of vertical structure due to the loss of canopy-forming species, as also reported from other areas impacted by sediments (Seapy & Littler 1982, Vogt & Schramm 1991, Airoldi et al. 1995, Airoldi 1998, Eriksson et al. 2002). Konar & Roberts (1996) reported differences in the composition of species between areas close to or distant from plumes originated by landslides. Patterns differed among sites, however, and the only consistent trend was a greater abundance of brown algae at the areas distant from the sediment plumes. Renaud et al. (1996, 1997) observed that the distribution and composition of macroalgae on subtidal rocky reefs affected by sediments were related to fluctuations in sediment characteristics and depth; cover of macroalgae was consistently greatest in areas with low cover of sediments, and a notable increase in the abundance of macroalgae was observed after a storm removed sediments from some areas. Saiz-Salinas & Urdangarin (1994) described a gradient of disappearance of macroalgae and increased abundance of opportunistic filter-feeding animals along the outer part of Bilbao harbour and discussed how estuarine sedimentation appeared to be the main environmental factor responsible for such gradient. Similarly, several authors have described patterns of zonation of species, or differences among assemblages on surfaces of different inclinations, and identified sedimentation as one of the environmental factors most closely related to those patterns (e.g. Chapman 1943, Stephenson 1943, Lilly et al. 1953, Lewis 1964, Pérès & Picard 1964, Clarke & Neushul 1967, Moore 1973b, Norton et al. 1977, Little & Smith 1980, Farrow et al. 1983, Castric-Fey 1988, Ballesteros 1992, Brattström 1992, Santos 1993, Mettam 1994, Johansson et al. 1998, Gabriele et al. 1999, Saiz-Salinas & Urkiaga-Alberdi 1999, Pedersén & Snoeijs 2001). Caution is needed, however, because in many studies distribution of sediments was correlated with other important environmental factors, such as wave action, depth or salinity. Low density of grazers and concomitant dominance of turf-forming and/or opportunistic foliose algae have been observed on several rocky coasts affected by sediments (e.g. Stewart 1989, Airoldi et al. 1995, Airoldi 1998, Pulfrich et al., in press, see pp. 187 and 189). Branch et al. (1990), for example, reported that following the flooding of the Orange River in South Africa, entirely different assemblages developed in areas most affected by abnormal dilution of water and high load of sediments and the shore changed from being dominated by patellid limpets to being dominated by opportunistic foliar algae. Among others, Daly & Mathieson (1977), Emerson & Zedler (1978), Robles (1982), Seapy & Littler (1982), Littler et al. (1983), Stewart (1983), D'Antonio (1986), Aleem (1993), Evans et al. (1993), Birje et al. (1996) and Kim et al. (1998) described changes in the composition and abundance of species following occasional, seasonal or long-term fluctuations in the levels of sediments. On a protected New England rocky beach, Bertness (1984) showed how accumulation of sediments, due to the removal of the snail *Littorina littorea* and consequent development of foliose algae, ultimately increased the abundance of organisms characteristic of soft-bottom habitats, such as polychaetes, tubiculous amphipods, mud crabs, and mud snails, and decreased the success of organisms characteristic of hard-bottom habitats, such as barnacles and encrusting algae. Changes in the abundance and composition of rocky coast assemblages have been frequently reported following enhanced sediment loads as a consequence of human activities (see p. 193). Finally, accumulation of sediments within mats of algae, mussels, or other invertebrates is known to be related to the abundance and diversity of species typically associated with soft bottoms, including macroinfauna and meiofauna (e.g. Gibbons 1988 and references therein, Grahame & Hanna 1989).

A few authors have also reported limited or non-persistent effects of sedimentation on the composition of rocky coast assemblages. Carballo et al. (1996), for example, found that the composition and distribution of sponges in subtidal hard-bottom habitats in Algeciras Bay, Spain, were not apparently related to rates of sedimentation. Baynes (1999) reported that differences in the composition of assemblages between horizontal and vertical surfaces on rocky reefs in southern Gulf of California were not related to differences in sediment deposition. Shaffer & Parks (1994) showed that a landslide had immediate effects on the abundance of algae in kelp beds adjacent to the slide area, but such effects did not persist over time, and differences between affected and unaffected areas were no longer evident after few months. Similarly, Moring (1996) reported immediate responses of assemblages to severe disturbance by sediments following a hurricane but by the following year excess sand was removed from the area by winter turbulence, and assemblages recovered to their pre-disturbance appearance. Many observations and experiments on the effects of sedimentation on rocky coast assemblages are carried out over very short times. However, the short-term nature of the effects reported by Shaffer & Parks (1994) and by Moring (1996), as well as the evidence from observations and experiments that effects of sediments vary over time in relation to other environmental and biological factors (e.g. Airoldi & Cinelli 1997, Airoldi 1998), suggest that timing is a critical and overlooked factor in studies on the impact of sedimentation on rocky coast assemblages.

Responses of individual species: evidence of direct and indirect effects

Although it appears evident that sediments may influence the species composition of assemblages on rocky coasts, by limiting the abundance of some species and favouring the development of others, in most cases the underlying mechanisms are not known. With few exceptions, the above reported relationships between sediments and species compositional changes have been attributed to direct effects on individual species that appeared to respond “negatively”, “positively”, or “indifferently” to their presence. Thus, observations have been focused on hard-bottom species that seemed to tolerate or even be enhanced by sediments (see pp. 179 and 187), or that seemed to undergo negative effects on their recruitment, growth, or survival (see p. 189). However, the lack of a clear understanding of the mechanisms by which sedimentation affects rocky coast organisms is reflected by the notably contrasting effects sometimes attributed to sediments. Species, or groups of hard-bottom species, that have been ranked from sensitive to tolerant to sediments are numerous, including, among others, species belonging to the genera *Ulva, Enteromorpha* and *Gelidium*, mussels, encrusting coralline algae, and sponges. These observations will not be analysed case by case, because quantitative data supporting evidence of either tolerance or intolerance are limited, and because scarcity of data on sediment loads makes it difficult to compare and interpret results as response to “high” or “low” levels of sedimentation (see p. 171). The case of encrusting coralline algae is taken as an example because there are lines of evidence that such apparently contrasting observations are not only related to different susceptibility among congeneric species, or to variations in the regime of perturbation by sediments, but are also connected with the complex direct and indirect effects of sedimentation.

Responses of encrusting coralline algae to presence of sediments are controversial. Some observations suggest that encrusting coralline algae may be negatively affected by sediments (e.g. Ayling 1981, Kennelly 1991, Moring 1996, Gorostiaga et al. 1998, Maughan 2001, Melville & Connell 2001, Pulfrich et al., in press, S. D. Connell, pers. comm.), whereas others suggest that encrusting coralline algae are often abundant, or even dominant, in a variety of sediment-impacted habitats (Littler 1973, Kendrick 1991, Saiz-Salinas & Urdangarin 1994, Airoldi et al. 1995, Falace & Bressan 1995, Konar & Roberts 1996, Airoldi 2000a). Such different responses are certainly in part related to the variable ecology of this vast and diversified group of species (e.g. Dethier 1994). Furthermore, observed effects may depend on the local characteristics of sedimentation regime. For example, recent experiments by Matsunaga et al. (1999) have shown that the presence of forest-derived, humic substances in sediments may inhibit the germination of encrusting coralline spores. There is evidence, however, that the contrasting responses observed for encrusting coralline algae may be related also to the complex indirect effects of sedimentation. Steneck et al. (1997), for example, suggested that most coralline algae are sensitive to sedimentation, although the encrusting coralline alga *Neogoniolithon strictum* formed unique algal ridges in the Bahamas, in environments characterised by low wave energy, high rates of sedimentation and low rates of herbivory. The authors discussed how this encrusting coralline alga tolerated sediment burial possibly as a result of anatomical adaptations (abundant multiple cell fusions and unbranched morphology). Even this species, however, required relatively sediment-free, hard substrata for successful germination and growth. The authors suggested that the success of *N. strictum* in such sediment-affected environments may be influenced by the low rates of herbivory observed in those habitats. Kendrick (1991) demonstrated that recruitment and growth of coralline crusts were enhanced by treatments simulating scour, whereas crusts were overgrown and outcompeted by turf-forming algae in treatments simulating erosion and accretion. Kendrick suggested that positive effects of scour were related indirectly to negative effects on the abundance of overgrowing algae (i.e. burial and abrasion by sand may provide the cleaning effects normally provided by grazers, and described as important to maintain encrusting coralline algae). Similar hypotheses have been suggested by other authors (e.g. Stewart 1989). Airoldi (2000a), however, demonstrated that some encrusting corallines, which occurred abundantly on sediment-stressed subtidal reefs, were more tolerant to overgrowth by turf-forming algae. It was hypothesised that crusts could benefit from being overgrown by turf through protection from abrasion by sediments, which seemed to negatively affect recruitment and growth of crusts. Furthermore, overgrowth by turf and trapped sediment could relieve crusts from competition for primary substrata with erect algae.

These observations suggest that the effects of sediments on rocky coast organisms may be complex, probably involving not only direct effects (e.g. from smothering and scour) on individual species but also indirect effects mediated by competitive or predator/prey outcomes. Indeed, results of recent field experiments have confirmed the potential indirect effects of sedimentation (see p. 207), the importance of which has long been overlooked. Consideration of indirect effects is fundamental to understanding responses of species to variations in sediment load.

Morphological, physiological and life-history attributes of "psammophytic" "sand-tolerant" species

Rocky coasts affected by sediments have always been viewed as extreme environments for hard-bottom species, characterised by highly stressful physical conditions. Therefore, morphological and physiological attributes of hard-bottom species occurring at and often dominating these habitats have long been the object of observation and discussion, particularly in the case of long-lived species that were able to persist and maintain spatial dominance from year to year in the presence of sediments. These species have often been indicated as "psammophytic" or "sand loving", which, as Littler et al. 1983 pointed out, implies that they are somehow directly favoured (e.g. in terms of enhanced growth and/or reproduction) by sediments. However, in recent years, observations and experiments have indicated that most "psammophytic" species are rather "sand-tolerant" species: they may be negatively affected by sediments but not as severely as other species, and the costs imposed by living in sediment-stressed habitats are probably compensated for by indirect advantages in terms of reduced competition and/or predation (Taylor & Littler 1982, Littler et al. 1983, Turner 1985, D'Antonio 1986, Kendrick 1991, Trowbridge 1992, Airoldi & Cinelli 1997, Airoldi & Virgilio 1998; see also pp. 196 and 207). The role of tolerance as an important mechanism influencing community structure relative to "negative" and "positive" interactions has been highlighted by the results of recent studies, which have suggested that the prevalence of space monopolising forms, such as algal turfs and crusts, may be related to their abilities to withstand a variety of physical and biological challenges (Airoldi 1998, 2000a). This emphasises the need for attention to life-history traits that enhance tolerance of species.

Littler et al. (1983) observed that rocky coasts impacted by sediments are colonised primarily by three groups of species with different life-history traits:

(1) long-lived species (either "psammophytic" or "sand-tolerant") that seem to be capable of adjusting to stresses imposed by the presence of sediments,
(2) opportunistic species, that rapidly recolonise space following mortalities caused by burial and scour, and
(3) migratory species, that move in and out of the habitat depending on the level of burial by sediments.

Rocky coasts affected by sediments are also often dominated by another group of species (Airoldi 1998, Airoldi & Virgilio 1998 and references therein), consisting of

(4) species that bind and trap sediments, and appear to tolerate burial and scour. Many of these species have life histories intermediate to long-lived and opportunistic species, and show a strong association with sediments. Because of its importance particular attention is dedicated to this group in the following section.

Very little experimental work has been done to test what attributes of a species result in differentiating tolerance or susceptibility to the presence of sediments (see Pineda & Escofet 1989). Nevertheless, observations from a variety of sediment impacted rocky habitats consistently suggest the prevalence of certain morphological, reproductive and physiological attributes (Table 1). These include:

- the regeneration of upright portions from remnant bases tolerant to sediment burial and scour;
- opportunistic cycles of reproduction and growth or the capacity to propagate vegetatively;
- tough and wiry thalli or bodies;
- growth, reproductive cycles, and/or migrating behaviours synchronised with fluctuations of sediments;
- apical meristems that maintain dividing cells above sediment;
- erect morphology that prevents settlement of sediment; and
- physiological adaptations to withstand darkness, anaerobic conditions and high hydrogen sulphide concentrations.

For example, Markham (1972) observed that *Laminaria sinclairii*, which grows in habitats affected by sediments, has a longer stipe and narrower blades than its congener *L. longipes* which grows in sediment-free habitats, and has distinctive deciduous blades. Markham &

Table 1 Morphological, physiological or life-history traits that have been suggested to confer tolerance to presence of sediments in species most frequent on rocky coasts with high levels of sediments (species sometimes defined as “psammophytic”).

Species	Morphological, physiological, life-history traits	Habitat/Location	References
Numerous algae, including *Rhodothamniella floridula* (as *Rhodochorton floridulum*), *Vaucheria velutina* (as *V. thuretii*), *Polyides rotundus*, and *Gracilaria gracilis* (as *G. confervoides*)	Terete branched thalli of tough construction.	Restricted to or very abundant on intertidal and shallow subtidal rocks covered by sand or in sandy tide pools. Clare Island (Ireland).	Cotton 1912
Phaeostrophion irregulare	Peak growth and reproduction synchronised with seasonal fluctuations of sand, deciduous blades, regeneration of upright fronds from perennial holdfast resistant to damage from sand burial.	Normally restricted to low intertidal rocky habitats subject to seasonal fluctuations of sand (up to 2 m). Pacific coast of North America.	Mathieson 1967, 1982, Turner 1983, 1985
Laminaria sinclairii	Peak growth synchronised with seasonal fluctuations of sand, long stipe and narrow deciduous blades, reproduction by vegetative propagation, regeneration of upright fronds from perennial holdfast resistant to damage from sand burial.	Normally restricted to low intertidal rocky habitats, moderately to fully exposed to wave action, and subject to seasonal fluctuations of sand (up to 2 m). Pacific coast of North America.	Markham 1968, 1972, 1973
Zonaria farlowii	Thallus plasticity, considerable growth of rhizoids, presumed reduction of respiratory rates and tolerance to hydrogen sulphide.	Intertidal and subtidal rocky habitats, often in areas subject to seasonal burial by sand. Alive thalli were collected from 150–100 mm thick layers of black anoxic sand. California, USA.	Dahl 1971
Halimeda spp., *Udotea* spp.,	Extensive rhizome system, tough	Species belonging to these genera	Scoffin 1970, Williams et al. 1985,

Table 1 *continued*

Species	Morphological, physiological, life-history traits	Habitat/Location	References
Penicillus spp., *Caulerpa* spp.	thalli.	occur in both rocky and sandy habitats in a variety of tropical and temperate environments.	Littler et al. 1988, Piazzi et al. 1997
Ahnfeltiopsis linearis (as *Gymnogongrus linearis*), *Ahnfeltia plicata, A. concinna*	Peak growth synchronised with seasonal fluctuations of sand, clump growth, terete branched thalli of tough construction due to thick cortical layers.	Normally restricted to low intertidal rocky habitats, moderately to fully exposed to wave action, and subject to seasonal fluctuations of sand (up to 2 m). Pacific coast of North America.	Markham & Newroth 1972
Numerous algae, including *Ahnfeltia plicata* and *Sphacelaria radicans*	Tough and wiry thalli, regeneration of upright fronds from perennial basal holdfasts, reproduction by vegetative propagation, incomplete alternation of generations.	Dominant in intertidal rocky habitats subject to irregular fluctuations of sand (up to 1 m). New Hampshire, USA.	Daly & Mathieson 1977
Anthopleura elegantissima	Reproduction by vegetative propagation, ability to elongate above the sediment surface, low oxygen demand, migratory behaviour (in solitary specimens).	Common in rocky intertidal habitats subject to seasonal burial by sand. California, USA, and Baja California, Mexico.	Taylor & Littler 1982, Littler et al. 1983, Pineda & Escofet 1989
Numerous plants and animals, including *Phyllospadix torreyi* and *Tegula funebralis*	Large size, tough thalli, rhizomatous growth, regeneration of upright portions from remnant bases, opportunistic life histories, migratory behaviour.	Abundant to dominant in intertidal rocky habitats periodically inundated by sediments. California, USA.	Littler et al. 1983

Table 1 *continued*

Species	Morphological, physiological, life-history traits	Habitat/Location	References
Numerous algae, including *Pterocladia capillacea, Dictyota* sp., *Sphacelaria rigidula* (as *S. furcigera)*	Apical meristems that maintain dividing cells above sediment, regeneration of upright portions from remnant bases resistant to burial, peak growth and reproduction synchronised with seasonal fluctuations of sand, tough and calcified thalli, vegetative propagation.	Abundant to dominant in intertidal rocky habitats periodically inundated by sediments. California, USA.	Stewart 1983
Gracilariopsis lemaneiformis (as *Gracilaria lemaneiformis*)	Regeneration of upright fronds from underground thallus system resistant to burial.	Adaptations were discussed for specimens in shallow subtidal sheltered bays, but the species can also occur in rocky habitats with sand. Chile.	Santelices et al. 1984
Neorhodomela larix (as *Rhodomela larix*)	Reproduction by vegetative propagation, regeneration of upright fronds from perennial basal holdfast resistant to burial.	Frequent on moderately exposed, horizontal, intertidal rocky habitats, particularly in areas subject to seasonal fluctuations of sand (up to 60 cm). Absent from vertical surfaces or areas with high urchin densities. Pacific coast of North America.	D'Antonio 1986
Sargassum sinicola	Small size, low sexual reproduction, reproduction by vegetative propagation.	Dominant in shallow subtidal rocky habitats, also in areas close to the mouth of streams and subject to high sand deposition. Southern Gulf of California, Mexico.	Espinoza & Rodriguez 1987

Table 1 *continued*

Species	Morphological, physiological, life-history traits	Habitat/Location	References
Several species of Dictyotales	Regeneration of upright branches from perennial creeping stolons.	Abundant in shallow water, sheltered rocky habitats, covered permanently by a layer of moving sand. Sydney Harbour, Australia.	King & Farrant 1987
Siphonaria capensis	Low oxygen demand, use of anaerobic pathways.	Frequent on sand-free, intertidal rocky areas, but can extend its distribution to sediment-affected areas. South Africa.	Marshall & McQuaid 1989
Corallina spp. (*C. pinnatifolia* and *C. vancouveriensis*)	Regeneration of upright fronds from perennial basal crust resistant to burial and scour, calcified thalli, apical meristems, large reproductive outputs, lateral vegetative propagation, slow growth rates.	Dominant on mid intertidal shores periodically disturbed by sand burial and scour. Southern California, USA.	Stewart 1989
Several algae including *Womersleyella setacea* (as *Polysiphonia setacea*), *Halimeda tuna* and *Dictyota dichotoma*	Reproduction by vegetative propagation, regeneration of upright fronds from perennial basal parts resistant to burial and scour, tough thalli, opportunistic life histories.	Abundant to dominant in subtidal rocky habitats, also in areas characterised by high deposition ($2\,\mathrm{g\,m^{-2}\,d^{-1}}$ to $178\,\mathrm{g\,m^{-2}\,d^{-1}}$) and movement of fine sediments. Mediterranean Sea.	Airoldi et al. 1995, Airoldi & Cinelli 1997, Airoldi 1998
Codium setchellii	No obvious demographic, phenological, anatomical or morphological features that indicate resistance to sand burial. The alga grows adherent to rocky surfaces, forming discrete crustose pads or	Present at low densities in low intertidal rocky habitats subject to seasonal up to nearly continuous burial by sand (up to $>1\,\mathrm{m}$). Growth was possible at non-sandy sites, if shielded from herbivory. Buried thalli	Trowbridge 1996

Table 1 *continued*

Species	Morphological, physiological, life-history traits	Habitat/Location	References
	irregular cushions. The author suggested that persistence may be due to slow growth and long life-span.	did not appear to be subject to anoxic conditions. Pacific coast of North America.	
Fucus vesiculosus forma *mytili*	Lack of holdfast, lack of air vesicles, lack of sexual reproduction, propagation by vegetative reproduction by means of drifting fragments of adult thalli.	On mussel beds in soft-bottom habitats. The form growing in soft-bottom habitats is so different from that in hard-bottom habitats that it was originally characterised as a distinct species (*F. mytili*). Wadden Sea, Germany.	Albrecht 1998
Sargassum microphyllum	Regeneration from perennial basal holdfast.	Adaptation to sediments were discussed for intertidal specimens in coral reefs, but species belonging to this genus are also frequent in rocky habitats.	Umar et al. 1998

Newroth (1972) observed that *Ahnfeltiopsis linearis* (as *Gymnogongrus linearis*), which can survive sediment burial over 6 months, has thicker cortical layers and a more terete thallus than the congener *G. platyphyllus*, which cannot survive in sediment affected areas. Solitary animals have been found to be less susceptible to sediments than colonial species (reviewed in Jackson 1977). Invertebrates with an erect morphology have been suggested to be less susceptible to sediments than prostrate forms (e.g. Saiz-Salinas & Urdangarin 1994, Irving & Connell 2002). Marshall & McQuaid (1989) demonstrated in the laboratory that the pulmonate limpet *Siphonaria capensis*, which extends its distribution to sediment-affected areas, has specific physiological adaptations to reduced oxygen tensions that presumably allow it to survive burial for considerably longer periods than does the prosobranch *Patella granularis* which is restricted to sediment-free areas. Albrecht (1998) reported that *Fucus vesiculosus* (forma *mytili*) growing on intertidal mussel beds on soft bottoms in the Wadden Sea differed in growth habit, morphology and reproductive ability from *F. vesiculosus* growing on mussel beds on rocky shores (Fig. 7). The former was characterised by lack of holdfast, lack of air vesicles, and especially by lack of sexual reproduction: reproduction only occurred vegetatively, by means of drifting fragments of adult thalli. In a detailed description of assemblages on intertidal rocky shores periodically inundated by sand at Bound Rock, California, Daly & Mathieson (1977) reported that several species, including *F. vesiculosus*, *Chondrus crispus* and *Mastocarpus stellatus* (as *Gigartina stellata*), exhibited extensive holdfast regeneration. Many species of algae that occur on both sheltered soft bottoms and rocky coasts, such as species belonging to the genera *Halimeda*, *Caulerpa*, *Penicillus* and *Udotea*, typically have tough thalli and develop extensive systems of rhizomes (Scoffin 1970, Williams et al. 1985, Littler et al. 1988, Airoldi & Cinelli 1997, Piazzi et al. 1997). Furthermore, the ability to reproduce vegetatively seems to be one of the features most consistently reported for species in sediment-impacted areas (see Table 1). Preva-

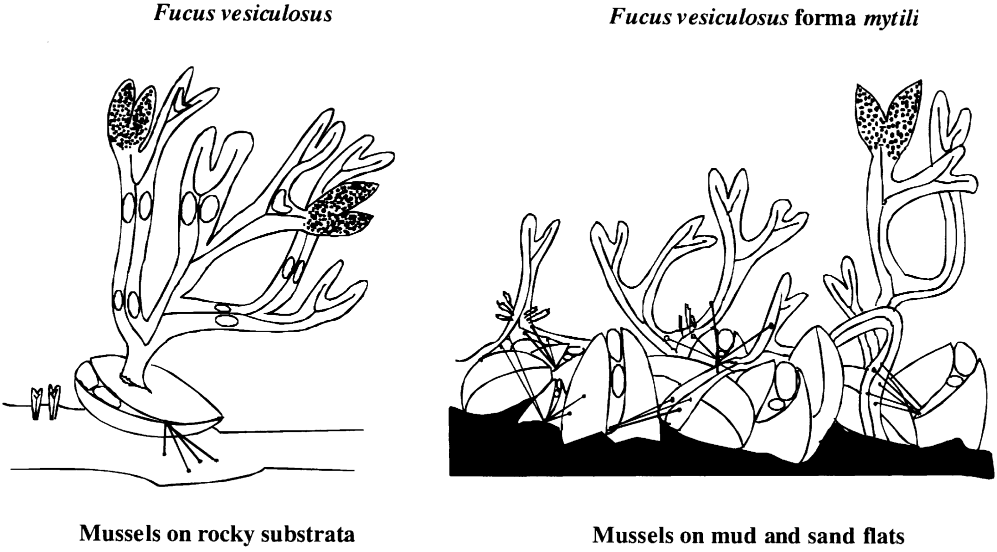

Figure 7 Growth habit and morphology of fertile *Fucus vesiculosus* colonising mussels on rocky substrata (left) and sterile *F. vesiculosus* forma *mytili* colonising mussels on mud and sand flats in the Wadden Sea (modified from Albrecht 1998, published with permission).

lence of vegetative propagation in these habitats may be related to the fact that this form of reproduction removes dependence upon spore attachment to buried, unstable substrata, and allows a rapid recovery from damage (Airoldi 1998). Indeed, observations and experiments suggest that vegetative propagating stages are less vulnerable to a variety of physical and biological factors than are sexually reproductive stages, and recover very quickly after most common disturbances, especially when damage to organisms is patchy (see Airoldi 2000b and references therein).

In contrast to these apparent adaptations, Trowbridge (1996) discussed how *Codium setchellii*, which forms low-density populations on sand-influenced rocky benches in Oregon, does not exhibit obvious anatomical or morphological traits that suggest tolerance to sand. She hypothesised that the alga persists in sand-stressed habitats because of its slow growth and long life-span, and stressed the need for more studies to understand better the adaptation of species to environmental conditions during burial.

Species that trap and bind sediments

Rocky intertidal and subtidal coasts affected by sediments appear to be often dominated by species which have a morphology that tends to accumulate and trap sediments. These species may include sessile invertebrates, such as the mud ectoprot *Cryptoarachnidium argilla*, which has been observed forming extensive mats up to 3 mm thick that entrap fine sand and silt (Palmer-Zwahlen & Aseltine 1994), or mussels which are known to accumulate large amounts of sediments (e.g. Albrecht 1998 and references therein). However, the most common and abundant group of species is represented by densely packed, small macroalgae which form mats that are frequently referred to as turfs (Airoldi 1998).

The composition and structure of turfs may be extremely variable, because they may be formed by filamentous, calcareous-articulated or corticated-terete algae (Airoldi 2001). Despite their variable morphology, however, they all tend to be associated with trapped sediments. The dense network of ramifications within turfs forms, in fact, a cohesive surface layer that tends to alter the flow microenvironment and entrap particles moving on the bottom (Neumann et al. 1970, Scoffin 1970, Carpenter & Williams 1993). Cotton (1912), for example, reported that on intertidal shores at Clare Island (Ireland), *Rhodothamniella floridula* (as *Rhodochorton floridulum*) was the most important species of a group of finely branched, upright growing algae which accumulated and retained sand. Boney (1980) observed stratified mineral accumulations of sand grains and particles of coal dust within small turfs formed by the filamentous alga *Rhodochorton purpureum* (as *Audouinella purpurea*) along the coasts of Scotland. Sousa et al. (1981) reported the presence of layers of anoxic sediments within turfs formed by perennial red algae, mainly *Chondracanthus canaliculatus* (as *Gigartina canaliculata*), *Laurencia pacifica* and *Gastroclonium coulteri*, on intertidal shores of southern California. Kennelly (1989) reported that a conglomerate of silt, microscopic filamentous algae and microinvertebrates built up in patches experimentally cleared of kelps. Among others, turfs formed by various species of red (e.g. *Corallina* spp., *Polysiphonia* spp., *Ceramium* spp., *Laurencia* spp., *Gelidium* spp., *Acrochaetium* spp.), brown (e.g. *Giffordia* spp.) and ephemeral green algae (e.g. *Ulva* spp., *Enteromorpha* spp., *Cladophora* spp.) have been frequently reported to trap sediments in rocky intertidal and shallow subtidal habitats in various geographical areas (Scoffin 1970, Towsend & Lawson 1972, Emerson & Zedler 1978, Ayling 1981, Stewart 1983, 1989, Herrnkind et al. 1988, Grahame & Hanna 1989, Branch et al. 1990, Kendrick 1991, Airoldi et al. 1995, Whorff et al. 1995, Piazzi & Cinelli 2001).

Sediment is considered to be a structural constituent of algal turfs (Stewart 1983, Kendrick 1991, Airoldi & Virgilio 1998). However, interactions between turf-forming algae and sediments have rarely been analysed directly and quantitative data on the amount or dynamics of sediments accumulated are scarce. The amount of sediment trapped within turfs formed by *Corallina* spp. on intertidal shores in southern California varied seasonally from <5 mm to >4.5 cm, and was closely related to the species composition and structure of the turf itself (Stewart 1983). Sediment trapped in filamentous algal turfs occurring on a shallow subtidal reef in the Galapagos archipelago ranged from 180 g m^{-2} to 1850 g m^{-2}, which corresponded to up to five times more than the biomass of the turf itself (Kendrick 1991). Whorff et al. (1995) found that algal turfs formed by a mixture of filamentous and corticated-terete algae on San Jose Island, Texas, trapped on average from about 270 g m^{-2} to 2600 g m^{-2} of sediment, depending on substratum slope and wave exposure. Airoldi & Virgilio (1998), working on turfs formed by the filamentous alga *Womersleyella setacea* (as *Polysiphonia setacea*) on exposed subtidal rocky reefs in the Ligurian sea (Italy), measured average amounts of sediment ranging from 86 g m^{-2} to 924 g m^{-2}, which represented up to 96% of the total mass of the turf (Fig. 8). The amount of sediment accumulated remained relatively constant over a year, despite significant temporal variations of rates of sediment deposition, supporting the hypothesis that turfs exert an important control on sediments. Furthermore, while the vertical growth of the turf was sensitive to the quantity and grain-size of sediment accumulated, its cover was unaffected: prostrate basal axes were resistant to sedi-

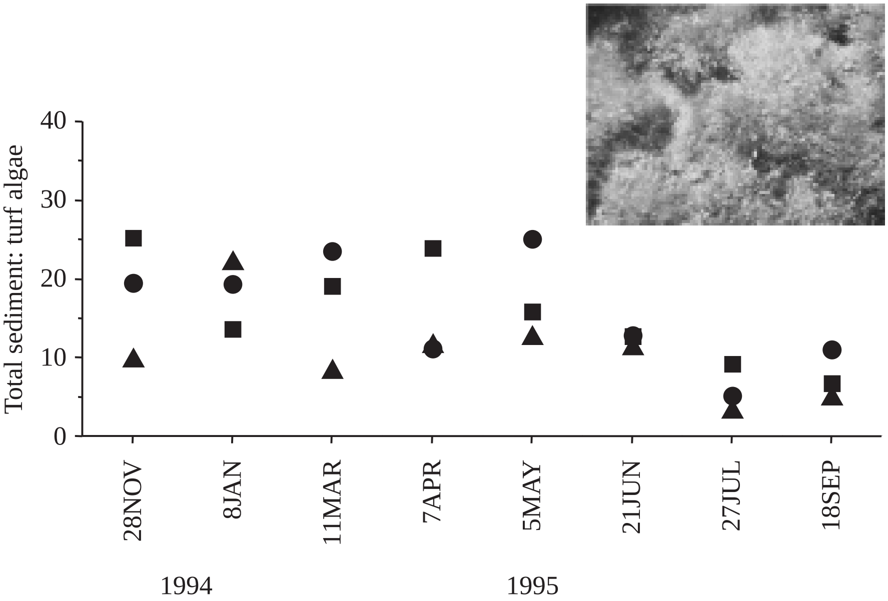

Figure 8 Sediment trapped in turfs formed by the filamentous alga *Womersleyella setacea* in subtidal rocky reefs south of Livorno, Italy (modified from Airoldi & Virgilio 1998, published with permission, photo by the author). Data are average ratios of dry mass of sediment trapped to biomass of turf-forming algae at three nearby sites (indicated by different symbols).

ment smothering, and, if damaged by severe scour, the turf was able to regain spatial dominance by quick vegetative propagation and regrowth of surviving axes (Airoldi 1998, Airoldi 2000b).

In recent years there seems to have been a worldwide trend of increasing abundance of turfs that has been hypothesised to be related to enhanced perturbations, including perturbation by sediments, in coastal areas (Airoldi et al. 1995, Airoldi 1998 and references therein). Observations and experiments suggest that the abilities to propagate by vegetative reproduction and to entrap and withstand sediments are among the possible determinants of the persistence and spatial dominance of turfs (Sousa et al. 1981, Airoldi 1998, 2000b, Airoldi & Virgilio 1998, but see Irving & Connell 2002). By propagating vegetatively, turfs may exploit opportunistically and pre-empt space. Subsequent accumulation of sediment is thought to inhibit both recruitment of algae that form canopies and grazing by sea urchins and other herbivores, thus favouring the prevalence of turfs (but see the review by Vadas et al. 1992 and work by Boaventura et al. 2002 for suggestions of facilitation of recruitment of canopy algae by turfs). So far, little experimental data either support or refute these hypotheses.

Inhibition of recruitment, growth, and survival

Sediments have been reported to be detrimental to a variety of rocky coast organisms. The most frequently postulated mechanisms are smothering and/or scouring of adult or juvenile stages, prevention from settling of larvae and propagules, and interference with normal foraging and feeding activities. Sometimes effects on growth, fertility and/or morphology have also been reported (e.g. Burrows & Pybus 1971, Dahl 1971, Espinoza & Rodriguez 1987, Sfriso & Marcomini 1996). Although direct observations of such effects are limited, several lines of indirect evidence suggest that the trends are real. The suggestion is that even the most tolerant hard-bottom organisms would eventually suffer inhibition and mortality above certain degrees of sedimentation. However, paucity of information on the regime of sedimentation greatly limits the interpretation and generalisation of the results, and prevents identification of the critical levels above which such detrimental effects of sediments become manifest.

Mortality Mortality of hard-bottom organisms as a consequence of severe smothering and scour by sediments has been reported frequently. Menge et al. (1994), for example, observed that at one study site affected by sand, mussels, barnacles and other invertebrates suffered severe mortality from burial by sand. Quantitative records of survival of mussels after different times and degrees of burial indicated that both partial and total burial by sediments reduced survival of mussels. In particular, *Mytilus californianus* was not able to survive total burial longer than 2 months, and in most cases mortality occurred within 12–18 days. Slattery & Bockus (1997) reported massive die-offs of the soft coral *Alcyonium paessleri* and other invertebrates along the shoreline of Ross Island: removal of organisms occurred from bands of substratum as extensive as 200 m^2, and the disturbance was clearly related to localised sediment slides. Laboratory experiments confirmed the intolerance of *A. paessleri* to a regime of sediment deposition and movement as that produced by sediment slides. Similar observations of dramatic mortality of epifaunal assemblages as a consequence of scour and smothering by landslides have been reported by Smith & Witman (1999). Seapy

& Littler (1982) and Branch et al. (1990) observed pronounced declines in covers of algae, and especially invertebrates, following flooding and sediment inundation events of rocky intertidal assemblages. In both cases, rates of mortality differed among species, resulting in shifts in the composition of dominant organisms. Robles (1982) reported that recurrent abrasion caused by shifting sediments was severe enough to remove most sessile organisms from local intertidal areas ranging in size from a few square metres to hectares. Similarly, extensive losses of invertebrates and algae from intertidal shores have been frequently reported in relation to severe sand scour and burial during storms (e.g. Seymour et al. 1989, Moring 1996, Underwood 1998). Burial by sediments was accounted to be the major cause of mortality of oysters and other sessile organisms in subtidal oyster reefs (Lenihan 1999). Several species of invertebrates, including cnidarians, sponges and ascidians, have been reported to suffer reduced growth and survival from sedimentation by burial, clogging of canals and chambers, or scour (reviewed by Moore 1977; see also Round et al. 1961, Bakus 1968, Gabriele et al. 1999).

Sediments have also been reported to enhance survival of some species of algae. For example, burial into sediments has been shown to be a good overwintering location for *Ulva* spp. (Kamermans et al. 1998) and *Gracilariopsis lemaneiformis* (as *Gracilaria lemaneiformis*, Santelices et al. 1984). It should be noted, however, that such observations referred to species most frequently occurring in soft-bottom habitats.

Inhibition of settlement and recruitment Effects of sediments on settlement or recruitment of rocky coast organisms have rarely been observed directly in the field. However, there is a great deal of circumstantial observation to suggest that detrimental effects of sediments on many species may be related to inhibition of their larval or juvenile stages. For example, the ability of transplanted adult sporophytes of *Hedophyllum sessile* to survive and prosper at one site where the species was absent suggested that lack of adults was due to negative effects of sedimentation on the gametophytes (Dayton 1975). Steneck et al. (1997) observed that whereas adults of the branching encrusting coralline alga *Neogoniolithon strictum* were capable of surviving and growing even when covered by sediments for long times, spores appeared to require hard, relatively sediment-free substrata for successful germination and growth. One of the postulated mechanisms by which many turf-forming algae and invertebrates, including mussels, have been demonstrated to interfere with recruitment and survival of other hard-bottom species is through enhanced deposition of sediments (e.g. Dayton 1973, Sousa et al. 1981, Airoldi 1998, Albrecht 1998). Reed et al. (1988) suggested that high rates of mortality of gametophytes of the kelp *Macrocystis pyrifera*, observed within the first week of settlement at one site in southern California, may have been due to high rates of sedimentation. Similarly, Deysher & Dean (1986) observed that a small but significant proportion of the variance in recruitment of sporophytes of *M. pyrifera* on artificial substrata deployed in the water column was correlated with sedimentation rates measured by using sediment traps. Santos (1993) observed that abundance of *Gelidium corneum* (as *G. sesquipedale*) was negatively related to sediment load, and suggested that sedimentation was more likely to influence spore settlement and recruitment of this species than adult plants. Enhanced algal recruitment in previously unsuitable habitats was observed as a consequence of an episodic storm that removed fine sediments from rocky reefs (Renaud et al. 1996, 1997) but such enhancement was not observed in those areas in which sediment persisted after the storm. Vogt & Schramm (1991) suggested that one of the causes of the decline of populations of *Fucus* spp. in Kiel Bay was the loss of substrata suitable for settlement through deposition of sediment from the eroded cliffs. Moran (1991) analysed changes in the rates of recruitment of fouling assemblages on artificial panels during dredging operations in a port in Australia. After 2 wk panels submerged before the dredging contained almost twice as many species as those that were submerged during dredging. The author suggested that direct physical removal of larvae was the probable limiting factor, because organisms appeared to survive the turbid and toxic conditions once settlement and metamorphosis had taken place. Observations made during experiments involving manipulation of rates of sediment deposition suggested that early recruitment of encrusting algae was negatively influenced by sediment scour (Airoldi 2000a) but rapid cover by turf made it difficult to quantify the importance of this process over appropriately long periods. Yoshida et al. (1997) transplanted embryos of *Sargassum horneri* at two sites, one where the species was naturally absent and another where it occurred at high densities. They observed that at the site where *S. horneri* was absent, the growth of germlings was greatly inhibited due to accumulation of fine sediments and concluded that sedimentation was probably the most important factor affecting the settlement, growth and consequently the distribution of *S. horneri* at their study sites. The prevalence in sediment affected areas of species that reproduce by vegetative propagation or that have reproductive cycles synchronised with seasonal fluctuations in the levels of sediments (see p. 179) also supports the hypothesis that early settlement stages are sensitive to mortality from sediments. Indeed, confirmation of the hypotheses that sediments can inhibit the settlement and recruitment of species that propagate by sexual reproduction has come from many laboratory and field experiments, which have shown the general susceptibility of larval and juvenile stages to sediments (see pp. 196 and 207).

It has been suggested that sometimes sediments also have positive effects on settlement and recruitment of species. Kennelly (1983), for example, reported a positive correlation between sedimentation and recruitment of macroalgae in a subtidal kelp forest. He suggested that sedimentation might have been beneficial to early growth of algae possibly by supplying nutrients or by protecting algae from disturbance from water movements or grazers. The author, however, also discussed the possibility that more silt might have been trapped where there is more algal cover, or that different effects might have been observed with greater sediment cover.

Inhibition of grazing and predation Suggestions that herbivorous organisms are deterred by sediments are numerous. This suggested deterrence is particularly important because one of the postulated mechanisms by which sediments may control the algal vegetation on rocky coasts is through inhibition of grazing. Scarcity of both large herbivores (e.g. sea urchins, limpets, chitons, herbivorous fishes) and small herbivores (e.g. amphipods, isopods, small gastropods) has been reported frequently from areas characterised by the presence of high levels of sediments both in rocky coasts (e.g. Emerson & Zedler 1978, Stewart 1982, 1989, Ebeling et al. 1985, Miller 1985, D’Antonio 1986, McGuinness 1987a, Trowbridge 1992, Schroeter et al. 1993, Airoldi & Virgilio 1998, Airoldi 2000a, Pulfrich et al., in press) and coral reef environments (e.g. Lim & Chou 1988, Steneck et al. 1997, Umar et al. 1998). However, direct evidence of negative effects of sediments on herbivores is scarce, and the mechanisms by which sediments might deter herbivores (e.g. direct damage to tissues by scour, smothering by clogging of respiratory apparatus or other physiological stresses, interference with movements or feeding activities, prevention of firm attachment, inhibition of recruitment) are unclear. D’Antonio (1986) hypothesised that the prevalence of *Neorhodomela larix* (as *Rhodomela larix*) in rocky shores affected by sand was related to

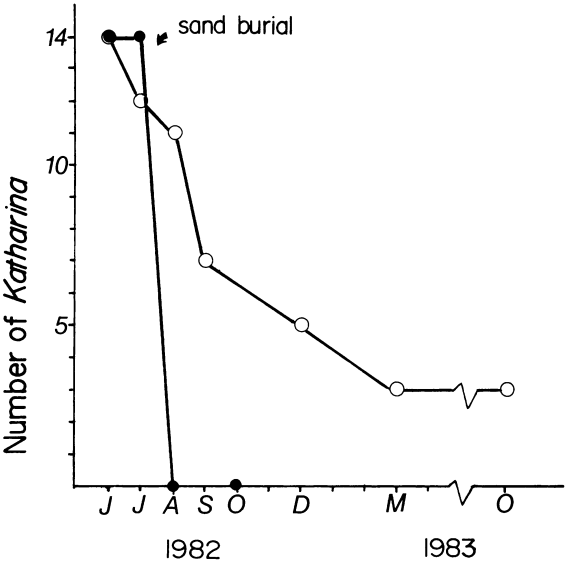

Figure 9 Effects of sand burial on survival of transplanted individuals of the chiton *Katharina tunicata* (from D'Antonio 1986, published with permission). Open circles represent chitons transplanted to areas that did not experience sand coverage, while solid circles represent chitons transplanted to areas which experienced sand coverage.

the notably scarcity of sea urchins, small herbivores, and especially chitons (*Katharina tunicata*) deterred by sediments. Experiments in which adults of *K. tunicata* were transplanted to areas that either experienced or did not experience burial by sand confirmed that these chitons were not able to tolerate sand burial, as their mantle suffered severe abrasion during coverage by sand (Fig. 9). Long-term monitoring at three sites that experienced different degrees of disturbance by sediments suggested that both abundance of herbivorous sea slugs and rate of attack of their algal prey *Codium setchellii* decreased with increased disturbance by sand (Trowbridge 1992). Experiments in which limpets were transplanted to areas affected or unaffected by sediments (Robles 1982), or in which they were exposed to burial conditions in the laboratory (Marshall & McQuaid 1989), suggested that some species of limpets are not able to tolerate burial by sediments. This result is consistent with observations of negative correlations between density of limpets and presence of sediments (Engledow & Bolton 1994, L. Airoldi & S.J. Hawkins, unpubl. data). Furthermore, laboratory experiments suggest that rate of grazing of limpets may be reduced by the presence of even a thin layer of sediment (L. Airoldi & S.J. Hawkins, unpubl. data).

There are also observations suggesting that sediments have negative effects on predator organisms. Schroeter et al. (1993), for example, reported a decline of abundance of sea stars following enhanced sediment load by a power plant. Pulfrich et al. (in press) observed significantly lower densities of predators, such as *Burnupena* spp. and *Nucella* spp., at sheltered sites affected by fine discharges from diamond mines compared with unaffected sites. Menge et al. (1994) reported weak predation by sea stars at a wave-protected site regularly buried by sand. They hypothesised that weak predation was due to direct negative effects of sediments on sea stars (e.g. interference with foraging and feeding activity, or physical and physiological stresses), or to indirect effects due to mortality and reduced abundance of prey.

Observations of effects of sediments from human discharges

There are observations of effects of sediments either indirectly related to enhanced erosion and runoff or as a direct consequence of discharges of industrial and urban wastes (see p. 187). These observations have consistently reported dramatic effects on rocky coast assemblages, including changes in the composition and distribution of species, and/or impoverishments in the richness and abundance of hard-bottom organisms, sometimes resulting in patterns of spatial dominance by a few monopolising species (e.g. Castilla & Nealler 1978, Ellis 1988, Moran 1991, Saiz-Salinas & Urdangarin 1994, Gorostiaga & Díez 1996, Konar & Roberts 1996, Turner et al. 1997, Kim et al. 1998, Roberts et al. 1998, Saiz-Salinas & Urkiaga-Alberdi 1999). An example of such changes is the decline in cover of canopy algae reported in the past decades by many authors from different parts of the world (e.g. Littler & Murray 1975, Thom & Widdowson 1978, Seapy & Littler 1982, Vogt & Schramm 1991, Benedetti-Cecchi et al. 2001, Eriksson et al. 2002). This pattern appears to be paralleled by a trend of increasing abundance of turf-forming algae (Airoldi et al. 1995 and references therein) that, once established, seem to inhibit invasion of canopy forming algae and other organisms (Sousa et al. 1981, Airoldi 1998, see also p. 187). Paucity of long-term quantitative data, however, makes it difficult to quantify the trends and unequivocally attribute the causes to enhanced sediment load from human activities. Furthermore, in many cases discharge of sediments was just one of many stresses affecting rocky coast assemblages, and effects due to sedimentation have not been separated from effects caused by potentially toxic organic and/or chemical compounds. For this reason, the present section is restricted to a few examples of effects of sediments from human discharges in which effects of sediments *per se* were considered predominant.

In a study on the ecological effects of cooling water discharges from a coastal nuclear power plant in southern California, Schroeter et al. (1993) reported significant reductions in density of snails, sea urchins and sea stars from the rocky substrata close to the diffusers over 2 yr after the power plant became operative. A reduction of the size and density of the kelp forest was also observed. Such decreases were paralleled by increases in abundance of two filter-feeding species, a gorgonian coral and a sponge. The most plausible cause of the changes in the composition and abundance of species was identified in the offshore discharging of turbid nearshore waters, which created turbidity plumes and enhanced sediment deposition over the kelp forest as far as 1.4 km from the diffusers. As a consequence, muddy sediments accumulated on the bottom at the closest affected site (0.4 km from the diffusers) and became armoured with coarser materials. Hyslop et al. (1997) compared the composition, abundance and distribution of dominant plants and animals at several rocky shores affected or unaffected by dumping of colliery wastes along the coastline of northeast England. They reported that while the distribution of animals was not related to colliery wastes, diversity of macroalgae was significantly negatively correlated with colliery waste inputs and particularly dramatic reductions in cover at the affected sites were observed for the species *Palmaria palmata* and *Ulva lactuca*. The authors suggested that, because colliery waste leaches much of its toxic chemical content into the sea, detrimental effects were most likely related to the physical presence of sediments. Indeed, a laboratory experiment confirmed the prevalent role of abrasion by sediments in affecting negatively the abundance of *U. lactuca* (Hyslop & Davies 1998). Dramatic declines of diversity and abundance of species on rocky coasts have been consistently reported as a consequence of the discharges of copper mine wastes (e.g. Castilla & Nealler 1978, Fariña & Castilla 2001 and references therein). In particular, Fariña & Castilla (2001) reported patterns of notably low species diversity on affected shores owing to the absence of many species of algae and filter-feeding animals, and monopolisation of space by *Enteromorpha compressa*. The authors emphasised that while previous work attributed such effects of copper mine wastes only to the high concentrations of trace metals, the mechanical effects due to the presence of sediments appeared to be an important and overlooked factor. Pulfrich et al. (in press) reported marked differences in species composition between rocky coasts close to and distant from the site of disposal of fine sediments from diamond mines in Namibia. The effects of fine deposits were restricted to sheltered sites, whereas no effects were observed at exposed sites where sediments were probably dispersed by wave action. Effects observed included reductions in the densities of grazers and predators, and proliferation of opportunistic foliose algae. Increased dominance of filter feeders was also observed, but only at intertidal sites.

Relationships between sediments and species diversity

Sediments are believed to affect the diversity of assemblages on rocky coasts. The prevalent opinion is that “high” sediment loads are detrimental to the overall diversity of rocky coast organisms, through inhibition of recruitment and mortality of less tolerant species (e.g. Devinny & Volse 1978) and/or through enhancement of spatial dominance by a few tolerant, space-monopolising species (Airoldi et al. 1995). Observations consistent with this hypothesis have been reported by many authors (e.g. Daly & Mathieson 1977, Little & Smith 1980, Mathieson 1982, Seapy & Littler 1982, Kennelly 1991, Evans et al. 1993, Crothers & Hayns 1994, Saiz-Salinas & Urdangarin 1994, Falace & Bressan 1995, Birje et al. 1996, Naranjo et al. 1996, Kim et al. 1998, Saiz-Salinas & Urkiaga-Alberdi 1999, Smith & Witman 1999), and have been emphasised in studies on the impact of human-related sediments on rocky coast organisms (see p. 193). Particularly interesting are the results of Engledow & Bolton (1994) who analysed patterns of diversity of macroalgal species at several low shore sites along the coasts of Namibia, and quantified several physical and biological factors that might potentially affect species diversity. Their results showed that species diversity (Shannon-Wiener index) within each plot was negatively correlated with the amount of sand present but only at levels of sediment greater than 5.6 $\mathrm{kg\,m^{-2}}$ (Fig. 10). This pattern was related to changes in equitability (Simpson’s Dominance index) rather than species richness. The authors suggested that sediments influenced the diversity of the assemblage by excluding less tolerant species and by favouring monopolisation of space by most tolerant species relieved from competition.

On the other hand, several authors have provided data that support the hypothesis that, in some cases, presence of sediments may promote diversity of species on rocky coasts by increasing patchiness and habitat heterogeneity, preventing monopolisation of space by competitively dominant species, controlling the balance between sand-tolerant and sand-intolerant species and providing new habitat to infaunal species typical of soft bottoms (Foster 1975, Robles 1982, Taylor & Littler 1982, Littler et al. 1983, Gibbons 1988,

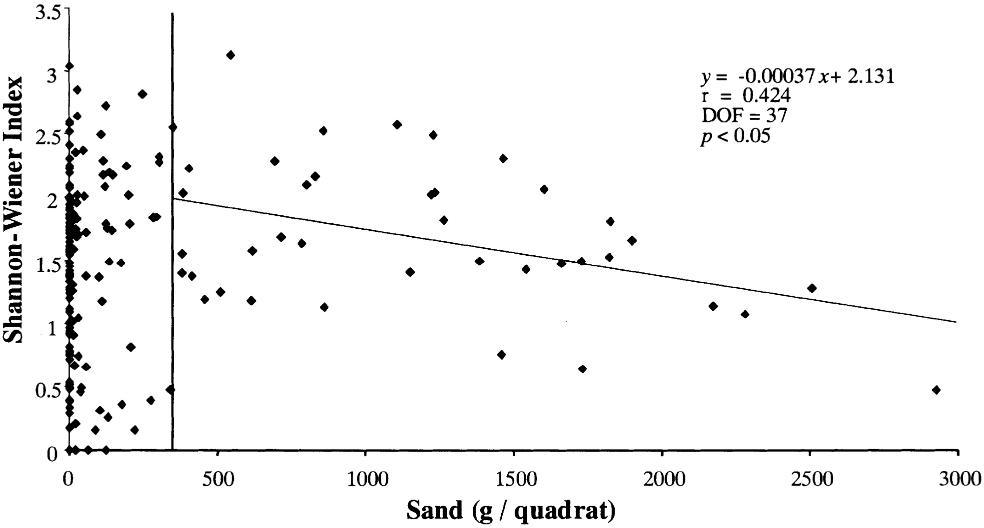

Figure 10 Relationship between diversity of macroalgae and degree of sand inundation in the lower eulittoral zone at 18 sites along the coast of Namibia (from Engledow & Bolton 1994, published with permission). The vertical line indicates the level of sand accumulation (350 g corresponding to 5.6 kg m^{-2}, size of quadrat was 25 cm × 25 cm) below which sand did not have an effect.

Jørgensen & Gulliksen 2001). McQuaid & Dower (1990), in particular, showed that along the coasts of South Africa, total faunal species richness was higher for rocky shores regularly inundated by sediments than for rocky shores unaffected by sediments and sandy shores combined. They attributed the causes of this pattern to two factors. The first was that the species recorded covered a spectrum of tolerance to sediments that varied from complete intolerance (species restricted to permanently sand-free areas, such as vertical cliffs), to complete dependence (species typical of soft-bottom habitats and thus restricted to the sand itself). The second was that within shores, patterns of accumulation of sediments were unpredictable and heterogeneous: species were thus often excluded locally by the presence of sand but patchiness of deposits resulted in a few being eliminated from the shore as a whole.

Interpreting these contrasting views is difficult, because in many studies the temporal and spatial context is not explicit, and because of lack of quantitative standardised measurements of the regime of perturbation by sediments. It is suggested here that differences arise because effects of sediments on rocky coast organisms vary in space and time, depending on the characteristics of the regime of sedimentation and their interactions with variable environmental and biological factors (see pp. 196 and 207). Thus, for example, the sub-lethal chronic smothering by a moderate layer of sediment may have different effects on the diversity of rocky coast organisms than severe and unpredictable scour events that create patches of open space (Airoldi 1998). Similarly, while a "moderate" regime of disturbance by sediments may promote diversity of species, "excessive" disturbance may result in dramatic declines in species diversity (Seapy & Littler 1982). Rocky coasts affected by sand may have fewer species of seaweeds than adjacent unaffected coasts: even so, within sand-abraded coasts, microhabitats may occur, causing differential diversity and/or abundance of species (Daly & Mathieson 1977, Littler et al. 1983, Airoldi & Cinelli 1997, Airoldi 1998). Effects of sediments could also vary across different habitats and geographical locations, depending on local environmental and biological characteristics, and could be influenced by the "vulnerability" (*sensu* Sousa 2001) of the organisms affected. For example, accumulation of sediments within mussel beds or turf-forming species may enhance richness and abundance of infauna (e.g. Tsuchiya & Nishihira 1985, Gibbons 1988, Grahame & Hanna 1989), while inhibiting growth of macroalgae (e.g. Dayton 1973, Sousa et al. 1981, Airoldi 1998, Albrecht 1998). Relationships between perturbations and diversity in natural systems are complex, and reflect the differential expression of life-history attributes under different regimes of disturbance (Petraitis et al. 1989, Airoldi 1998, Sousa 2001). Deeper knowledge of the causal mechanisms by which sediments interact with affected organisms, greater consideration of scale issues, and quantitative information on the characteristics of the regime of perturbation by sediments are necessary to improve our present understanding of the relationships between sedimentation and species diversity on rocky coasts.

Laboratory experiments

The first laboratory experiments on the effects of sedimentation on rocky coast organisms were carried out in the 1970s, and became relatively frequent in the 1990s (Table 2). Experiments have focused on the effects of smothering by sediments on settlement, recruitment, growth, survival, or behaviour of a variety of species, whereas only a little work has been done on the effects of scour or substratum instability. Despite the short-term nature of laboratory experiments and their shortcomings (including the frequent arbitrary choice of treatment levels), these studies have detected a variety of responses of rocky coast organisms to sediment load, and have given insight into the possible mechanisms of the action of sediments.

A general trend that emerges from these experiments is that adult individuals of many species (e.g. *Zonaria farlowii*, *Ahnfeltiopsis linearis*, *Neorhodomela larix*, *Gracilariopsis lemaneiformis*, *Laminaria saccharina*, *Codium setchellii*, *Ulva* spp., *Siphonaria capensis*) can survive some degree of burial, and resume growth or regenerate vegetatively from remaining fragments, despite often remarkable negative effects on biomass, growth, or photosynthetic activity (Table 2). Conversely, larvae, propagules, early post-settlement stages and juveniles generally suffered severe stress and mortality from sediments. Moss et al. (1973), for example, observed that growth of zygotes of *Himanthalia elongata* was inhibited under a layer of silt 1–2 mm thick, and that attachment on silt was insecure. Similarly, Norton (1978) showed that an underlying layer of silt prevented attachment of young sporophytes of kelps, whereas an overlying layer of silt inhibited the development of gametophytes. Devinny & Volse (1978) showed that sedimentation both prevented spore settlement and smothered gametophytes of *Macrocystis pyrifera* although survival increased markedly when spores were allowed to attach for 24 h (Fig. 11). Arakawa & Matsuike (1992) showed that presence of sediments inhibited the insertion, germination, survival and maturation of gametophytes of the kelps *Ecklonia cava* and *Undaria pinnatifida*. In these species adhesion of zoospores and maturation of gametophytes were the most sensitive phases, whereas germination and survival of gametophytes were more

Table 2 Summary of selected laboratory experiments on the effects of sedimentation on rocky coast organisms. S = experiment done under still conditions, T = experiment done under turbulent conditions, ? = unknown water movement conditions. *The algae of in this study occurred as free-floating thalli in a lagoon with a sandy bottom. However, the species also occurs at rocky coasts.

Species	Factor/type of sediment (size)	Experimental set-up	Results	Reference
Laminaria saccharina, Ulva lactuca	Presence of silt. ?	Settlement of *L. saccharina* on slides was followed in absence and presence of a layer of silt. Detail of experiment and abundance of silt were not specified. Reported effects were qualitative.	Settlement of *L. saccharina* was inhibited in the presence of silt covering the slides.	Burrows 1971
	Presence of mud, polluted by sewage, from Dublin Harbour. S	Disks of *U. lactuca* were grown, both in the light and in dark, in presence of control filtered sea water or water from Dublin Harbour with or without mud. Details of experiments and concentration of mud were not specified. Effects on growth (disk diameter) were measured after 14 and 21 days.	Growth of *U. lactuca* was enhanced by the presence of mud but only in the presence of light. Effects were likely related to organic enrichment due to sewage.	
Zonaria farlowii	Burial by natural sand. S	Plants were exposed to burial for increasing intervals (up to 6 months). Experiments were not replicated. Reported effects were qualitative. Degree of sand burial was not specified.	Apical growth ceased short after burial. Living tissue gradually reduced as burial time increased. Only basal proliferations survived over 6 months. Resumed growth was often observed, but it was vulnerable to light exposure. Burial also affected thallus morphology. Effects were similar to those observed in natural populations in the field.	Dahl 1971
Ahnfeltiopsis linearis	Sand burial (natural	Plants of both species attached to rocks	After 1 month, *G. platyphyllus* plants were	Markham &

Table 2 *continued*

Species	Factor/type of sediment (size)	Experimental set-up	Results	Reference
(as *Gymnogongrus linearis*), *G. platyphyllus*	sand). T	were subjected to burial of the lower portions and shaken. Details of experimental design were not given. Reported effects were qualitative.	dead. Conversely *G. linearis* plants survived and produced new branches, fronds and cystocarps. Growth was still observed after 6 months. Results were in agreement with observations in the field and results of transplant experiments.	Newroth 1972
Himanthalia elongata	Presence of an underlying or overlying layer of silt, 1–2 mm thick. S	Fertilised eggs were exposed to addition of a layer of silt before and after settlement. Details of experimental design were not given. Reported effects were qualitative.	Zygotes settled on a silt substratum, but attachment was insecure and they assumed a different shape. Growth of settled zygotes ceased under a layer of silt.	Moss et al. 1973
Porphyra umbilicalis, *Plumaria plumosa* (as *P. elegans*), *Polysiphonia lanosa*, *Cladophora rupestris*, *Pelvetia canaliculata*	Presence of four different types of iron ore dust (8–25 μm). T	Experiments were done before the construction of an unloading terminal. Ore dust (0.5 g in 100 ml filtered sea water) was shaken with algal thalli. Amount of ore dust retained and transmission of radiant energy through thalli were measured. Details of experimental design were not given. Concentration was chosen arbitrarily, due to lack of information on amount of spillage.	All algae retained considerable amounts of iron ore dust. Differences in retention ability between algae were observed.	Boney 1978
Macrocystis pyrifera	Sand burial, scour, and presence of underlying sand (construction sand, <74 μm). S and T	Spores were exposed to addition of increasing amounts of sediments (0 mg cm^{-2} to 108 mg cm^{-2}) before and after settlement. Effects on spore density were quantified. An additional experiments, in which treatments were exposed or not to light, tested whether effects were due to light deprivation.	Spore attachment was reduced by 90% in the presence of 8 mg cm^{-2} of sediments and was prevented at 10 mg cm^{-2}. Survival of established germlings was reduced by 90% at 108 mg cm^{-2}. Effects were not attributable to light deprivation. Effects of sediments were more severe in moving water.	Devinny & Volse 1978

Table 2 *continued*

Species	Factor/type of sediment (size)	Experimental set-up	Results	Reference
		Effects of sediments in moving water were also tested. Experiments were run for 4 days, as pilot studies suggested that most effects occurred during the first days of germination.		
Saccorhiza polyschides, *Laminaria saccharina*	Presence of an underlying or overlying layer of natural silt. S	Spores of both species were exposed to addition of natural non toxic sediments ($0.3\,\mathrm{mg\,mm^{-2}}$) before and after settlement. Details of experimental design were not given. Reported effects were qualitative.	Spores of both species germinated and grew normally if settled on top of silt, but could not attach. If spores were covered by sediment after attachment, they germinated, but few gametophytes were produced and no sporophytes were formed. Results could only in part explain the distribution of the two species in the field.	Norton 1978
Gracilariopsis lemaneiformis (as *Gracilaria lemaneiformis*)	Burial by natural sand. S	Branched and unbranched pieces (about 10 cm long) of thalli were buried under 0 cm, 2 cm and 10 cm of sand, either in vertical or horizontal position with respect to the sand surface. Growth of thalli was measured over 90 days.	Thalli survived burial, but none increased in weight or length.	Santelices et al. 1984
Neorhodomela larix (as *Rhodomela larix*) and its epiphytes, *Microcladia borealis*, *Cryptosiphonia woodii*, *Ulva* sp., *Mastocarpus papillatus* (as *Gigartina papillata*), Coralline crust	Burial by natural sand (125 μm to 250 μm). S	Two experiments in which plants were placed under 15–20 cm of fine sand for over 3 months, and survival was compared with controls. Observations on survival continued after removal of the plants from sand.	After 3 months of burial, holdfasts and basal crusts of *R. larix* were intact, but growth was inhibited and upright portions had decayed. Epiphytes disappeared after 6 wk. Buried coralline crusts were similar to control specimens, but reduced in size and slightly discoloured. *Ulva* sp. suffered severe mortality, less than 10% surviving. Other species did not survive 1 month of burial. Results were consistent with field observations.	D'Antonio 1986

Table 2 *continued*

Species	Factor/type of sediment (size)	Experimental set-up	Results	Reference
Panulirus argus	Effects of natural silt trapped by algal turfs. S	Pueruli or juvenile spiny lobsters were exposed to clumps of *Laurencia* spp. with silt removed or unmanipulated, in order to test the effects of silt trapped into algal turfs on time-to-metamorphosis and early postsettlement survival, and on postlarval settlement and juvenile habitat selection.	More pueruli settled in unsilted than silted algal clumps, and similar habitat preference was shown by juveniles. Silt had no effects on survival of pueruli through time to metamorphosis or metamorphosis. Scarcity of spiny lobsters observed in habitats with silt was attributed to low rates of postlarval settlement in these habitats.	Herrnkind et al. 1988
Patella granularis, *Siphonaria capensis*	Effects of sand burial and reduced oxygen tension. S	Repeated experiments tested the effects of burial (0 mm or 15 mm of sand) and reduced concentrations of oxygen ($<0.8\,\mathrm{ml\,l^{-1}}$, $2.0–2.8\,\mathrm{ml\,l^{-1}}$ and $3.6–4.8\,\mathrm{ml\,l^{-1}}$) on survival of replicated limpets. An additional experiment separated the effects due to presence or weight of sand. Experiments lasted 7 days. The oxygen consumption at reduced tensions and the capacity of anaerobiosis of the two species were also quantified.	*S. capensis* survived for significantly longer periods than *P. granularis* in sand burial and reduced oxygen tensions. Negative effects on *P. granularis* were only in part attributable to weight of sand. Differences in mortality between the two species could be explained by differential respiratory responses during exposure to reduced oxygen tensions. Results could explain the distribution of the two species on rocky shores inundated by sand.	Marshall & McQuaid 1989
Anthopleura elegantissima	Effect of sand burial. S	Experiments tested the effects of burial (0 cm or 12 cm of sand) on behaviour of replicated aggregated clonal, wandering clonal, small solitary and large solitary forms of *A. elegantissima*. Experiment lasted 4 days. Effects were measured as proportion of individual per experimental unit that remained buried, were detached or successfully escaped	Wandering and aggregated forms showed little mobility when buried by sand, small solitary forms escaped burial by increasing their mobility, while large solitary forms avoided burial by elongating their columns above the sand. It was concluded that solitary forms are better adapted to sand-influenced habitats, because of their large final size or high mobility. Results	Pineda & Escofet 1989

Table 2 *continued*

Species	Factor/type of sediment (size)	Experimental set-up	Results	Reference
		from sand burial (anemones with their oral disc above the sand while still attached to the substratum).	partially explained the distribution of colonial and solitary forms on rocky shores inundated by sand.	
Ecklonia cava, *Undaria pinnatifida*	Suspended particles of kaolinite.	Plants were treated with increasing concentration of particles. Experimental set-up is difficult to understand as the article is in Japanese (abstract in English).	Settling velocity of zoospores was negatively affected by adsorption on suspended particles. Insertion of zoospores on the base-plate was also negatively affected by settled particles.	Arakawa & Matsuike 1990
	Settled particles of kaolinite.	Four experiments in which plants were treated with increasing amounts of settled particles (from 0 mg cm^{-2} up to 50 mg cm^{-2}). Experimental set-up is difficult to understand as the article is in Japanese (abstract in English).	Adhesion of zoospores decreased to 50% at 0.5 mg cm^{-2} and was prevented at 3 mg cm^{-2}. Germination of gametophytes decreased to 40% at 1 mg cm^{-2} and was prevented at 10 mg cm^{-2}. Survival of gametophytes decreased to 50% at 1 mg cm^{-2} and was prevented at 10 mg cm^{-2}. Maturation of gametophytes decreased to 50% at 0.25 mg cm^{-2} and was prevented at 1 mg cm^{-2}.	Arakawa & Matsuike 1992
	Suspended particles of kaolinite.	Experimental set-up is difficult to understand as the article is in Japanese (abstract in English).	Settling of zoospores decreased to 0.023% at levels of turbidity greater than 2 mg l^{-1}. A reduction of kelp bed extension to 10% at levels of turbidity greater than 10 mg l^{-1} was predicted.	Arakawa & Morinaga 1994
Laminaria saccharina	Presence of fine grained sediments from test dredging. ?	Plants were incubated after exposure to a sediment suspension for 2 h. No information is given about the type of treatment (e.g. amount of sediment tested or how treatment was applied to plants). Effects on growth,	Growth, nitrogen uptake and chlorophyll *a* concentrations were significantly reduced in treated plants with respect to controls. No effects were observed for photosynthetic capabilities or phosphorous uptake. Direct physical damage to the	Lyngby & Mortensen 1996

Table 2 *continued*

Species	Factor/type of sediment (size)	Experimental set-up	Results	Reference
		photosynthesis, nitrogen and phosphorous uptake and chlorophyll *a* concentrations were quantified at weekly intervals. A similar study was repeated in the field.	treated plants was observed, as a consequence of thick layers of fine-grained material deposited on the thalli.	
Codium setchellii, *Ahnfeltiopsis linearis* (as *Gymnogongrus linearis*), *Neorhodomela larix*	Burial by natural sand. S	Replicated pieces of *C. setchellii* were buried in 5 cm of sand. Controls were unburied thalli and thalli buried in 5 cm coarse aquarium gravel, in order to separate the effects of reduced light and reduced water flow. Biomasses of thalli were measured for 5 wk. A second similar experiment, tested responses of the 3 sympatric species to burial in 2 cm sand for 4 wk.	*C. setchellii* lost substantial biomass during 4 wk to 5 wk of sand burial due to both reduced light and reduced water flow. Conversely the other two species lost little or no biomass. The high loss in biomass of *C. setchellii* in the laboratory was in apparent discrepancy with high survival to burial observed on the shore, and could be possibly explained by the use of algal discs in experiments.	Trowbridge 1996
Haliotis rufescens, *Paracyathus stearnsii*	Effects of water-based drilling muds from an active platform. T	Experiments tested the effects of different concentrations ($0\,mg\,l^{-1}$ to $200\,mg\,l^{-1}$) of drilling muds on fertilisation, early development, survivorship and settlement of *H. rufescens* and on adult survivorship, viability and tissue loss of *P. stearnsii*. Concentrations were chosen based on field data. Effects due to toxicity of dissolved fractions were not separated.	Drilling muds did not affect fertilisation or early development of *H. rufescens*. Settlement of competent larve was sometimes weakly positively affected. Settlement of larvae on coralline crusts (natural settlement inducer) was strongly negatively affected. Survivorship and viability of *P. stearnsii* were strongly negatively affected, due to increased tissue mortality: at highest concentrations individuals died after 6 days.	Raimondi et al. 1997
Alcyonium paessleri	Effects of periodic deposition of sediments from a slide. T	Replicated specimens of *A. paessleri* from rocky and soft-bottom habitats were exposed to sediments (100 g) added every 4 h for either 24 or 96 h.	*A. paessleri* exhibited significant mortality as a consequence of sediment addition regardless of its habitat origin. Mortality increased over time up to values	Slattery & Bockus 1997

Table 2 *continued*

Species	Factor/type of sediment (size)	Experimental set-up	Results	Reference
		Sediment was released along a Plexiglas "slide" directed towards the soft corals, in order to mimic the effects of a landslide. Control specimens were mechanically agitated with a water flow at similar time intervals. Effects on soft coral behaviour (expansion or contraction of the polyps) and conditions (tissue necrosis) were followed over 4 wk. Sediment packaged in mucus or accumulated to the bottom of the aquarium were quantified.	above 70%. *A. paessleri* was able to package silt into mucus to be sloughed away, which might explain the ability of this species to colonise soft-bottom habitats. However, scour by sediments produced necrotic wounds leading to mortality. Results were consistent with observations in the field.	
Fucus vesiculosus forma *mytili*	Effects of biodeposition by mussels under high concentrations of suspended sediments. S	Survival of *Fucus* germlings inoculated on live (l) and mortar filled (mf) mussel shells was compared among 3 treatments with different combinations of l and mf shells (25 l + 5 mf, 15 l + 15 mf, 5 l + 25 mf), in order to separate effects of biodeposition from mussels (affecting germlings on both l and mf shells) from effects of shell cleaning activity by mussels (affecting germling only on l shells). The experiment lasted 5 wk. Amount of biodeposits in different treatments was not specified.	Germling survival was lowest on both l and mf shells in aquaria with the highest proportion of live mussels (although differences were not significant), suggesting that biodeposition was the most critical factor. It was hypothesised that lack of sexual recruits observed on mussel beds in soft bottoms compared to hard bottoms might be related to post-settlement detrimental effects due to large biodeposition in the former habitats related to high particle concentrations in the water column.	Albrecht 1998
Ulva lactuca	Presence of colliery waste of 3 grain sizes (<500 μm, 500–2000 μm and 0–2000 μm). S and T	Replicated plants were exposed to colliery-waste treatments (0 g l^{-1} or 1 g l^{-1}) in both still and turbulent (shaking for 1 h each day) conditions, for 8 days. The physical and chemical effects of colliery waste on weight of	*U. lactuca* lost weight significantly in presence of colliery waste; weight loss was most pronounced with particles 500–2000 μm in size, under shaken conditions. Significant weight gain with respect to controls was observed in still	Hyslop & Davies 1998

Table 2 *continued*

Species	Factor/type of sediment (size)	Experimental set-up	Results	Reference
		plants were partitioned by using particles in contact with the plants or separated by bags. Criteria used to choose treatment levels were not explained.	conditions with particles of 0–2000 μm or in the presence of bags. It was concluded that under turbulent conditions colliery waste acts as a physical detrimental abrading agent, while in still conditions it promotes the growth of *U. lactuca*.	
Ulva spp. (mixture of *U. scandinavica*, *U. curvata*, *U. rigida* and *U. lactuca*)	Burial under anoxic (from lagoon) and oxic (bird-cage sand) sediments, under freezing conditions. S	Replicated pieces of *Ulva* spp. were buried under 5 cm of anoxic or oxic sediments. Viability after 4 wk was tested by incubation and compared with that of unburied thalli kept in the dark or in a light-dark cycle. All treatments were frozen to mimic the natural winter conditions in the lagoon. Viability of naturally buried thalli was also tested.	Treatments affected viability and growth rate of *Ulva* spp. Growth was fastest after freezing in natural anoxic sediments, followed by freezing in oxic sediments and freezing under dark conditions. No recovery was found after freezing in a light-dark cycle. All thalli naturally buried were able to resume growth. It was concluded that burial in natural sediments may allow *Ulva* spp. to survive freezing conditions during the winter.	Kamermans et al. 1998*
Fucus serratus	Differential effects of burial (i.e. light deprivation, sediment type, and sediment chemistry). Sediments from a tidal inlet. S	Zygotes settled on slides were exposed to different combinations of: (1) sediment types, i.e. fine (<63 μm) low (1 mm), fine high (3 mm), coarse (255–350 μm) low, mussel biodeposits low, and no sediments, (2) light, i.e. incoming vs dark, and (3) sediment chemistry, i.e. oxygenated, de-oxygenated, de-oxygenated with presence of sulphyde. There were 4 replicates for each combination of treatments. Slides were retrieved after 5 days. Survival and growth of embryos were measured after 5 days of recovery.	Presence of hydrogen sulphide had overriding negative impacts on both survivorship and growth of *F. serratus* embryos, independently of sediment type and light availability. Simple anaerobiosis did not impair survival or growth. High levels of fine sediments and organic rich mussel biodeposits significantly reduced survival of embryos. Low irradiance did not influence survival of embryos but affected growth negatively.	Chapman & Fletcher 2002

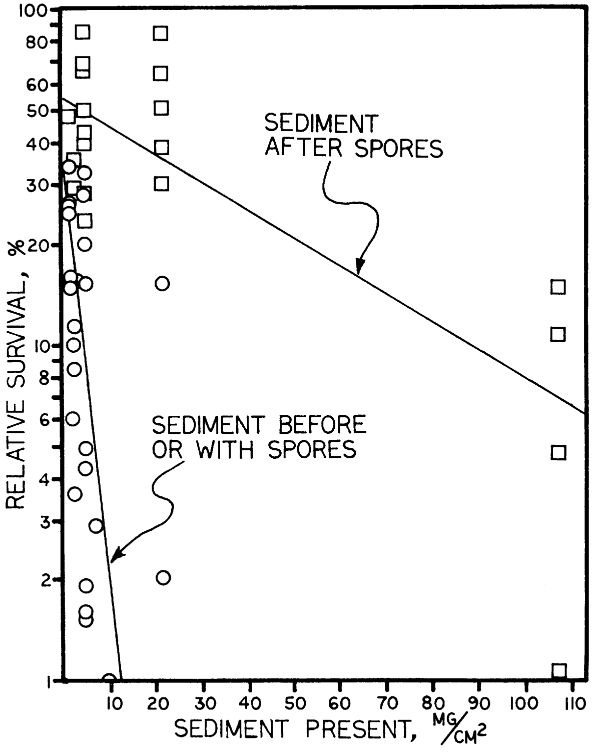

Figure 11 Effects of variable amounts of sediment on relative survival of spores of *Macrocystis pyrifera* during laboratory experiments (from Devinny & Volse 1978, published with permission). Circles represent experiments in which sediments were applied before spores or were initially mixed with spore solution. Squares represent experiments in which spores were given 1 day to attach before sediment was added.

tolerant to presence of sediments. Raimondi et al. (1997) showed that while settlement of competent larvae of the red abalone *Haliotis rufescens* was sometimes affected weakly yet positively by the presence of drilling muds, settlement of larvae on coralline algal crusts (known to induce red abalone larvae to settle) was severely decreased. Overall, these results support the hypothesis that rocky coast organisms that persist by sexual reproduction are more vulnerable to the presence of sediments than organisms that reproduce vegetatively, apparently because the former require stable substrata for settlement and attachment, and/or their juvenile stages are more sensitive to smothering by sediments than adult individuals.

In most experiments, presence of sediments exerted some degree of stress on rocky coast organisms, as indicated by the negative effects observed on growth, biomass, survival or photosynthetic activity (Table 2). The suggestion is that any hard-bottom species would suffer stress above certain levels of sedimentation. Some species, such as *Zonaria farlowii*, *Ahnfeltiopsis linearis*, or *Neorhodomela larix*, were, however, clearly able to tolerate those stresses better than others. For such “sand-tolerant” species, it has been suggested that costs directly imposed by sediments are compensated for by indirect advantages. For example, D’Antonio (1986) showed that burial of *Neorhodomela larix* (as *Rhodomela larix*) by sediments imposed stress in terms of reduced growth and loss of upright portions. This species, which dominated sediment-affected rocky shores along the northwest coast of the USA, could, however, better tolerate burial than its epiphytes or other species sometimes occurring in the same habitats. D’Antonio suggested that stresses imposed by burial were possibly compensated for by indirect positive effects, including reduced predation by herbivores, reduced cover by epiphytes, protection from desiccation during the summer months, and reduced competition by potential space occupiers.

Only a few experiments tested the effects of different sediment loads and, surprisingly, some studies did not report the levels of sediment applied to treatments (Table 2). Devinny & Volse (1978) showed that attachment of spores of *Macrocystis pyrifera* was reduced by 90% in the presence of $8\,\mathrm{mg\,cm^{-2}}$ of sediments, and was inhibited at levels above $10\,\mathrm{mg\,cm^{-2}}$, which formed a thin layer enough to occlude all the surface of the culture dishes. Established germlings, however, tolerated greater amounts of sediments, survival being reduced by 90% at $108\,\mathrm{mg\,cm^{-2}}$. Arakawa & Matsuike (1992) showed that adhesion of zoospores of *Ecklonia cava* and *Undaria pinnatifida* and maturation of gametophytes were prevented in presence of levels of sediments above $3\,\mathrm{mg\,cm^{-2}}$ and $1\,\mathrm{mg\,cm^{-2}}$, respectively, while germination and survival of gametophytes were inhibited at levels above $10\,\mathrm{mg\,cm^{-2}}$. These results clearly indicate that effects of sediments vary in relation to their quantity. Scarcity of information about responses of species to different levels of sediments, however, limits, at present, the possibility of identifying threshold levels of sedimentation for rocky coast organisms.

Effects of sediments have sometimes been compared under still and turbulent water conditions. Experiments on *Ulva lactuca* (Hyslop & Davies 1998) indicated that while this species seems to tolerate well, and sometimes even be enhanced by, the presence of colliery waste particles under still water conditions, it was severely affected negatively under turbulent conditions. Devinny & Volse (1978) measured greater negative effects of sediments on survival of gametophytes of *Macrocystis pyrifera* in moving rather than in still water. Norton (1978) observed that spores of kelps could germinate and grow normally on still sediments but if the medium was disturbed, they drifted away. Slattery & Bockus (1997) observed that presence of silt was less problematic for the survival of the soft coral *Alcyonum paessleri* than scour, which produced necrotic wounds that lead to mortality. Overall, laboratory experiments suggested more severe effects of sediments on both adults and settlement stages under turbulent than still water conditions, presumably because of both abrasive scour and washing effects on individuals with an insecure attachment. It should, however, be noted that most experiments lasted for short times and although short-term burial by sediments may be less stressful in still than turbulent waters, the opposite pattern may occur during long-term burial conditions because circulation of water might enhance diffusion of gases and nutrients through the sediments.

Very few attempts have been made to separate different aspects of sedimentation that affect rocky coast organisms. Chapman & Fletcher (2002) have investigated the mechanisms by which sediments negatively affect survival and growth of embryos of *Fucus serratus*. In particular, they separated three components related to smothering by sediments, specifically: a) physical components associated with different sediment types and grain sizes, b) light deprivation due to cover by a layer of sediment, and c) chemical components associated with changes in oxygen and hydrogen sulphide levels that often occur under sediments in nature. Their results showed that the presence of hydrogen sulphide had overriding negative impacts on both survival and growth of *F. serratus* embryos, independently of type of sediment and availability of light. Interestingly, simple anaerobiosis generally did not have negative effects. Deprivation of light did not affect survival of embryos but influenced their growth, which is consistent with results by Devinny & Volse (1978) on effects of light on survival of germlings of *Macrocystis pyrifera*. Fine sediments and organically-rich biodeposits had more detrimental effects on embryo survival than coarse sediments, which the authors attributed to accumulation of metabolic waste products of the embryos as a consequence of constrained diffusion.

Results from laboratory experiments thus give clear indications that sediment quantity as well as quality may have important effects on rocky coast organisms, and that severity of effects of sediments may be related to variable environmental and biological factors, such as the degree of water movements, or the stage of development of the organisms themselves.

Field experiments

While experimental work on the effects of sedimentation has been relatively common in coral reef environments (reviewed in Rogers 1990), field experiments to analyse the effects of sedimentation on rocky coast organisms were undertaken only recently, and such studies are still few (Table 3). Explanations for such scarcity of experimental studies in rocky coasts probably include the high labour costs required to do such experiments in temperate habitats, and the difficulties that are often encountered in planning and executing such experiments. Furthermore, the spatial and temporal scales of field manipulative experiments are necessarily small, which limits the possibility of generalising results at large spatial scales relevant for predicting changes in sedimentation rates as a consequence of human activities. The results of the few available experiments (including a study by Umar et al. 1998 which was done on coral reefs but tested the effects of sediments on algae belonging to the genus *Sargassum* that is common on rocky coasts) are reviewed here and the methodological difficulties encountered discussed.

Methodological problems

Manipulating sedimentation rates in the field is difficult because patterns of deposition of sediments are often influenced by many physical and biological factors (see p. 164), which can invalidate the effectiveness of the manipulation. The commonest approach used in rocky habitats has been the reduction of sedimentation rates through the removal of sediment by water motion, for example, by wafting water with one hand or flushing (Neushul et al. 1976, Kendrick 1991, Umar et al. 1998, Irving & Connell in press a,b), or by using transparent panels (e.g. Fig. 12) that intercept settling particles (Duggins et al. 1990, Airoldi & Cinelli 1997, Relini et al. 1998, Maughan 2001). Alternatively, sediment load has been increased through the addition of known amounts of sediment to the experimental plots (Kendrick 1991, Airoldi 1998, Airoldi & Virgilio 1998, Umar et al. 1998), or by burying natural or artificial hard substrata into sediments (McGuinness 1987b, Gotelli 1988). In both cases, the effectiveness of the manipulation is clearly dependent on the frequency of the application or

Table 3 Summary of field experiments on the effects of sedimentation on rocky coast species or assemblages. *This experiment was done on a fringing coral reef. Nevertheless, species belonging to the genus *Sargassum* are common on rocky coasts.

Species-assemblage/habitat characteristics/location	Type of manipulation/experimental set-up	Results	Reference
Fouling assemblages on Plexiglas plates (12 m in depth). Santa Barbara, California, USA. Sedimentation rates up to 2000 $\mathrm{g\,m^{-2}\,d^{-1}}$ during the winter.	Effects of sedimentation on recruitment of fouling organisms were tested by comparing colonisation between replicated settlement plates from which sediment was removed manually by divers (25 times during 1 yr) or that were left unmanipulated.	No differences were observed between plates from which sediments were removed and unmanipulated plates. It was assumed that sediment removal was not frequent enough to decrease significantly sediment deposition.	Neushul et al. 1976
Intertidal assemblages on boulders on two rock platforms inundated by sand. Sydney, Australia.	Effects of disturbance by sand on existing assemblages were tested by burying replicated boulders and their associated assemblages about 1–3 cm deep into sand, or leaving them on sand as control. Effects of short (13 days) and long-term (119 days) burial were compared. Similarly, effects on developing assemblages were tested by using bare boulders that were completely buried, half-buried or left unburied. Colonisation was followed over 266 days. Both experiments were repeated at high- and low-shore levels.	Recruitment onto fully buried boulders was virtually zero. Disturbance by sand also reduced the number and abundance of species in existing assemblages. Effects were particularly severe and rapid for grazers, while negative effects on algae (such as *Polysiphonia* sp. and *Ulva lactuca*) or sessile invertebrates became visible after long burial. Short-burial boulders generally had more species than long-burial ones, but differences were not always significant. Effects also varied as a function of height on the shore and size of boulder.	McGuinness 1987b
Leptogorgia virgulata on a limestone outcropping (1.5 m in depth) with patchy cover of sand (few mm thick). Evidence of frequent sand movements. Franklin County, Florida, USA.	The effects of sand burial on recruitment and growth of *L. virgulata* were analysed by experiments and observations. Replicated cement patio stones were either raised on limestone, raised on sand or buried into sand. Recruitment, and survival of *L. virgulata* were recorded over 1 yr, and	Recruitment of *L. virgulata* was reduced by 50% on buried stones compared with stones raised on sand. Inexplicably, recruitment was reduced also on stones raised on limestone. Observations suggested that sand reduced recruitment also on natural substrata. Mortality rates	Gotelli 1988

Table 3 *continued*

Species-assemblage/habitat characteristics/location	Type of manipulation/experimental set-up	Results	Reference
	compared with those measured on natural rock in relation to the heterogeneous distribution of sediments. Effects on growth were tested by transplanting juvenile gorgonians on top of sand or almost completely buried into it. Growth was measured after 55 days.	and mean colony sizes were similar among treatments, although the largest colonies were collected from the buried treatment. Buried colonies grew significantly more than unburied colonies. It was concluded that recruitment of *L. virgulata* was affected by the distribution of sand, and that spatial patterns established at the time of recruitment persisted in the adult population. It was also suggested that increased growth rate of buried colonies enhanced their survival.	
Invertebrates in subtidal understorey kelp environments (7–11 m in depth) in Washington State, USA. Kelps increased sedimentation by 2.4–4.8 times with respect to no kelp areas.	Experiments tested the effects of kelp on recruitment of invertebrates, and tried to separate the roles of physical factors controlled by kelps (i.e. flow speed, sediment and light). Replicated recruitment plates were deployed either facing up or facing down in each of kelp and no kelp treatments. Plates facing down were either opaque or transparent. Effects of sedimentation were tested by comparing plates facing up and opaque plates facing down only in kelp treatments. There were differences in flow rates between the two types of plates, but these were considered irrelevant. Possible confounding effects due to the different orientation of the substrata were not considered.	Rates of recruitment of the polychaetes *Pseudochitinopoma occidentalis* and spirorbid spp., and the bryozoans *Membranipora membranacea* and *Tubilopora* spp. were inhibited in treatments facing up (with sediments) compared with treatments facing down (without sediments). It was concluded that kelps exerted an important indirect influence on recruitment of benthic invertebrates by affecting sedimentation.	Duggins et al. 1990

Table 3 *continued*

Species-assemblage/habitat characteristics/location	Type of manipulation/experimental set-up	Results	Reference
	An analogous experiment was done to separate the effects of the same physical factors on growth of adult invertebrates. As above, possible confounding effects due to the different orientation of the substrata were not considered.	Growth of *Pseudochitinopoma occidentalis*, *Membranipora membranacea*, the bryozoan *Cheilopora praelonga*, and the sponge *Myxilla incrustans* was reduced in treatments facing up (with sediments) compared with those facing down (without sediments). Extent of responses differed among species. Negative effects of sedimentation on growth were not consistent with the observation that most species exhibited greatest growth and survival below kelps. It was suggested that negative effects of kelps due to enhanced sedimentation were compensated by positive effects due to reduced rates of flow and abundance of microalgal turfs.	Eckman & Duggins 1991
Crustose coralline and filamentous turf algae onto lava boulders in a lagoon (<3 m in depth), Galapagos Archipelago. Sedimentation rates ranged from $100\,g\,m^{-2}\,d^{-1}$ to $550\,g\,m^{-2}\,d^{-1}$. Small size particles (<0.02 mm) accounted for up to half of total sediment.	Replicated bleached and sun-dried lava boulders were subjected to sediment accretion (physical addition of sediment), sediment erosion (removal of sediment by water motion once every 2 or 7 days) and scour (physical abrasion). Effects on recruitment of turf and coralline algae were followed over 51 days.	Turf recruited in all treatments. Percent cover and biomass were enhanced by sediment erosion. Accretion of sediment negatively affected cover of turf, but this did not result in negative effects on biomass. Biomass was significantly lower in treatments simulating scour. Effects on crusts were difficult to quantify as crusts were overgrown by the turf, except in treatments simulating scour. It was suggested that persistence of crusts may be favoured indirectly by sand scour that removes the overgrowing turf.	Kendrick 1991

Table 3 *continued*

Species-assemblage/habitat characteristics/location	Type of manipulation/experimental set-up	Results	Reference
Assemblages dominated by turf-forming algae on rocky subtidal reef (13–17 m in depth) at Calafuria, Italy. Sedimentation rates ranged from 2 $g\,m^{-2}\,d^{-1}$ to 178 $g\,m^{-2}\,d^{-1}$. Turfs trapped up to 924 $g\,m^{-2}$ of sediment. This was mostly composed of fine (<200 μm) inorganic particles. Maximal disturbance by sediments occurred in late autumn and winter, from storms and scouring by sediments, when small patches of bare rock could be produced.	Two experiments tested whether the structure and diversity of adult or developing assemblages (plots experimentally cleared at different times of the year) differed between replicated plots unmanipulated or in which sedimentation was reduced by using transparent Plexiglas panels. Cover and biomass of dominant species were quantified over 1 yr. Potential artefacts were assessed and were found to be irrelevant. Panels effectively reduced natural sedimentation rates by 35%.	Reduction of sedimentation influenced the structure of the algal assemblage. Effects were most evident on the developing assemblage, and were dependent upon the time when succession was initiated. Cover of algal turf was unaffected by sediments, while its biomass was enhanced by reduced sediment load. Conversely erect algae only grew in plots scraped in June and exposed to natural sedimentation. Overall, species diversity was lower in plots with lessened sedimentation. It was suggested that sediments affected the diversity of the assemblage both directly, by controlling the biomass of turf, and indirectly, by modulating competitive interactions between turf and erect algae.	Airoldi & Cinelli 1997
	One experiment tested whether variable size (different size of plots), intensity (chronicle smothering, or abrupt disturbance), timing (time when disturbance started) and spatial location of disturbance by sediments affected the success of turf-forming and erect algae. Sediment smothering was manipulated by weekly additions of sediments as to obtain sedimentation rates increased by 0 $g\,m^{-2}\,d^{-1}$ and 100 $g\,m^{-2}\,d^{-1}$. Sediment scour was	Variable size, intensity, timing and location of disturbance by sediments significantly influenced the success of erect algae that persisted by sexual reproduction, but did not affect spatial dominance by the turf that persisted by vegetative reproduction. Severe disturbance by sediment favoured the development of erect algae by locally removing the turf from small patches of substratum. These positive indirect effects, however, only occurred if turf was	Airoldi 1998

Table 3 *continued*

Species-assemblage/habitat characteristics/location	Type of manipulation/experimental set-up	Results	Reference
	mimicked by abrading or completely scraping off the assemblage.	disturbed at certain times of the year, and probably did not persist over time. It was suggested that by propagating vegetatively and trapping sediment, the turf monopolises space, and relegates erect algae to the status of fugitive species.	
	Responses of turf-forming algae to spatial variations in the deposition of sediments at different spatial scales were analysed by observations and experiments. The experiment tested the hypotheses that (1) different amounts ($0\,g\,m^{-2}\,d^{-1}$, $100\,g\,m^{-2}\,d^{-1}$ and $200\,g\,m^{-2}\,d^{-1}$) and grain sizes (fine, medium and coarse) of sediment affected the cover and biomass of the turf, (2) any effects of sediments were independent of the stage of development of the turf, and (3) patterns were consistent at different spatial scales, ranging from centimetres to metres.	Sediments affected negatively the biomass of the algal turf at values greater than $200\,g\,m^{-2}\,d^{-1}$. Effects occurred only with medium and coarse sediments, and were mainly evident on an established turf. Patchiness in the deposition of sediment affected the biomass of the turf at the scale of metres, however turf cover was not affected by sediments at any spatial scale. It was concluded that negative direct effects of sediments on turf thickness over small spatial scales (cm to m) were probably compensated for by indirect positive effects on turf cover over large spatial scales (10 s to 100 s m), possibly though limiting grazing by herbivores or inhibiting recruitment of potential competitors.	Airoldi & Virgilio 1998
	Effects of timing and location of disturbance (as produced in the area by severe episodic perturbations from storms and sediment scour) on colonisation of encrusting, turf-forming and erect algae	Encrusting, turf-forming and erect algae responded differently to spatial and temporal variation of disturbance, depending on life histories. Turf colonised space by vegetative propagation	Airoldi 2000b

Table 3 *continued*

Species-assemblage/habitat characteristics/location	Type of manipulation/experimental set-up	Results	Reference
	were investigated by clearing replicated plots at 8 different times during 1 yr. The experiment covered spatial scales ranging from about 1 to 100 s m. Colonisation of patches by different algae was followed over 1 yr.	and quickly regained spatial dominance in patches disturbed at all times of the year and at all locations. Encrusting and erect algae occupied space mostly by colonisation of propagules, and their recruitment was much influenced by timing and location of disturbance. A regime of disturbance by storms and sediment scour adverse to recruitment of erect algae was identified as the probable cause of their scarcity in the study area.	
Subtidal epibenthic assemblages on an artificial reef (18 m in depth) at Loano, Italy. Sedimentation rates ranged from 10 $g\,m^{-2}\,d^{-1}$ to 213 $g\,m^{-2}\,d^{-1}$.	Effects of sedimentation on recruitment of epibenthic assemblages were tested by using horizontal settlement panels protected or non protected by glass screens. Panels (two replicates for each treatment) were deployed over 24 months. Both upper and undersides of panels were sampled.	Multivariate analyses separated panels protected or non protected by sediments. Total abundance (biomass) and diversity of species were greatest on panels protected by sediments, which were colonised by diversified assemblages of oysters, ascidians and encrusting and erect bryozoans.	Relini et al. 1998
Sargassum microphyllum on an intertidal fringing coral reef usually covered by a thin deposit of fine sand, Great Barrier Reef, Australia.	Several experiments tested the effects of three levels of sediment load (addition up to 20 mm in order to double natural sediment thickness, removal by flushing plots with seawater, and unmanipulated) on recruitment, growth, survival, degeneration and vegetative propagation of *S. microphyllum*.	Increased amounts of sediments significantly decreased rates of recruitment, growth, survival and vegetative regeneration, but did not affect degeneration. Sediment removal did not have relevant effects. It was suggested that the greatest abundance of *Sargassum* spp. often observed in habitats with greatest sediment load was related to other factors	Umar et al. 1998*

Table 3 *continued*

Species-assemblage/habitat characteristics/location	Type of manipulation/experimental set-up	Results	Reference
		correlated with sediments, such as nutrients, or to indirect effects of sediments on potential competitors or predators.	
Encrusting algae and invertebrates on a sheltered plateau reef (6 m in depth), Lough Hyne, Ireland. Natural sedimentation rates ranged from 2 $g\,m^{-2}\,d^{-1}$ to 12 $g\,m^{-2}\,d^{-1}$. Organic content varied from 15% to 30%.	Effects of light and sedimentation in influencing prevalence of invertebrates on down facing surfaces were tested by exposing replicated slate settlement panels to 4 different combinations of sedimentation and light: light but no sediment, light and sediment, no light and no sediment, and down facing panels. Sediment and light were manipulated by using opaque or transparent perspex panels (or frames). The experiments did not include unmanipulated panels. Development of the assemblage was followed over 13 months. Similar sets of panels were deployed at two different times for 39 days.	Downward facing panels supported greater number of species and total per cent cover than all other treatments, followed by panels with no light and no sediment, panels with light but no sediment, and panels with light and sediment. Cover of some species, such as *Lithothamnion* spp. was negatively affected by the presence of sediments, whilst other species, such as *Anomia ephippium* were not affected. Differences among panels exposed for short times were less pronounced than differences among panels exposed for 13 months, suggesting that differences among treatments were mainly related to post-settlement mortality. It was suggested that the negative phototactic response of many larvae may be a response to sediments as well as light. Differences between down facing panels and panels with no light and no sediment could not be explained.	Maughan 2001
Epibiotic assemblages on artificial panels (5 m depth). Outer Harbour, South Australia.	Effects of light and sedimentation in influencing prevalence of algae and invertebrates on up facing and down facing surfaces, respectively, were tested by	Alternate states of algae vs invertebrate dominated assemblages appeared to be primarily maintained by light intensity, which facilitated algal cover on up facing	Irving & Connell 2002a

Table 3 *continued*

Species-assemblage/habitat characteristics/location	Type of manipulation/experimental set-up	Results	Reference
	manipulating light and sedimentation in orthogonal combinations. Epibiota was allowed to develop on down facing surfaces. After 100 days, some plates were rotated 180° and attributed to 3 levels of light intensity (full shade by using dark roofs, procedural control with clear roofs, unmanipulated) and two levels of sedimentation (natural or reduced by removing sediment manually every 2–3 days). Effects on per cent cover of epibiota were assessed after 65 days. Potential artefacts were assessed and were found to be irrelevant.	surfaces (full light) and invertebrates on down facing surfaces (reduced light). Although sedimentation was only partially responsible for differences between habitat types, it acted as a negative disturbance on the abundance of algae and survival of invertebrates. Effects were particularly evident under shaded conditions, suggesting important interactive effects between light and sedimentation. It was observed how the ability of invertebrates to withstand sedimentation was related to their morphology, where erect forms tolerated sediments better than prostrate forms.	
Turf-forming algae (*Feldmannia* spp.) on artificial panels (5 m depth). Outer Harbour, South Australia. Natural sedimentation rates ranged from 322 $g\,m^{-2}\,d^{-1}$ to 2033 $g\,m^{-2}\,d^{-1}$.	Effects of microtopography and sediment deposition on recruitment of turf were tested by exposing replicated settlement plated to an orthogonal combination of two sediment treatments (sediment removed manually every 2–3 days and unmanipulated) and two microtopographies (smooth or roughened surfaces). Cover and biomass of turf were quantified after 50 days.	Reduced sedimentation enhanced cover of turf independently of substratum microtopography. Reduced sedimentation also enhanced biomass of turf: these effects were much greater on topographically complex than simple surfaces, while no differences between smooth and roughened plates were observed at natural rates of sediment deposition. It was suggested that heavy sedimentation can obliterate differences in turf abundance related to substratum microtopography	Irving & Connell 2002b

Figure 12 Plexiglas roofs (34 cm × 39 cm) used to manipulate rates of sedimentation on rocky subtidal reefs south of Livorno, Italy (modified from Airoldi & Cinelli 1997, published with permission, photo by the author).

removal of sediment, as well as on environmental conditions (e.g. natural sedimentation rates, water flow, composition of the biological community). Neushul et al. (1976), for example, reported that, during an experiment designed to test whether sedimentation affected settlement and growth of subtidal algae, the manipulation was unsuccessful, probably because removal was not frequent enough in relation to the local depositional regime. Similarly, Airoldi & Virgilio (1998) experienced uncharacteristic storms, which probably reduced the effectiveness of their manipulation due to removal of sediments that were experimentally added to their plots. Although such problems are not unlikely to occur, the effectiveness of the manipulations of sedimentation regime and the resulting levels of sediment deposition, accumulation and movement in experimental treatments are rarely quantified or even questioned (but see Airoldi & Cinelli 1997), which represents a major shortcoming of most field experiments.

Airoldi & Cinelli (1997) also discussed possible overlooked problems related to the use of panels or similar devices to reduce sedimentation rates. These structures are valuable instruments but they require a constant maintenance because they need to be perfectly clean so as not to limit the level of incoming irradiance. Furthermore, the presence of a panel may introduce the risk of potential artefacts (e.g. on the flow microenvironment, levels of irradiance, access to predators, or larval supply). Similar potential artefacts could also arise from the removal of sediments by water motion or flushing. A careful assessment of possible artefacts is necessary for the interpretation of the results (Airoldi & Cinelli 1997, Irving & Connell 2002a). So far, however, the possible influence of artefacts has been largely overlooked.

Measured effects

Field experiments demonstrate that sedimentation affects the composition and distribution of rocky coast organisms and the overall structure and diversity of assemblages (Table 3, p. 208). Negative effects of sediments were demonstrated for various species of invertebrates, including sponges, gorgonians, polychaetes, bryozoans and grazing gastropods (McGuinness 1987b, Gotelli 1988, Duggins et al. 1990, Eckman & Duggins 1991 but note possible confounding effects in the last two studies, Relini et al. 1998, Irving & Connell in press a), and for several species of algae (McGuinness 1987b, Kendrick 1991, Umar et al. 1998, Irving & Connell 2002a,b). In some cases responses were complex and difficult to disentangle. Airoldi & Cinelli (1997), for example, observed that a reduction of sediment inputs enhanced the biomass of turf-forming algae but did not affect their cover; conversely, erect algae only grew in patches of bare rock exposed to natural, moderately high ($2\,g\,m^{-2}\,d^{-1}$ to $178\,g\,m^{-2}\,d^{-1}$) sedimentation rates and produced at certain times of the year. Airoldi & Virgilio (1998) showed that, whereas cover of turf-forming algae was not affected by sediments, biomass was influenced negatively at rates of sedimentation $>200\,g\,m^{-2}\,d^{-1}$ and with grain sizes $>250\,\mu m$. Maughan (2001) suggested, and Irving & Connell (2002a) clearly demonstrated, complexes patterns of recruitment of algae and invertebrates in relation to combined effects of sedimentation, light intensity and surface orientation (see also the pioneer study by Muntz et al. 1972). In particular, Irving & Connell (2002a) emphasised that attempts to separate the effects of sedimentation and light intensity, which are not independent in nature, may not reveal the true effects of sedimentation on epibiotic assemblages.

In agreement with results from field observations and laboratory experiments, susceptibility to sediments was generally more pronounced in larval and juvenile stages than in adult mature assemblages. For example, the presence of sand reduced recruitment of *Leptogorgia virgulata* but enhanced the growth of established juveniles (Gotelli 1988). Disturbance by sand inhibited the development of assemblages on boulders, while mortality of established assemblages became notable only after long burial (McGuinness 1987b). Sediments significantly reduced the recruitment, growth, survival and regeneration ability of *Sargassum microphyllum* (Umar et al. 1998). These authors, however, observed that adult populations were never completely killed, and indicated that the major mechanisms by which enhanced sediments inhibited *S. microphyllum* at their study site involved preventing attachment of new recruits and smothering of young fronds. Airoldi & Cinelli (1997) observed that effects of sediments on the structure of subtidal assemblages were more evident on developing than established assemblages and were dependent upon the time of the year when succession was initiated.

Most field experiments did not attempt to elucidate the underlying mechanisms by which sediments affect rocky coast organisms. Nevertheless, there are lines of evidence which suggest that responses of species to sediments are complex, and are probably the result of both direct effects on individual species and their propagules, and indirect effects related to changes in abundance of other potential competitors or predators (see also p. 191). Umar et al. (1998), for example, demonstrated that sediments negatively affected the development and growth of *Sargassum microphyllum*. Results, however, contrasted with the observation that *S. microphyllum* was most abundant in areas with greatest sedimentation. The authors suggested that although sediments imposed a stress on *S. microphyllum*, the costs of living in sediment-affected habitats were probably compensated for by indirect advantages due to detrimental effects of sediments on other potential competitors or herbivores. Similarly, Kendrick (1991) demonstrated that recruitment of coralline crusts was enhanced by treatments simulating scour. These treatments were the only ones where crusts were not completely overgrown by turf at the end of the experiment because turf appeared to be sensitive to scour. Kendrick concluded that positive effects of scour on crusts were possibly related to indirect negative effects on the abundance of overgrowing turf (but see Airoldi 2000a).

The complexity of the effects of sedimentation has been elucidated by studies carried out over six years at an exposed subtidal rocky reef in the Ligurian Sea, Italy (Fig. 13). The area was subject to sediment loads that were moderately large compared with other rocky reefs, as a consequence of enhanced runoff and erosion from extensive fires of coastal vegetation (Airoldi et al. 1996). Accumulation of and disturbance from sediments were variable in space and time (Airoldi & Virgilio 1998). Sediment deposition and scour were greatest following storms, particularly intense during late autumn and winter, and the regime of sedimentation varied significantly among nearby sites, suggesting the important role of hydrodynamic conditions in influencing transport of sediment along the coast. Superimposed on these large-scale patterns, sediment was redistributed within each site. At a scale of metres, accumulation of sediment was patchy, probably reflecting differences in the microtopography of the bottom and in profiles of flow-speed at the boundary-layer. The assemblage was

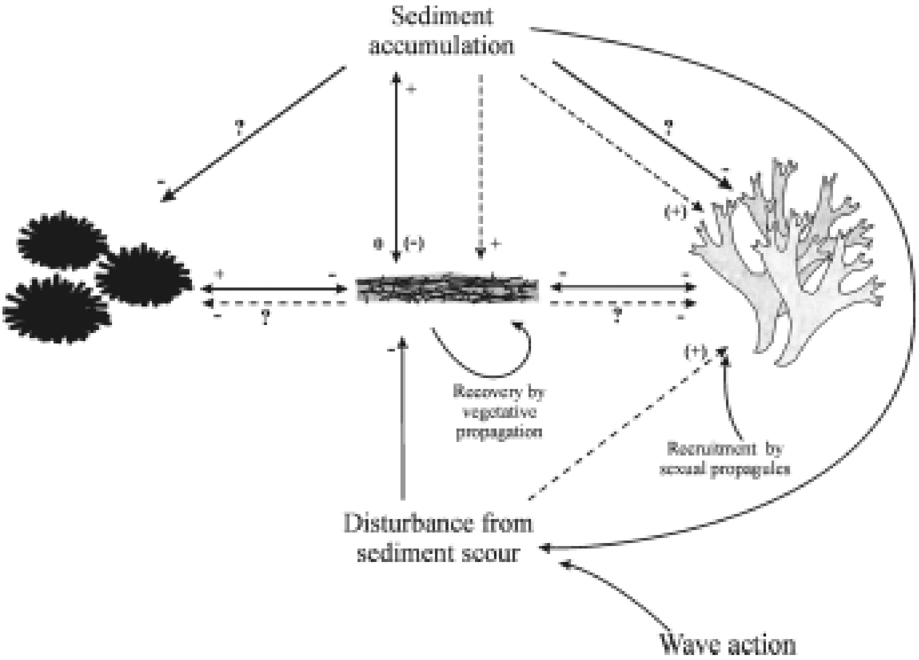

Figure 13 Example of complex direct (solid arrows) and indirect (dashed arrows) effects (+ = positive, − = negative and 0 = no effects) of sedimentation in rocky coast assemblages. Parentheses indicate effects that occur only under certain circumstances, while question marks indicate processes that need further experimental verification. The scheme derives from results of experimental studies of rocky subtidal assemblages in the Ligurian sea by Airoldi & Cinelli (1997), Airoldi & Virgilio (1998) and Airoldi (1998, 2000b). Filamentous turf accumulates sediment. In turn sediment can sometimes reduce turf thickness which does not affect turf cover. Accumulation of sediment is thought to deter grazers and inhibit recruitment of erect algae that compete for space with turf. Severe scour and accumulation can locally remove turf, allowing the temporary development of erect algae. Such positive indirect effects, however, only occur at certain times depending on propagule availability. Turf always recovers quickly from eventual damage by vegetative propagation. For further explanations see text and Table 3.

characterised by a notable low diversity of species and by the dominance of filamentous turf-forming algae that entrapped large amounts of sediments (Airoldi et al. 1995, Airoldi & Virgilio 1998). Observations and experiments indicated that sediments affected the structure of this assemblage in many direct and indirect ways. Airoldi & Cinelli (1997) demonstrated that species diversity decreased in plots where sediment inputs were reduced by using transparent screens. This pattern was related to an increase in the biomass of dominating turf-forming algae and a decrease in the cover of erect algae. They suggested that sediments affected the diversity of the assemblage both directly, by controlling the biomass of turf, and indirectly, by modulating competitive interactions between turf and erect algae. Subsequent experiments (Airoldi & Virgilio 1998), confirmed these hypotheses but showed that effects were more complicated than initially thought and varied at different spatial scales. Local accumulation of sediments could affect negatively the vertical growth of the turf but effects varied depending on the amount and grain size of sediments, the stage of development of the turf, and the concomitant action of other factors, such as the regime of disturbance and water movement in the area (Fig. 14). Conversely, cover of turf was not affected by sediments because prostrate basal axes appeared to be resistant to smothering and scour and, if damaged, the turf quickly regained spatial dominance by vegetative propagation. Overall, small-scale direct detrimental effects of sediments on the vertical growth of the turf appeared to be compensated for by indirect advantages to its horizontal distribution at large spatial scales. In particular, experiments showed that turf inhibited the recruitment of erect

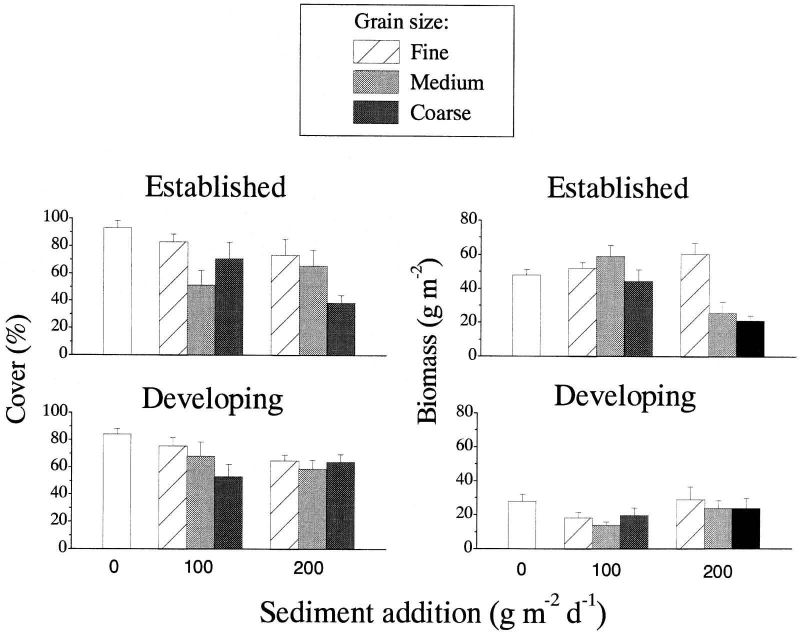

Figure 14 Variable effects of sediments on cover and biomass of subtidal turf-forming algae as a function of sediment characteristics (amount and grain size) and stage of development of the assemblage (modified from Airoldi & Virgilio 1998, published with permission). Data are mean values (+1 SE), measured 4 months after the beginning of the experiment.

algae that propagated by sexual reproduction (Airoldi 1998). Such effects were attributed to the ability of turf to entrap sediments; however experiments designed to test this hypothesis through manipulations of the relative abundances of turfs and entrapped sediments were unsuccessful (Airoldi & Cinelli 1996b). It was suggested that entrapped sediments also limited grazing by herbivores and experiments are now in progress to test this hypothesis (L. Airoldi and S.J. Hawkins, unpubl. data). Ultimately, severe disturbance by sediments could remove the turf from small patches or decrease its thickness, thus allowing the local development of erect algae which were relegated to the status of fugitive species (Airoldi 1998). Further experiments (Airoldi 2000b), however, showed that these positive indirect effects on erect algae occurred only if turf was removed at certain times of the year; overall, the temporal regime of disturbance in the area adversely affected the recruitment of erect algae, contributing to their notable scarcity. Airoldi (1998) concluded that the ability of turf to accumulate large amounts of sediment and to quickly recover vegetatively to eventual damages were major determinants of the spatial dominance of the turf, and of the low diversity of species observed in the study area.

Overall, results from field experiments indicate that effects of sediments on rocky coast assemblages are complex because they are probably the result of both direct effects acting on individual species and indirect effects through mediation of competitive and/or predator/prey outcomes. Furthermore, the responses of species to variations in the characteristics of the depositional environment vary with changes in the scale of observation and are influenced by a number of factors acting at different spatial and temporal scales. Consideration of scale is particularly important because it emphasises the need for caution when trying to extrapolate results observed at the relatively small spatial scales of most field experiments to larger spatial scales relevant to predict threshold levels of disturbance by sediments in coastal areas.

Modelling

Limited work has been done to quantify the magnitude of the effects that different sedimentation regimes have on rocky coast organisms, and to predict threshold levels of perturbation by sediments. For example, deposits of sediment above $10\,\mathrm{mg\,cm^{-2}}$ and above $3\,\mathrm{mg\,cm^{-2}}$ have been shown to inhibit settlement of *Macrocystis pyrifera* (Devinny & Volse 1978) and *Ecklonia cava* and *Undaria pinnatifida* (Arakawa & Matsuike 1992), respectively. Results of field observations and experiments suggest that prevalence and monopolisation of space by filamentous, turf-forming algae, might be favoured by chronic, "moderately high" (i.e. up to about $15\,\mathrm{mg\,cm^{-2}\,d^{-1}}$) rates of sedimentation (Airoldi et al. 1996, Airoldi 1998, Airoldi & Virgilio 1998). Overall, in agreement with indications from coral reef habitats (Rogers 1990), available information suggests that chronic rates of sedimentation $>10\,\mathrm{mg\,cm^{-2}\,d^{-1}}$ may be considered potentially stressful for rocky coast organisms, but generalisations are premature. Even fewer attempts have been made to model and predict the effects of enhanced sediment load, as a consequence of natural or human processes, on individual species or assemblages. Based on laboratory experiments and numerical simulations, Arakawa & Morinaga (1994) predicted a reduction to 10% of the extension of beds of the kelp *Ecklonia cava* at levels of turbidity $>10\,\mathrm{mg\,l^{-1}}$. Based on computer simulations (using a hydrodynamic model to calculate sediment concentrations) of the effects of spillage of sediments and release of nutrients as a consequence of the construction of a bridge between

Denmark and Sweden, Bach et al. (1993) predicted that up to 90% of the eelgrass meadow and 50% of macroalgae in the area would be seriously affected by concentrations of suspended sediments of $5\,\text{mg}\,\text{l}^{-1}$ to $20\,\text{mg}\,\text{l}^{-1}$, with losses of biomass up to more than 30%. However, there appear to be no subsequent verifications of the predictions. Developing and testing sound quantitative models about the consequences of changes in the regime of perturbation by sediments on rocky shore assemblages is undoubtedly most urgent.

Discussion and conclusions

Sedimentation has long been acknowledged as a major determinant of the composition, distribution and diversity of rocky coast organisms. Despite the early recognition of this possibility, the present review highlights the rarity with which this hypothesis has been assessed with informative quantitative observations and specifically targeted research to quantify the effects of sedimentation and identify the underlying mechanisms has been surprisingly scarce (Fig. 5). In the past few years there has been an increasing number of quantitative and experimental studies investigating the effects of sedimentation on temperate rocky coast assemblages (Tables 2 and 3). However, many questions still remain unanswered and present knowledge makes it difficult to formulate predictions of the effects of sedimentation on individual species and assemblages on rocky coasts. In the following sections available information on the ecological role of sedimentation on rocky coasts is synthesised, present inability to predict responses of individual species and assemblages to the threshold sediment loads is addressed and an attempt is made to identify emerging general trends. Those factors that most hinder generalisations and predictions are highlighted, including limited knowledge of the underlying mechanisms, insufficient description of the regime of perturbation by sediments, and scarce consideration of scale issues. A critical discussion of these limitations is important for the effective planning of future work.

Ecological role of sedimentation

There is substantial evidence that the ecological role of sedimentation in rocky coasts is one of major significance. Sedimentation is an important factor of stress and disturbance for hard-bottom organisms (*sensu* Grime 1977). As with other natural and anthropogenic perturbations, presence of sediments may deeply affect the composition, structure, dynamics and diversity of natural assemblages (e.g. Daly & Mathieson 1977, Littler et al. 1983, D'Antonio 1986, Kendrick 1991, Airoldi 1998, Irving & Connell 2002a,b,), and may play a role in the evolution of life histories (Brown 1996). Sediments that accumulate on rocky substrata can cause burial, scour and profound modifications to the characteristics of the bottom surface, and interact with other physical and biological processes, including grazing and predation, water motion, turbidity, substratum topography and pollutants (see p. 170). The degree, extent, location, frequency and duration of burial and/or scour, and the characteristics of sediment particles (e.g. grain size, shape, density, mineral and chemical composition) are all important in determining the regime of perturbation by sediments and its ecological consequences.

Interactions between sediments and organisms on rocky coasts are complex (Fig. 13).

Many species accumulate and trap sediments, thus controlling their transport, deposition and accrual rates (see pp. 168 and 187). In turn, sediments significantly affect the abundance and distribution of hard-bottom organisms by limiting the abundance of some species and favouring the development of others (Tables 2 and 3). The underlying mechanisms of these processes are little known, and often ecologists have referred to the effects of “sedimentation” ambiguously, without explicit consideration of the different components and effects of “sedimentation” (e.g. burial, scour, turbidity). Observations and experiments suggest that sediments affect rocky coast organisms through both direct effects (generally negative, such as smothering, scour, replacement of stable with unstable substrata) on settlement, recruitment, growth or survival of individual species (see pp. 189 and 196), and indirect effects (positive and/or negative) through mediation of competitive and predator–prey outcomes (e.g. Taylor & Littler 1982, Littler et al. 1983, D’Antonio 1986, Airoldi & Cinelli 1997). Effects vary over space and time, depending on the characteristics of the depositional environment, life histories of species and the stage of development of individuals and assemblages, and in relation to variable physical factors, including hydrodynamics, light intensity and bottom topography (e.g. Airoldi & Cinelli 1997, Airoldi & Virgilio 1998, Irving & Connell 2002a,b).

Can we predict the impacts of sediments?

Identifying the magnitude of the effects that different sedimentation regimes have on individual species and assemblages and the critical levels above which detrimental effects become manifest is a major requirement for predicting the impacts of sediments and for effective management of rocky shore habitats. Observations and laboratory experiments suggest that even the most tolerant hard-bottom organisms would eventually suffer inhibition and mortality above certain degrees of sedimentation (see pp. 189 and 196). Furthermore, there is evidence that “excessive” sediment load can be a threat to the diversity and functioning of rocky coast assemblages, and a prime initiator of shifts between alternate states in the composition of species (see pp. 176, 193 and 207). Paucity of quantitative data and poor understanding of the mechanisms by which sediments interact with rocky shore organisms limit our present ability to predict the effects of enhanced sediment loads on rocky coast assemblages. Nevertheless, several common patterns emerge from the body of literature that is reviewed here, and a few qualitative trends may be tentatively suggested:

(1) Rocky coast organisms that persist by sexual reproduction appear to be more vulnerable to the presence of sediments than organisms that propagate vegetatively, probably because larvae and propagules require stable substrata for settlement, and/or juvenile stages are more sensitive to smothering by sediments than adult stages;

(2) There seems to be a trend in sediment affected areas for the prevalence of species with sediment-trapping morphologies, opportunistic, vegetative propagating or migratory life histories and physiological and morphological adaptation to withstand stressful physical and chemical conditions during burial. Many of these species can probably be characterised as “sand-tolerant” species, for which negative effects due to the presence of sediments are possibly compensated for by indirect advantages, including reduced competition and predation.

(3) Low density of grazers and concomitant dominance of turf-forming and/or

opportunistic foliose algae frequently characterise rocky coasts affected by sediments, suggesting that sediments may control rocky coast vegetation through inhibition of grazing.

(4) Areas affected by sediments appear to be frequently characterised by low diversity of species, often because of the prevalence of space-monopolising forms. At the same time, however, variable patterns of sediment deposition and movement may be important sources of spatial and temporal heterogeneity in the structure and dynamics of affected assemblages, sometimes promoting diversity.

(5) There seem to be trends in areas with high human perturbations, including high sediment load, for the decline in cover of erect, canopy-forming algae and increased abundance of turf-forming algae. The latter, once established, trap sediments and seem to inhibit reinvasion of canopies and other organisms. The underlying mechanisms for the prevalence of turf-forming algae and their tendency to monopolise space in sediment impacted areas are not fully clarified but recent research has suggested that the abilities to entrap and withstand sediments and to pre-empt space by propagating vegetatively are major determinants of the success of these species. It can be further speculated (but evidence either supporting or refuting this hypothesis is limited) that assemblages dominated by canopy-forming and turf-forming algae might represent alternative stable states in shallow temperate rocky reefs, and that sediments might be one of the factors triggering the shift in balance between those two states.

Verification of any of the above scenarios requires quantitative and experimental work, including large-scale temporal and geographic comparisons among systems with different regimes of stress and disturbance by sediments. Such examination is only possible if sedimentation is quantified with comparable methods and over a range of spatial and temporal scales, that are relevant to the ecological processes being examined.

The overlooked importance of scale

Although the problem of scale has been recognised as a central issue in ecological studies (e.g. Petraitis et al. 1989, Levin 1992), consideration of scale has been surprisingly limited in studies on the impacts of sedimentation on rocky coast assemblages, and analogous concern has been raised by Rogers (1990) for studies done in coral reefs. The characteristics of the depositional environment, the attributes of rocky coast habitats and assemblages, and the interactions between the two are highly variable over a range of spatial and temporal scales. Thus, the perception of coupling between sedimentation and rocky coast assemblages is influenced by the spatial and temporal extent of a study (Airoldi & Virgilio 1998). However, in many cases, effects of sedimentation have been interpreted and generalised in the absence of data on the regime of perturbation by sediments undergone by the assemblages and there is a lack of information on the spatial and temporal variability in both patterns of deposition of sediments and benthic assemblages. Very few studies have been done at more than one place or time and most observations and experiments have been undertaken at the scale of individual organisms or small habitat patches. The effects of changes in the regimes of sedimentation over large spatial scales have rarely been addressed and observations were often confounded by the concomitant variations of other physical, chemical or biological parameters. Furthermore, most studies on the effects of sedimentation on rocky coast assemblages were carried out over very short times. Observations and experiments indicate, however, that timing is a critical and overlooked factor in studies of the effects of sedimentation on rocky coast assemblages (e.g. Shaffer & Parks 1994, Airoldi & Cinelli 1997, Airoldi 1998).

Current knowledge is limited and does not allow conclusions about the range of scales that are relevant to interactions between sediments and rocky coast assemblages. However, there are a few studies that have identified important spatial and temporal components of variability. For example, it has been demonstrated that the effects of disturbance by sediments can vary depending on the time of the year when disturbance occurs, or on the location and topography of the shore (e.g. Littler et al. 1983, Trowbridge 1996, Airoldi 2000b). The sub-lethal chronic presence of a moderate layer of sediment has been shown to have different effects on the diversity of rocky coast organisms than sporadic, severe burial or scour (e.g. Shaffer & Parks 1994, Airoldi 1998). Detrimental effects on growth of some species observed at the small spatial scales of habitat patches have been found to weaken if not be reversed at larger scales of sites and shores (Airoldi & Virgilio 1998). Similarly, there are indications that the heterogeneous and unpredictable distribution of sediments affects the small-scale patchiness of the environment (Littler et al. 1983, McQuaid & Dower 1990, Airoldi & Cinelli 1997, Airoldi 1998), but the consequences at the scale of a whole shore (e.g. in terms of control of species diversity) are less clear. These results stress the need for explicit consideration of scale issues in future studies.

Conclusions and future research needs

Substantial progress has been made in the past few decades in detecting effects of sedimentation in coastal environments. However, we still know little about how individual species and assemblages on rocky coasts respond to spatial and temporal changes in the characteristics of the regime of sedimentation, and about the direct and indirect mechanisms by which sediments affect rocky coast organisms. Current limitations to knowledge can be attributed largely to a paucity of quantitative and experimental research, and especially to the scant attention devoted to quantitative measures of the regime of perturbation by sediments and responses of organisms at relevant spatial and temporal scales. Whereas limited information exists, our ability to make generalisations is restricted. Predicting the consequences of changes in sediment loads and the critical levels above which detrimental effects of sediments become manifest remains a key issue for the ecology of rocky shores and a challenge for future studies.

There is a need for rigorous research, with a meaningful experimental component, to quantify the effects of sedimentation on individual species and assemblages, clarify the underlying direct and indirect causal mechanisms, and identify possible interactions with other environmental factors, including hydrodynamic conditions, substratum topography, organic and chemical pollutants, and water turbidity. There is a need for comparable estimates of the regime of perturbation by sediments across different habitats and locations, in order to interpret which are the levels of sedimentation that should be considered as “high” or “low” for rocky coasts. Such a comparison is only possible if standardised methodologies or sets of methodologies are used, and especially if the temporal and spatial context of any study are explicit. There is probably also a need to be more explicit about what is meant by “sedimentation” (i.e. sediment deposition, accumulation or movement, scour, or turbidity), because the effects of sediments are complex, variable over space and time and non-independent from a variety of physical and biological factors. Finally, there is much demand for studies over large spatial and temporal scales, because the scales of impact of enhanced sediment load as a consequence of human activities are much larger than those that can be covered by laboratory or field experiments. Extrapolating results from small to larger scales is still a major problem and challenge in ecology (Gardner et al. 2001). Large-scale and long-term monitoring programmes would be very useful in helping to solve these problems, because they would provide fundamental baseline information about trends of changes in sediment loads and assemblages, identify whether the causes of change are to be attributed to natural processes or human activities, and possibly take advantage of unplanned experiments that occur as a consequence of management actions (Carpenter et al. 1995).

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