*Environmental Conservation* **29** (2): 168–191 © 2002 Foundation for Environmental Conservation DOI:10.1017/S0376892902000115

# Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years

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Date submitted: 10 August 2001 Date accepted: 20 February 2002

## SUMMARY

**Rocky shores occur at the interface of the land and sea. Typically they are open ecosystems, with steep environmental gradients. Their accessibility to man has rendered them susceptible to a variety of impacts since prehistoric times. Access can be regulated, however, and they are more amenable to management than open ocean habitats. This review uses examples from throughout the world to demonstrate the extent to which rocky shores have been, and are currently, affected by pollution (examples used are endocrine disrupters, oil, eutrophication), over-collection of living resources, introduced alien species, modification of coastal processes (coastal defences, siltation) and global change (climate, sea level). These impacts are put into the context of natural fluctuations in time and variability in space of both the environment and the organisms. The relative magnitudes of some anthropogenic disturbances differ between the industrialized, developed world and the developing world. For example, in developed, industrialized countries pollution based impacts should diminish over the next 25 years due to improved regulation and a reduction in older 'dirtier' heavy industry. Conversely, in many developing countries pollution will increase as a consequence of growth in the human population and industrialization. Except for large-scale disasters such as oil spills, pollution tends mainly to influence embayed coastlines. Chronic effects such as eutrophication can have broader-scale impacts over whole coastlines and elevated nutrient levels have also been implicated in a trend of increasing frequency of catastrophic kills due to harmful algal. Direct removal of living resources has had major effects on coastlines at both local and regional scales and is likely to increase over the next 25 years, especially in developing countries where rapidly expanding human populations will put further pressure on resources. Impacts from recreational activities are likely to increase with greater leisure time in wealthier regions of the world, and cheaper travel will spread these impacts to poorer regions. Invasions by alien species have increased in frequency during the last 20 years leading to some dramatic effects on native assemblages. Problems associated with alien species, especially pathogens, will continue to increase over the next few decades. The proportion of the coastline modified by artificial structures (breakwaters, seawalls, groynes) will increase because of coastal development and defences against sea-level rise and the greater frequency of storms. This will increase connectivity between areas of rocky habitat. Siltation will continue to increase due to urbanization of catchments and estuaries, and changes in agricultural practice. This may have considerable impacts at local and regional scales, favouring sediment tolerant organisms such as turf algae and anemones. In the future, greater frequency of environmental extremes is likely, including large-scale events such as the El Niño Southern Oscillation (ENSO). Global change in temperature, sea-level rise and increases in the frequency of storms will affect rocky shores throughout the world, but this will occur over long time scales; over the next 25 years most of the responses by rocky shore communities will mostly be quite subtle. Thus rocky shores will be subject to increasing degradation over the next 25 years. They are, however, less vulnerable than many other aquatic habitats due to their hard substratum (rock), their relative lack of large biogenic structures and to their generally open nature. They are also remarkably resilient, and recovery can occur rapidly due to recruitment from unaffected areas. Their susceptibility to both terrestrial and marine disturbances does make them more vulnerable than sublittoral and offshore habitats. There are considerable gaps in knowledge, particularly of certain microhabitats such as crevices, boulders, sand-scoured areas and rock pools. These have been much less studied than more accessible assemblages on open, freely draining rock. More research is needed to establish the effects of increasing sediment loads, ultraviolet radiation and introduced species on rocky shore communities.**

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https://doi.org/10.1017/S0376892902000115 Published online by Cambridge University Press

**Strategic and applied research programmes should integrate field experiments and carefully selected monitoring programmes to verify management regimes. Hindcasting from the palaeo-record would be valuable, to compare rates of predicted change with periods when change was rapid in the past. This information could, in principle, be used to help conserve rocky shores through networks of marine protected areas and a general reduction of environmental pollution.**

*Keywords*: impacts, prediction, littoral, rocky intertidal, anthropogenic disturbance, global change, conservation, management

## INTRODUCTION

Rocky shores occur at the margins of the oceans throughout the world. They are the most common littoral habitat on open wave-exposed coasts and also constitute many sheltered and enclosed coastlines, such as sea lochs, fjords and rias. This already extensive natural habitat is further increased by the plethora of artificial hard structures such as offshore platforms, docks, dykes, breakwaters, groynes, and sea walls, all of which essentially function as artificial rocky shores.

Their accessibility to man has rendered them susceptible to a variety of impacts since prehistoric times. They are subject to anthropogenic impacts originating from both the land and the sea. They are obviously also subject to a wide range of natural fluctuations (see later) on various temporal and spatial scales. Therefore there is a considerable challenge in unravelling anthropogenic change from natural variability. From a management perspective, rocky shores are more amenable to regulation than the open sea as access and discharges can be restricted. Furthermore, a wealth of knowledge of rocky shore ecology is available to inform management decisions and compliance monitoring programmes.

The overall aims of this review are to summarize the principal anthropogenic impacts on rocky shore organisms (individuals, populations and assemblages) and place them in the context of natural environmental changes. We have reviewed past and present impacts, attempted to establish the relative importance of trends and used this information to help inform predictions for the future. We also identify gaps in our current knowledge and directions for future research in terms of focus and approach. Given current concerns about global change and sustainability of natural resources this review is intended to inform the selection and design of research programmes for the next two decades.

After a brief summary of characteristics of rocky shore habitats, we start by examining how anthropogenic disturbances are superimposed upon existing environmental gradients and naturally fluctuating environmental conditions. We then survey past and present impacts and attempt to rank them and synthesize long-term trends in order to make predictions about future states. We then summarize major themes of the review and consider the relative vulnerability of rocky shores in comparison to other habitats before making recommendations for management and future research needs.

## THE NATURE OF ROCKY SHORE HABITATS

Rocky shores are bounded to the landward by fully terrestrial systems beyond the influence of sea spray. This boundary can be very sharp on sheltered shores, with terrestrial higher plants closely abutting and even intermingling with algae and marine invertebrates. To their seaward side rocky shores are part of a continuum to subtidal reefs but can also give way, both horizontally and vertically, to depositing shores of large boulders, cobbles, gravel and sand (see reviews by Lewis 1964; Stephenson & Stephenson 1972; Little & Kitching 1996; Raffaelli & Hawkins 1996). Thus rocky shores are typified by steep environmental gradients between land and sea and between exposed headlands and sheltered bays and inlets (see Raffaelli & Hawkins 1996 for review). The vertical gradient is essentially unidirectional with increasing stress from emersion at higher shore levels. There is also a horizontal gradient associated with exposure to wave action with greater wave force and frequency at exposed headlands than in bays or inlets. The latter is not a unidirectional stress gradient; some organisms function better and are naturally more abundant in wave swept conditions (e.g. suspension feeders such as mussels), whilst others thrive in shelter (e.g. some large algae such as *Ascophyllum* and *Hormosira*).

Another major environmental gradient is that of salinity, which is evident in estuaries and rock pools. On a much larger biogeographic scale, there is an all-encompassing influence of climate associated with latitude and modified by ocean currents and upwelling regimes. Thus the biota found at any location are determined ultimately by their ability to colonize sites and tolerate the various stress gradients acting upon them, and proximately by the smaller-scale physical influences and interactions with other organisms (see reviews by Lewis 1964; Connell 1972; Stephenson & Stephenson 1972; Little & Kitching 1996; Raffaelli & Hawkins 1996).

Most rocky shores are strongly influenced by the hydrographic conditions immediately offshore, especially in areas where upwelling occurs (Menge *et al.* 1997; Menge 2000). Material and hence energy are transported onto, away from and within rocky shores by waves, tides and currents. Sheltered bays, particularly fjordic systems, are often semi-enclosed with strong functional linkages between benthic habitats and the open water column. Rocky shores form extensive feeding, resting, spawning and nursery areas for mobile marine animals, including fish and crustaceans, as well as birds, reptiles and mammals (e.g. Rangeley & Kramer 1995; Bradshaw *et al.* 1999; Burrows *et al.* 1999; Coleman *et al.* 1999; Thompson *et al.* 2000*a*). Rocky shores have major functional links with other inshore habitats and the land itself. Populations of most rocky shore organisms are

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considered 'open' because the larvae and propagules that settle and recruit to populations are often from outside sources (Gaines & Roughgarden 1985; Underwood & Fairweather 1989; Menge 1991; Small & Gosling 2001), although there is recent evidence that not all rocky shore populations should be considered open (Todd 1998; Todd *et al.* 1998; Cowen *et al.* 2000). This openness, leading to recruitment variability, combined with varying environmental factors, generates considerable spatial patchiness and temporal fluctuations at a range of scales (e.g. Lewis 1976; Bowman & Lewis 1977; Underwood *et al.* 1983; Hartnoll & Hawkins 1985; Johnson *et al.* 1998; Underwood 1999; Jenkins *et al*. 2001).

## NATURAL ENVIRONMENTAL FORCING FACTORS VERSUS ANTHROPOGENIC INFLUENCES

Rocky shores are subjected to considerable natural environmental change. The most obvious example is tidal amplitude that varies, predictably, on short-term (daily to monthly) and long-term (annual and decadal) time scales (Denny & Paine 1998). There will also be diurnal and seasonal variation in stresses experienced when the tide is out and through weather generated disturbance by wave action and scour. Occasional natural catastrophic events such as cold winters, hot summers, extreme storms, toxic algal blooms, earthquakes and volcanic events also occur. Rocky shore ecosystems are also influenced strongly by offshore and near shore processes, such as upwelling, the El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO). Similarly increased freshwater input from flooding rivers can also influence adjacent coastlines.

Rocky shore organisms have mechanisms to deal with the stresses associated with alternating submersion and emersion in air (desiccation, temperature extremes, osmotic stress; for examples see Newell 1979; Davison & Pearson 1996; Karsten *et al.* 1996). The tolerance mechanisms involved are also effective for withstanding some anthropogenic stresses. Of particular note are behavioural mechanisms that shut animals off from the environment. These, coupled with the ability to withstand anaerobosis are effective in avoiding short pulses of pollution as well as spells of low salinity or desiccation. Many animals have well developed sensory mechanisms to detect and hence respond to natural stressors (e.g. Akberali & Davenport 1982) and pollutants such as heavy metals (e.g. Redpath & Davenport 1988). Many intertidal algae are also resilient and can tolerate considerable uptake of heavy metals (Barreiro *et al.* 1993; Castilla 1996) and withstand oil spills (Southward & Southward 1978). Thus, it is sometimes difficult to detect the effects of anthropogenic stress even at the level of the individual organism.

Anthropogenic stresses have a range of effects on the physiology and behaviour of intertidal organisms, influencing their metabolism, activity patterns, respiration, growth, reproductive output and immune responses (Newell 1979; Beardall *et al.* 1998; Harvell *et al.* 1999). Physiological tolerances vary both within and between species, (e.g. algae: Pakker & Breeman 1996; amphipods: Gaston & Spicer 1998; see Spicer & Gaston 2000 for review). Numerous studies have examined mortality of intertidal organisms in relation to environmental stresses and attempted to relate these to their distribution (e.g. Newell 1979; Lüning 1984). Some organisms live right on the edge of their physiological tolerances and the burden of additional anthropogenic or natural stress and could lead directly to mortality (Stillman & Somero 1996; Tomanek & Somero, 1999). For most species, however, their actual or realized distribution falls well within their ultimate physiological tolerances and is determined by interactions among several physical and biological factors (e.g. Connell 1961; Wolcott 1973; see Raffaelli & Hawkins 1996 for review). Hence the consequences of anthropogenic stress are often expressed by sublethal effects, which alter the competitive balance between species and indirectly influence their distribution and abundance.

Populations and communities exhibit considerable natural variability in space and time under the influence of many physical and biological factors (e.g. Hartnoll & Hawkins 1985; Underwood 1985, 1999; Foster *et al.* 1988). For example, dramatic natural fluctuations can be caused by extremes in temperature (Crisp 1964), red tides (Southgate *et al.* 1984), and variations in recruitment (e.g. Bowman & Lewis 1977; Caffey 1985; Underwood & Fairweather 1989; Menge 1991; Underwood 1999). Unravelling causes of long-term changes in community structure is extremely complex, due to the number of physical and biological interactions involved. This is especially so where small changes in the abundance or performance (e.g. photosynthetic output, growth, reproduction or activity) of a species, which has a key role as a predator or grazer or by providing habitat for other species, lead to substantial changes in overall community structure. For example, feeding rate of the starfish, *Pisaster ochraceus,* a key predator regulating community structure (e.g. Paine 1974, 1994), can be altered substantially by small changes in temperature (Sanford 1999).

Against a background of such variation it is can be extremely difficult to detect the additional effects of human activities (Dayton *et al.* 1998; Underwood 1991; 1992; 2000*a*, *b*). As a general principle, research should be conducted at replicate sites to ensure generality. This is not always possible; for example where there is only one example of a particular impact or management strategy in the region of interest. Replicated control, background or reference sites can still be used in most cases. Even where this is not possible insight derived from research must be clearly weighed against the limitations. For example, some of the clearest demonstrations of effects of collection of intertidal resources come from before and after studies at a single site in Chile (e.g. Duran & Castilla 1989; Castilla 1999, 2000, 2001; and see later). Where the effect size is large compared to natural variability the influence of anthropogenic disturbance can be established with modest replication. Of greater concern is the

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likelihood that experiments may fail to detect anthropogenic effects (type II error) because of inadequate experimental designs (Mapstone 1995; Underwood 1991, 2000*a*, *b*).

## HUMAN IMPACTS: PAST PRESENT AND FUTURE

Rocky shores are subject to a variety of impacts on a range of spatial and temporal scales and even in the most remote regions there are few pristine shores. Most impacts are localized, associated with either point sources or densely populated areas with a diversity of diffuse inputs of contaminants and elevated recreational and food collection activities. On a broader scale, intensive use of the shore for food collection can cause impacts at a regional level over 100s to 1000s of kilometres (e.g. in Chile, reviewed by Paine 1994; Siegfried 1994; Castilla 2000). Eutrophication can also occur over a broad scale as in the Baltic (Bonsdorff *et al.* 1997; see below). Acute impacts are generally localized; for example oil spills rarely cover more than a few tens of kilometres of coastline, the exception being the Gulf War.

Some stretches of coastline have been chronically impacted by collection of organisms for food, for thousands of years (Siegfried *et al.* 1994). In some economically developed countries such as the UK this impact has probably lessened since medieval times, while in others such as Italy (Fanelli *et al.* 1994; Fraschetti *et al.* 2001) and California, USA (Murray *et al.* 1999) collection by humans is still considerable. Disposable income and leisure time have increased dramatically over the last 50 years or so in industrialized countries and this has been associated with an increase in recreationally related impacts (Fletcher & Frid 1996). Industrial and domestic pollution has increased over the last 200 years or so with greatest impacts being on urban coastlines, especially in embayed areas. In developing countries, industrialization and population growth are accelerating rapidly (Morton 1990; Da Silva *et al.* 1997; Liu & Morton 1998) and environmental impacts may well follow a similar trajectory to past proliferation in the developed world. In countries that are losing their traditional heavy industries or that have increased pollution control many coastal ecosystems are recovering, albeit slowly, and rocky shores in these areas are no exception (e.g. the Mersey and Liverpool Bay region; Hawkins *et al.* 1999*a*, *b*).

Table 1 shows an overview of human impacts on rocky shores, outlining long-term trends, current knowledge, topics on which more work is required and predictions for the future. Here we describe the evidence in more detail for selected impacts. We present a summary of understanding of long-term trends, current knowledge and predict the extent of these impacts in the 2020s based on current forecasts. For each impact, the summary focuses on relevant levels of biological organization, ranging from the sub-individual level

**Table 1** Past perspectives and evidence of impacts on rocky shores from the 1960s, 1980s and now (2000s), predictions for trends in severity by the 2020s, plus an estimate of our ability to make predictions based on existing evidence. Evidence of impacts: negligible evidence (–), evidence of isolated incidents/occurrence (*), concerns and some evidence of impacts (**), evidence of major impacts (***). Expected trends in severity: little overall change (–), increasing severity (↑), decreasing severity (↓). Ability to predict impacts based on current evidence: low (•), moderate (••), good (•••)

| | *1960s evidence* | *1980s evidence* | *2000s evidence* | *2020s* | |
|---|---|---|---|---|---|
| | | | | *Severity* | *Predictability* |
| *Pollution* | | | | | |
| Endocrine disrupters | – | * | *** | ↑ | •• |
| Oil spills | *** | ** | *** | ↓ | ••• |
| Eutrophication | – | * | *** | – | •• |
| Toxic algal blooms | – | ** | *** | ↑ | •• |
| *Living resources and recreation* | | | | | |
| Gathering food and bait | * | ** | *** | ↑ | ••• |
| Recreation, research and education | – | – | * | ↑ | •• |
| Introduced species | * | ** | *** | ↑ | • |
| Genetically modified organisms | – | – | – | ↑ | • |
| *Global change* | | | | | |
| Warming | – | * | ** | ↑ | •• |
| Ultraviolet radiation | – | – | * | ↑ | • |
| Sea-level rise | – | – | * | ↑ | •• |
| Storms and extreme weather | – | * | ** | ↑ | •• |
| ENSO | – | * | ** | ↑ | •• |
| *Modification of coastal processes* | | | | | |
| Sea defences | – | * | ** | ↑ | •• |
| Sedimentation | * | ** | ** | ↑ | • |
| Renewable energy | * | * | ** | ↑ | • |

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to populations and communities through to ecosystem-scale effects.

## Pollution

Pollution can have impacts at all levels of biological organization from cellular to ecosystem levels. For example, toxicological challenges from pollution impair immune responses and could be responsible for the dramatic increase in reports of diseases affecting populations of marine organisms over the last few decades (Harvell *et al.* 1999). Impacts including oil spills and eutrophication can lead to community level changes, such as shifts in the relative abundance of primary producers and consumers, which may influence primary productivity at an ecosystem scale. We have chosen some specific examples: endocrine disrupters such as TBT (tributyl tin), influence organisms from a cellular level up to populations, with possible implications at higher levels of organization; oil spills and toxic algal blooms directly affect populations and communities; eutrophication directly influences communities and ecosystems, but via toxic blooms may also indirectly impact susceptible populations.

### *Endocrine disrupters*

During the last decade there has been increasing concern about the ability of anthropogenic substances to disrupt normal endocrine function in animals. Research on marine organisms has lagged behind that in terrestrial and freshwater habitats but one of the best-publicized examples is from effects on stenoglossan molluscs worldwide of TBT pollution derived from the leachates of antifouling paints (Ellis & Pattisina 1990; Matthiessen & Gibbs 1998). These molluscs respond to much lower concentrations than other marine organisms, showing imposex and, in badly affected cases, female sterility. This had devastating effects on populations, leading to local extinctions in sheltered bays and estuaries, where they were already at the edge of their distributional range (Bryan *et al.* 1986; Gibbs & Bryan 1987; Spence *et al.* 1990; Hawkins *et al.* 1994), and sublethal effects on open coasts.

Imposex is an irreversible condition stimulated at the onset of sexual maturity and because dogwhelks are long-lived it persists in populations for extended periods. Following legislation in 1987 to ban TBT paints on small boats in the UK recovery has occurred, but has taken at least 10–15 years (Fig. 1; Hawkins *et al.* 2002*a*). A worldwide ban on TBT has been proposed (by 2003) and so impacts from this particular pollutant are likely to decrease further. However, a range of other substances have also been recognized as having endocrine disruptive effects for a variety of marine organisms, including other molluscs, crustaceans, echinoderms and polychaetes (Depledge & Billinghurst 1998).

As awareness of new impacts increases other compounds or classes of compounds will become regulated. Experience has shown, however, that there is likely to be a time lag between impacts being recognized and enactment of legislation. Impacts are likely to increase before legislation eventually begins to bite. For example, with TBT it took 15–20 years to first legislation and a further 15 years will have elapsed before the proposed ban comes into force.

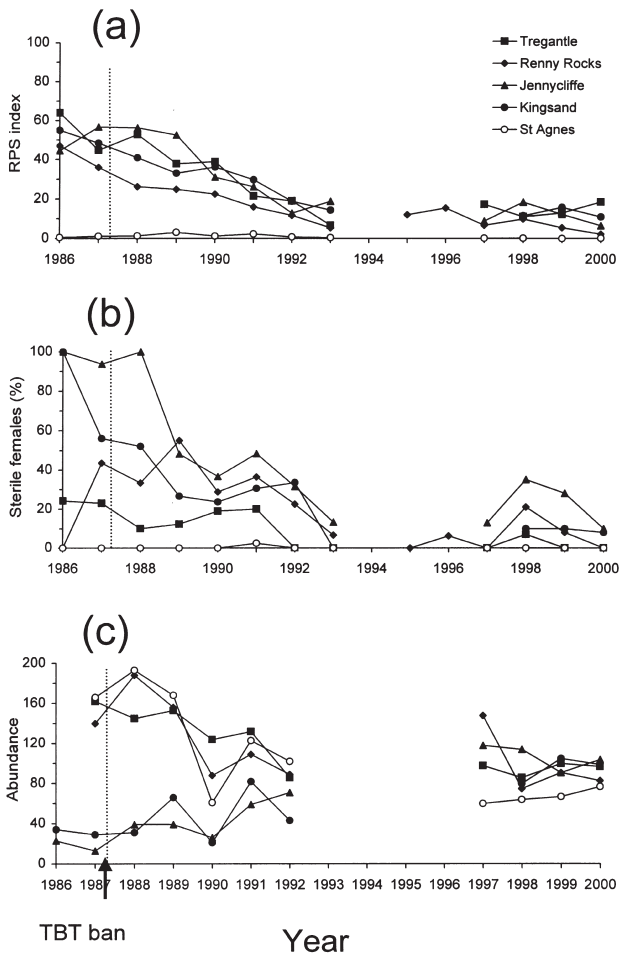



**Figure 1** Recovery of individuals and populations of dog whelks (*Nucella lapillus*), from imposex induced by tributyl tin pollution, following its ban in 1987 (dotted line) at contaminated sites around Plymouth Sound, UK (shaded symbols) and St Agnes, UK, a relatively uncontaminated site on the north Cornwall coast (open circles). (*a*) Relative penis size index (average size of penis found on females compared to males within a population (Bryan *et al.* 1986); (*b*) percentage sterile females (vas deferens sequence 5 and 6 of Gibbs & Bryan 1986); (*c*) abundance estimated as number of individuals found in a 30 minute search (Hawkins 2002*a*).

### *Oil spills*

Some of the best-recorded community-level impacts of anthropogenic stress are from oil spills (Clark *et al.* 1997). Some species can be remarkably tolerant of oiling (e.g. barnacles: Southward & Southward 1978; mussels: Newey & Seed 1995); others have been impacted more by the clean up than the oil (see Southward & Southward 1978; Foster *et al.* 1990 for reviews). Grazing molluscs seem to be particularly susceptible to both oil and chemical dispersants (e.g. Smith 1968; Hawkins & Southward 1992; Newey & Seed 1995).

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Physical cleaning can also cause considerable disturbance especially if high water pressures or temperatures are used, for example following the *Exxon Valdez* spill (Shaw 1992; Peterson *et al.* 2000).

The effects of the *Torrey Canyon* oil spill in Cornwall were especially well recorded, with regular sampling many years after the incident. Here, the major damage was not caused by the estimated 14 000 tonnes of oil that came ashore, but by excessive treatment with over 10 000 tonnes of dispersants, which killed the principal grazers, *Patella* spp. (mainly *P. vulgata*) and, to a lesser extent, *Osilinus* (*Monodonta*) *lineata* and *Littorina* spp. This led to dense growth of ephemeral green algae and then fucoids on many shores. Barnacles were only directly affected in areas that were cleaned repeatedly, but over the next few years they succumbed to smothering by algae and predation by dogwhelks (see Smith 1968; Southward & Southward 1978; Hawkins & Southward 1992; Hawkins *et al.* 1994). The dense macroalgal cover that formed subsequently provided a favourable environment for early survival of *Patella vulgata*. Treated shores recovered through a series of damped oscillations over the next 10–15 years, while an untreated shore recovered within 2–3 years (Southward & Southward 1978; Hawkins & Southward 1992). Similar patterns of impact and recovery were also reported after the more recent *Exxon Valdez* spill. Here the clean up did not involve dispersants. A variety of methods were used including manual wipe up, removal of oiled rocks and seaweed, bioremediation, and pressurized hot water washing. The latter method will kill animals as effectively as dispersants. Despite these precautions recovery of rocky shore assemblages was still quite slow. For instance *Fucus gardneri* still had not recovered at high shore levels some seven years after the spill (see Paine *et al.* 1996; Peterson 2001 for reviews).

Oil spills are one of the most visible and newsworthy forms of pollution and will no doubt continue to happen on shores adjacent to major shipping routes and oil refineries. With increases in the size of vessels, and improvements in design and legislation, the frequency of spills is likely to decline, however the potential for large-scale devastation from incidents with super tankers will probably increase over the next 25 years. Most attention to ecological effects has focused on catastrophic oil spills (see above). However, in terms of total volume, the input from low-level chronic sources such as urban run-off and routine tanker and refinery operations is much greater (Foster *et al.* 1988; Suchanek 1993) and is likely to increase over the next 25 years.

*Eutrophication and toxic algal blooms*

Eutrophication occurs over large areas and is now recognized as a significant problem in enclosed seas and estuaries in many parts of the world (e.g. the Baltic: Bonsdorff *et al.* 1997; Irish Sea: Allen *et al.* 1998; Canada: Meeuwig *et al.* 1998; USA: Cloern 2001). The rise of coastal eutrophication is driven largely by agricultural run-off contaminated by high fertilizer loads, and, to a lesser extent, sewage discharges (Nixon 1995). Over the last 20 years there has been an increase in intensive agriculture and attempts to reduce such practices have proven politically difficult (Iversen *et al.* 1998). Atmospheric deposition is also an important input of anthropogenic nitrogen to the marine environment (Paerl & Whitall 1999). The main effect observed on shores in the Baltic has been a decline in the perennial macroalgae (*Fucus vesiculosus*), including reduction in depth range (Kautsky *et al.* 1986), and increases in the abundance of ephemeral algae growing epiphytically or on rock surfaces (Schramm 1996; Worm *et al.* 1999). Microbial communities on rocky substrata can also be directly affected by eutrophication (Meyer-Reil & Koster 2000), with potential indirect effects on intertidal grazers.

Management of sewage and fertilizers may reduce eutrophication in some developed regions by 2025 and some dramatic improvements have already been observed (Cloern 2001). Developing countries, however, are expanding their use of inorganic fertilizers and increasing sewage discharges into the sea (Nixon 1995). Levels of eutrophication are therefore expected to follow a trajectory similar to that observed in developed countries (Nixon 1995). Oligotrophic tropical systems are expected to exhibit stronger responses to eutrophication than those in the temperate zone (Corredor *et al.* 1999). Atmospheric inputs of nitrogen are increasing (Paerl & Whitall 1999) and forecasted increases in rainfall may also exacerbate eutrophication by leaching terrestrial organic nitrogen (Hessen *et al.* 1997).

In addition to direct effects, eutrophication has been linked to an increase in incidence of harmful algal blooms. Widespread increases in the frequency and magnitude of blooms of harmful algae, mostly dinoflagellates (Smayda 1997), have been observed, particularly during the last decade (see Wu 1999 and references therein) but the causes are unclear. Some authors have suggested links with eutrophication (e.g. Paerl & Whitall 1999; Wu 1999; Cognetti 2001); warm water associated with ENSO was implicated in initiating blooms on the coasts of China in 1997–1998 (Yin *et al.* 1999). The cysts of harmful algae can be spread in ballast water, providing another mechanism for increased and more widespread occurrence (Hallegraeff 1998). When toxic blooms do occur, substantial mortality of rocky shore filter feeders, grazers (e.g. Southgate *et al.* 1984) and predators (Robertson 1991) has been observed. For example, when a bloom of *Chrysochromulina polylepsis* was washed ashore over large areas of the Scandinavian coast in 1988, it eliminated almost entire populations of dogwhelks and other marine invertebrates in some areas (Bokn *et al.* 1990; Robertson 1991; Wu 1999). The impacts on the whole community can resemble that of a badly treated oil spill, with a proliferation of algae due to decreases in the abundance of grazers (Southgate *et al.* 1984).

Given the uncertainty about the biology and ecology of bloom-forming algae (Zingone & Enevoldsen 2000), it is difficult to predict future trends in the occurrence of algal blooms, but links with eutrophication and El Niño suggest that they are likely to increase significantly by 2025 (see Wu 1999).

https://doi.org/10.1017/S0376892902000115 Published online by Cambridge University Press

### Direct removal of living resources, recreation and introduced species

*Food gathering*

Evidence from middens and other archaeological sites suggests subsistence collection has generally taken place in a sustainable manner since prehistoric times (Cunliffe & Hawkins 1988; Siegfried *et al.* 1994), and in some locations organisms are still being harvested sustainably (Kyle *et al.* 1997). However, the general pattern is of increasing impact because of growth in the human population and use of non-traditional equipment to facilitate harvesting, transport and storage (Hockey & Bosman 1986; Kingsford *et al.* 1991; Underwood 1993*a*; Siegfried *et al.* 1994; Santos *et al.* 1995; Crowe *et al.* 2000).

Direct exploitation of resources has had a major impact on rocky shore communities and the species targeted have been badly affected, showing declining populations. When recruitment is high the average size of individuals is affected because larger individuals tend to be collected (Hockey & Bosman 1986; Underwood 1993*b*) and populations display classic signs of growth overfishing. When intensive collection occurs at a large spatial scale then numbers can decline as the spawning biomass decreases leading to recruitment overfishing. There are several examples of this on isolated islands, where recruitment is already low and has been made much worse by overexploitation. Intertidal limpets in Hawaii (*Cellana* spp.), the Azores, Madeira and Canaries (*Patella* spp.) have all shown declines, and in the case of the Azores, dramatic population crashes (Hawkins *et al.* 2000 for review).

Castilla (1999, 2000, 2001) and co-workers (Moreno *et al.* 1984; Duran & Castilla 1989) have extensively documented effects of intertidal collection in Chile. Here creation of a no-take reserve at Mehiun led to an increase in the size and abundance of keyhole limpets (*Fissurella picta*), which had previously been harvested, and an associated decline in the abundance of the algae on which these limpets feed (Fig. 2). At Las Cruces, exclusion of humans led to an increase in the body size and abundance of the predatory muricid gastropod *Concholepas concholepas*, which had previously been exploited, followed by a reduction in the abundance of mussels, which are its main prey items. Keyhole limpets also increased in abundance. Loss of the mussels created areas of open space, which became colonized by barnacles (Castilla & Duran 1985). Subsequently there was a decline in the abundance of *Concholepas* and *Fissurella*, which was attributed to food shortages. Hence reducing collection by humans led to predictable direct and less predictable indirect changes in community structure (Fig. 3). Artisanal and commercial collections are widespread along the coastline of Chile and many other countries (Kingsford *et al.* 1991; Newton *et al.* 1993; Kyle *et al.* 1997; Crowe *et al.* 2000). In Chile, the intensity and extent of such activities have probably influenced community structure at a landscape scale (Paine 1994).

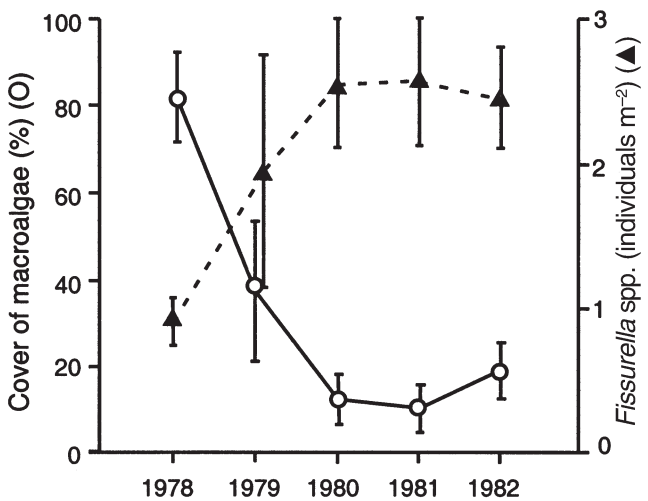



**Figure 2** Changes in the abundance of limpets and cover of macroalgae (mean ± SD, $n = 3$) as a consequence of human exclusion beginning in May 1978 from the intertidal at Mehiun, Chile (modified from Paine 1994; after Moreno *et al.* 1984; from Hawkins *et al.* 1999*a*).

Lasiak (1998) also demonstrated changes in community structure on shores of Southern Africa as a consequence of the establishment of marine reserves two decades previously. Here the effects of gathering were evident by comparing intertidal communities within the reserves with nearby exploited areas (see also Hockey & Bosman 1986). Multivariate analyses of the 248 macrofaunal species revealed patterns of increased biomass and/or greater abundance of both exploited and non-exploited species, some of which were more abundant in the reserve areas while others were more abundant in exploited areas (Fig. 4).

As a consequence of an increasing demand for food resources, use of non-traditional harvesting methods, improved transportation and storage, we anticipate that subsistence collection will become increasingly commercialized over the next few decades. In extreme cases, exploitation might follow trends observed for finfish, where fish that were once a staple diet in some subsistence economies are increasingly being harvested for export rather than local consumption.

*Recreation, research and education*

Recreational gatherers collect a wide variety of organisms, mainly invertebrates, for use as fishing bait, for their ornamental value or for food. Although the daily take may be small, the cumulative effects can be substantial (Underwood 1993*b*). Additionally, human trampling and disturbance associated with collection (Newton *et al.* 1993) and other forms of recreation, such as access to the sea for scuba-diving (Hawkins & Roberts 1992), with tourism and educational visits (Fletcher & Frid 1996; Bellan & Bellan-Santini 2001), can damage habitats.

Disposable income, leisure time and availability of personal transport have all increased dramatically over the last 50 years in the developed world. This has been associated

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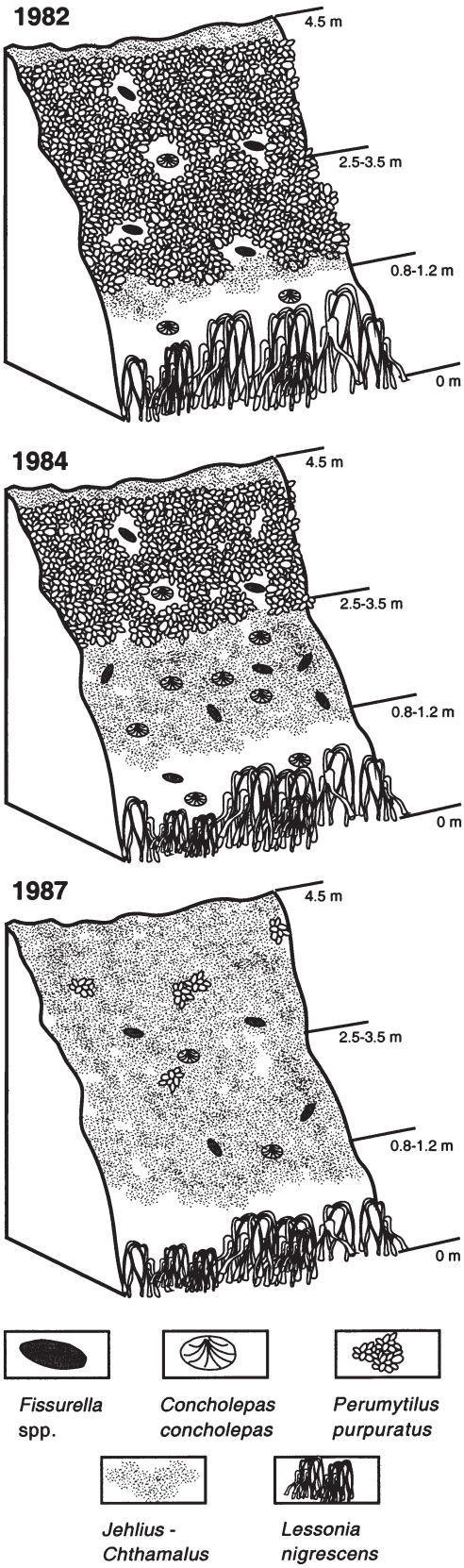



**Figure 3** Changes in community structure on an exposed rocky shore at Las Cruces, following human exclusion in 1982 (modified from Paine 1994, based on Duran & Castilla 1989, from review by Hawkins *et al*. 1999*a*; with permission).

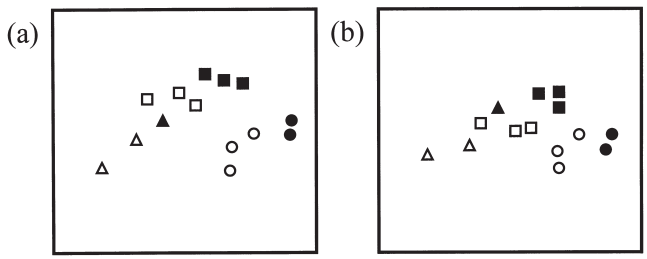



**Figure 4** Impacts of intertidal collection on (*a*) macrofaunal abundance and (*b*) biomass on rocky shores in South Africa: MDS (multi-dimensional scaling) ordinations based on Bray–Curtis indices of similarity derived from root-root transformed means; circles, triangles and squares represent study sites in the southern, central and northern region of Transkei, South Africa, respectively. Open and shaded symbols represent exploited and non-exploited sites, respectively (see Lasiak 1998 for details; with permission).

with a decline of subsistence gathering of food and collection of algae, but an increase in recreationally-related impacts (Fletcher & Frid 1996) including recreation in areas of the third world which are being developed for tourism (Hawkins & Roberts 1992). Paradoxically, these impacts can be particularly heavy in conservation areas where public access is encouraged to promote awareness of marine wildlife (Fletcher & Frid 1996). Increases in the amount of time available for leisure are likely to lead to an increase in this form of disturbance by 2025. Recently concern has also been expressed about the levels of disturbance associated with scientific research in some locations (Hawkins 1999). Clearly there are trade-offs. Despite some localized negative impacts of research and educational activities, wider implications will be beneficial in influencing perceptions and attitudes to coastal environments and providing information for management.

*Introduced species*

Accidental or deliberate introduction of species either as a consequence of transporting stocks for aquaculture, via release of ballast water from ships or from fouling on the underside of ships can lead dramatic effects on native species (see Raffaelli & Hawkins 1996; Reise *et al.* 1999 for review). Examples include introduction of the barnacle *Elminius modestus* from Australasia and the Japanese alga, *Sargassum muticum* to Europe (Carlton 1989; Critchley *et al.* 1990; Southward 1991; Carlton & Geller 1993). Experimental work in northern Spain has shown that *Sargassum* modifies native algal assemblages sometimes leading to a decline in abundance of leathery species such as *Bifurcaria bifurcata* (in two out of three experimental plots); although foliose algae (mainly Ulvaceae) and articulated calcareous algae were not affected (Fig. 5; Viejo 1997).

In some locations introductions have not had dramatic influences on rocky intertidal communities and have added to local diversity rather than displacing native species (Reise *et*

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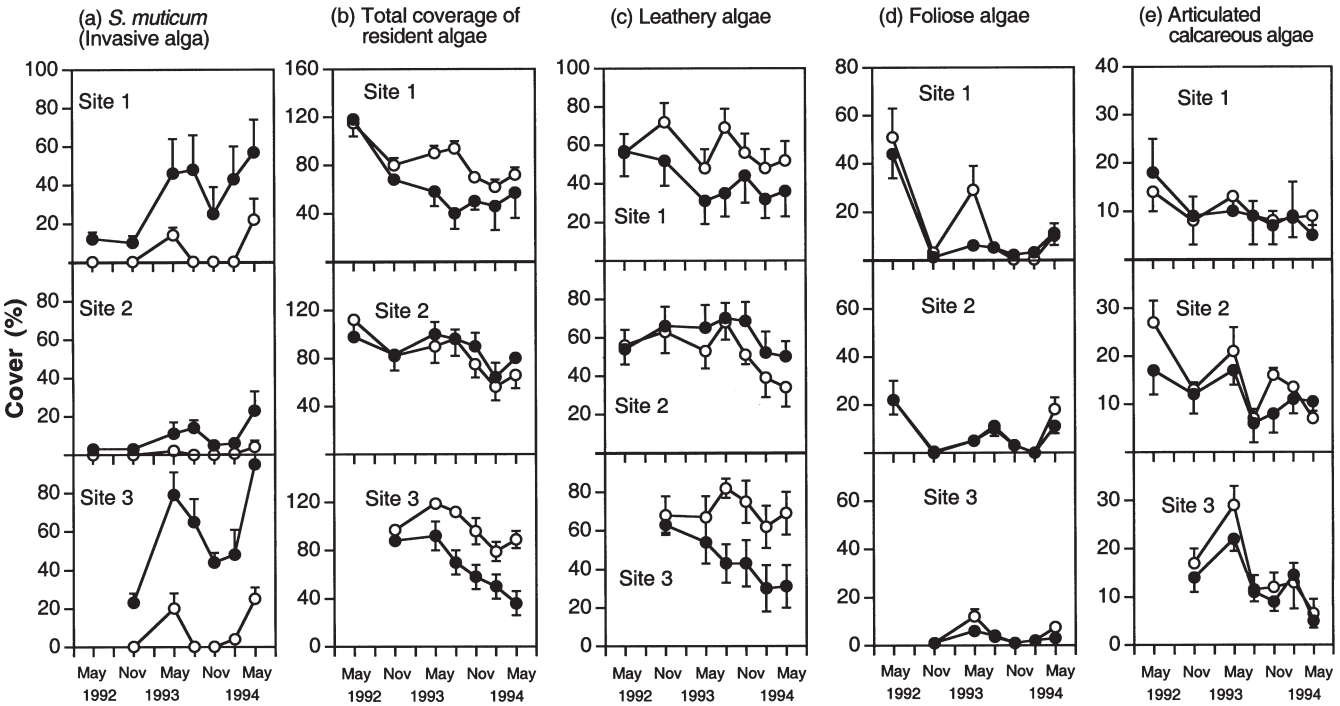



**Figure 5** Impacts of colonization by the invasive alga *Sargassum muticum* on resident macroalgal assemblages during a two-year experiment in tide pools at three sites in northern Spain. *S. muticum* was allowed to colonize and spread in some pools (●) and was periodically removed in the others (○). The effectiveness of these treatments on percentage cover of *S. muticum* is shown in (*a*). As a consequence of the removal, (*b*) the total cover of native macroalgal species (excluding encrusting algae and *Sargassum*) and (*c*) leathery algae, mainly *Bifurcaria bifurcarta*, became significantly more abundant than in pools where *Sargassum* was allowed to colonize, (at two of the three sites), while (*d*) foliose algae, mainly Ulvaeae, and (*e*) articulated algae were not affected. Data are mean ± standard error (Viejo 1997).

*al.* 1999). Elsewhere invasions have caused major and permanent changes to the abundance of native species. For example, the European crab *Carcinus maenas* has had a dramatic effect in California during the last ten years. Since 1989, when it was first recorded in California, direct effects of predation by *C. maenas* have caused five- to ten-fold reductions in the abundance of the native crab *Hemigrapsus oregonensis* together with significant reductions in the abundance of the native clams *Nutricola tantilla* and *N. confusa* (Grosholz *et al.* 2000). Conversely, indirect effects have lead to an increase in the abundance of two polychaete taxa (*Lumbrineris* sp. and *Exogene* sp.) and the tube dwelling crustacean *Leptochelia dubia* during the same period. In South Africa the Mediterranean mussel *Mytilus galloprovincialis* has largely displaced the native species *Aulacomya ater* since the 1970s leading to an increase in the biomass of mussels on the shore and a reduction in the space available for algal colonization and limpet foraging (Griffiths *et al.* 1992).

We predict that arrival of alien species is likely to increase over the next few decades, representing one of the most important threats to intertidal habitats. This is especially so for invasive pathogens, which may find new hosts that lack natural resistance (see Harvell *et al.* 1999), parasites (Sindermann 1992; Burreson *et al.* 2000), and high rank competitors or predators that could cause substantial changes to native communities. One of the principal concerns is that unlike pollution, gathering or harvesting, introductions are irreversible.

## Global change and large-scale phenomena

Global changes in the intensity of a range of climatic variables (temperature, isolation stress, ultraviolet light [UV], sea level and wave action) are anticipated by 2025 (IPCC [Intergovernmental Panel on Climate Change] 1996). These will no doubt lead to shifts in the geographic distribution of some intertidal organisms. However, most of these organisms have morphological or physiological adaptations to cope with changes in environmental stresses greater than those anticipated by 2025. Consequently, although there may be changes in species abundance at the fringes of their distribution, these are only likely to affect organisms at local to regional scales and will depend on the gradient concerned. For instance, shifts might be expected to occur along the vertical emersion gradient at a scale of metres, along horizontal gradients of wave exposure at a scale of 10s to 100s of metres and along geographic climatic gradients at a scale of 10s to 100s of kilometres. Species distributions are likely to have significant effects where they are associated with shifts in the relative proportions of functional groups or in the abundance of organisms that have a key role in structuring communities. Similarly, considerable shifts in species distributions would

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occur if small changes in climate lead to large-scale changes in ocean circulation.

*Warming*

Climate can directly influence the distribution of intertidal species. This operates through shifts in competitive abilities at the northern and southern distributional boundaries, and at the upper vertical distributional boundary (e.g. Denny & Paine 1998) where temperatures are either too low or too high for growth and reproduction. For example, in response to elevated temperature, species will become increasingly stressed at the equatorial margins of their distribution leading to local extinctions. At higher latitudes, if low temperatures are also a major factor limiting their distribution, the margins of distribution will expand polewards (see Clarke 1996 for review). Species with broad dispersal will be able to colonize polewards quite rapidly, while those with limited dispersal will face a bottleneck with their distribution being squeezed by increasing temperature from the equator and their restricted ability to disperse towards the poles.

Clarke (1996) identified four ways that organisms may respond to an environmental challenge: (1) they may move somewhere else, (2) they may stay, (3) they may adapt to the changes or (4) they may go extinct. Although historical examples of all of these responses can be demonstrated for climate change (e.g. range expansion and morphological evolution, see Hellberg *et al.* 2001), there is no real understanding of the balance between them. Given the gradual nature of changes in the biogeographic axis, the steepness of vertical gradients and the ability of shore organisms to tolerate environmental fluctuations, the likelihood that animals and algae will survive and eventually move seems high.

Different species will, however, move in distinct ways depending on their dispersal characteristics (Hiscock *et al.* 2001). The influence of climate on the distribution and abundance of invertebrates is also mediated through reproductive output (see Southward & Crisp 1954; Southward 1967; Kendall *et al.* 1985; Lewis 1996). For example, southern species of barnacles reaching their northern geographic limits in the British Isles have fewer broods than further south in Europe and the success of early broods released into the plankton is very poor (Burrows *et al.* 1992).

Because of the connectivity of rocky shore habitats, rocky shore organisms will probably respond to climate change by shifts in distribution and abundance along environmental gradients over biogeographic scales. Hence local extinctions will generally be matched by colonization of new areas. For example, abundances of boreal cold-temperate *Semibalanus balanoides* and subtropical *Chthamalus* spp. fluctuate markedly over time, with numbers being strongly positively correlated with sea surface temperature with a time lag of two years (Southward 1991; Hawkins *et al.* 2002*b*; Fig. 6). Similar fluctuations have been seen in Northern (*Patella vulgata*) and Southern (*P. depressa*) limpet species (Southward *et al.* 1995). Broadscale surveys have shown that abundance of the southern species, *P. depressa,* was much more common in the warmer 1950s, when Crisp and Southward (1958) undertook extensive semi-quantitative surveys, than in the early 1980s (Hawkins *et al.* 2002*b*) and numbers at many locations have now returned to levels observed in the 1950s (S.J. Hawkins, unpublished 1980–2002). Consequently, rocky-shore plants and animals may provide cheap indicators of more extensive changes offshore (Southward 1980, 1991; Southward *et al.* 1995).

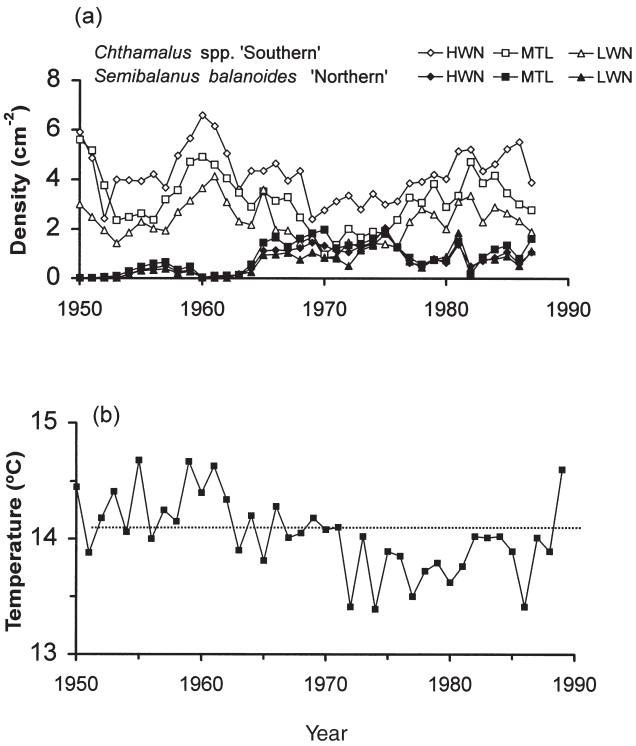



**Figure 6** (*a*) Long-term changes in the relative proportions of northern and southern species of barnacles on the south coast of Devon and Cornwall, UK. Data from three tidal levels are shown: high water neaps (HWN), mid-tide level (MTL) and low water neaps (LWN). See Southward (1991) for further details (from A. J. Southward and S.J. Hawkins, unpublished 1950–1987). (*b*) Annual mean seawater temperature in the Bay of Biscay. Average for the period is shown as a dotted line.

The effects of changes in temperature may be amplified or reduced by interactions between temperature and other physical factors. For example, based on thermal tolerances alone, the ranges of some tropical and warm temperate macroalgal species are expected to extend to higher latitudes as a consequence of increases in global temperature. Apart from temperature, however, the distribution of many algae is also regulated by day length (photoperiod). Hence expansions in algal distribution from lower latitudes may be limited by their inability to adapt to prevailing photoperiods rather than by temperature (Beardall *et al.* 1998).

Interactions with other organisms will also modify the direct effects of temperature further restricting our ability to predict the consequences of climatic changes. For example,

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small changes in temperature (about 2ºC air temperature) across the Cape Cod peninsula appear fundamentally to alter the influence of *Ascophyllum nodosum* canopy on survival of the barnacle *Semibalanus balanoides*. In the south, macroalgal canopy provided a refuge from thermal stress, enhancing barnacle survival (Fig. 7). Further north, where shading was less important, the algae provided refuge for a predatory whelk that fed on the barnacles and reduced their survival relative to areas higher on the shore above the *Ascophyllum* zone (Leonard 2000; Fig. 7).

Based on predictions of a 0.28–0.58 ºC rise in temperature by 2020 (IPCC 1996), we anticipate typical horizontal shifts in species distributions in the region of 10s to 100s of kilometres and small changes in vertical distribution (depending on the tidal range at a given location) by 2025. Assuming the current pattern of gradients in sea and air temperature remains, the speed of horizontal shifts in distribution will tend to be more rapid in regions where isotherms are widely separated. However, there will be exceptions and there is the potential for local extinctions and major shifts in community structure and ecosystem process in some regions.

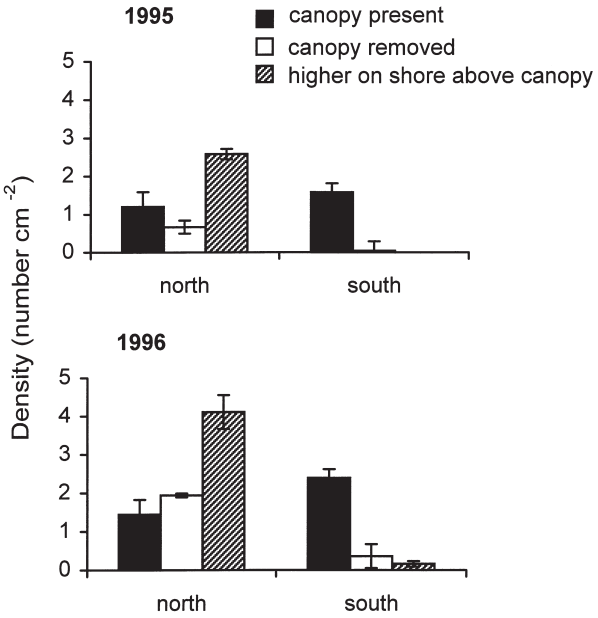



**Figure 7** Mediation of climate by biological interactions in Cape Cod peninsula, New England, USA: survival of barnacles that recruited on the shore during spring of 1995 and 1996 and were resurveyed in October of those years. Counts are from 25 cm × 25 cm quadrats located under macroalgal canopy ('canopy'), in areas cleared of canopy, or above the zone influenced by the canopy. Densities (mean ± SE) have been adjusted to take account of initial differences in recruitment between areas using analysis of covariance (from Leonard 2000; with permission).

*Ultraviolet radiation*

Ultraviolet radiation, principally UV-B, can have inhibitory effects on photosynthetic performance, growth, and nutrient uptake, and can cause DNA damage in algae (Beardall *et al.* 1998). It can also alter behaviour (e.g. covering response in sea urchins; Adams 2001), shift the sex ratios and reduce survival in invertebrates (Chalker-Scott 1995). Although UV-B radiation is maximal in the tropics, the greatest ecological effects are likely to occur at higher latitudes where organisms may lack adaptive mechanisms such as screening compounds, methods of repair, or behavioural strategies that help reduce the deleterious effects of UV-B (Beardall *et al.* 1998). To date the majority of work has focused on individual responses and more research is required to identify the potential community and ecosystem level effects (see El-Sayed *et al.* 1996 for review).

*Sea-level rise, storms and extreme weather events*

Changes in sea level are of considerable concern to human populations inhabiting low-lying coastal areas. The changes anticipated by 2025 are small (IPCC 1996; 'best estimate' for 2020 is a rise in sea level of 7.4cm). Direct consequences for rocky shore organisms are likely to be minimal compared to the effects of changes in climate or storminess and to natural fluctuations in tidal rhythms associated with short term (18.6 year) changes in the astronomical cycle (Denny & Paine 1998). An exception to this might occur in regions where a small change in tidal level leads to a substantial shift in the extent of horizontal versus vertical rocky shoreline with associated consequences for the area and aspect of intertidal substrata (A.J. Underwood, unpublished data 2000).

One of the predicted consequences of global change is a greater frequency of extreme events such as storms and increased rainfall in winter or hot spells in summer (IPCC 1996). An increase in wave action associated with storms will lead to an increase in the relative abundance of filter feeders and predators, which do well in these conditions, and a reduction in the abundance of grazers and macroalgae. These changes are likely to be associated with an increase in biomass and a reduction in species diversity (see Bustamante & Branch 1996; Ricciardi & Bourget 1999). Extreme thermal events are likely to result in kills at the upper limits of distribution of many intertidal species during both hot (e.g. Schonbeck & Norton 1978; Hawkins & Hartnoll 1985) and cold weather (Todd & Lewis 1984). The abundance of intertidal epilithic microalgae is also strongly influenced by weather conditions, declining during summer. Hence climatic extremes will also affect primary productivity in intertidal communities leading to alternating conditions of either feast or famine for species such as molluscs, which graze on these microbial films (reviewed by Thompson *et al.* 2000*b*). These features would all lead to increased temporal variability in the structure of rocky shore communities with extreme conditions leading to periodic mortality of some species and an associated increase in the frequency with which space is made available for recolonization. Indirect effects of sea-level rise and increases in storminess are anticipated since a greater proportion of the coastline will be 'hardened' by construction of sea defences, increasing the total area of hard intertidal habitat (see below).

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*El Niño Southern Oscillations*

ENSOs and the NAO are natural events in which the 'usual' patterns of atmospheric and oceanic circulation within entire ocean basins change (Jaksic 1998). There is growing evidence that increased frequency of ENSOs may be linked to climate change driven by increased anthropogenic carbon dioxide in the atmosphere (see discussion by Urban *et al.* 2000). On rocky shores, the most significant impact of El Niño is to reduce the frequency and extent of upwelling of cold, nutrient-rich water along the west coast of the Americas. Relatively warm, nutrient-poor surface waters replace these usually productive coastal waters. ENSO events also change currents and storm regimes (Allison *et al.* 1998) and have been associated with changes in species distributions, prevalence of marine diseases and the primary production of marine systems (see Fields *et al.* 1993; Harvell *et al.* 1999). Similar phenomena occur in other upwelling areas.

The influences of the ENSO on pelagic fisheries and subtidal kelp forests have been widely publicized (e.g. Dayton *et al.* 1992, 1998) and effects on intertidal communities are equally apparent with both positive and negative effects depending on the species concerned. For example, in Chile, the 1982–1983 ENSO was thought to have caused massive die-offs of brown algae (Soto 1985) and of littoral invertebrates (Tomicic 1985). Settlement of a keystone predator (*Concholepas concholepas*) was low in years associated with either El Niño or La Niña (negatively related to the Southern Oscillation Index; Moreno *et al.* 1998), with potential consequences for both intertidal communities and food gathering (Castilla & Camus 1992). Similarly in California recruitment of intertidal barnacles (Connolly & Roughgarden 1999) and tide pool fish (Davis 2000) were affected during the 1997 ENSO.

Geological evidence suggests that ENSO events have been a persistent feature of late Quaternary climate variation and have been occurring since at least the Pleistocene (Keefer *et al.* 1998; Bull *et al.* 2000). There has been an apparent trend towards more severe El Niños at the end of the 20th century (Jaksic 1998; Stone *et al.* 1999). If this forms part of a longer-term trend, impacts on affected rocky shores are likely to become more frequent and intense over the next few decades.

### Modification of coastal processes

*Sea defences*

Many of the world's sedimentary coastlines adjoin low-lying land or are threatened by flooding or coastal erosion. The severity of these problems is likely to increase during the next few decades because of sea-level rise and the increasing frequency of storms (Rodwell *et al.* 1999; Grevemeyer *et al.* 2000). Consequently, the number of coastal defence structures such as breakwaters is likely to increase considerably over the next twenty-five years, providing stepping-stones between populations presently isolated by distance. This can have consequences for population genetics (see Kimura & Weiss 1964; Keenan 1994) and may lead to range extensions of species with restricted dispersal, for example, littorinids extending their range along the Belgian coastline, which lacks natural rocky shores, via breakwaters (Johannesson & Warmoes 1990). Most artificial rocky shores support communities similar to natural ones (e.g. Southward & Orton 1954; Hawkins *et al.* 1983). Thus, from a rocky shore perspective, increasing hard substrates can be viewed as increase in the extent of habitat available for rocky shore organisms.

*Sedimentation*

The amount of suspended sediment in the water column is expected to increase by 2025 as a consequence of increased coastal erosion, riverine inputs and artificial replenishment of coastlines. When deposited, this material may smother rocky habitats, particularly in sheltered locations. This will lead to an increase in the abundance of sand-dwelling organisms such as polychaetes and sand-tolerant species such as the anemone, *Anthopleura elegantissima,* and the red alga *Chondrus crispus* (Daly & Mathieson 1977; Taylor & Littler 1982). Organisms with opportunistic life histories, such as ephemeral and some turf-forming algae, will also be favoured on rocks that are subject to intermittent inundation (Airoldi 1998). Hence diversity at the 'shore' scale of resolution will tend to increase as a consequence of an increase in the variety and fragmentation of habitats (Littler *et al.* 1983; McQuaid & Dower 1990).

## HABITAT FRAGMENTATION

Unlike many other habitats worldwide, we anticipate that rocky shores will, at a broad scale of resolution, become less fragmented by 2025 as a consequence of increases in the number of coastal defences. For example, in the Netherlands, the Adriatic and Japan (e.g. Koike 1993) virtually all of what were originally sedimentary coastlines have now been 'hardened' by sea defences. Similar changes will occur in the future on other low lying land around the world, with associated increases in the extent and connectedness of rocky shore habitats as more soft shores are 'hardened' (e.g. Johannesson & Warmoes 1990).

## ECOSYSTEM PROCESSES

Rocky shores have a high degree of connectivity with other coastal ecosystems. Hence there is the potential for shifts in community structure to have an influence on ecosystem level processes such as primary productivity, detrital supply and water quality.

The power of the ecosystem services provided by filter feeders such as mussels has been amply demonstrated on the artificial substrata of disused dock walls (Allen & Hawkins 1993; Hawkins *et al.* 1999 *a*, *b*) and in semi-enclosed ecosystems such as the Rade de Brest (Hily 1991). If filter feeders such as mussels and oysters are removed from sheltered and semi-enclosed areas, the potential control of phytoplankton

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blooms will be reduced. This will be exacerbated in enclosed eutrophic waters and cumulative effects could result in toxic algal blooms killing shellfish and further reducing the capacity for biofiltration.

So far we have considered the effects of anthropogenic disturbances and global change largely in isolation of each other. However, this approach represents an oversimplification since several changes are likely to occur in parallel amplifying or reducing the effects of any given variable in isolation (see Dayton *et al.* 1998; Paine *et al.* 1998). For example, current latitudinal patterns of algal distribution (Hawkins *et al.* 1992) indicate that an increase in global temperature (IPCC 1996) might lead to a shift in algal abundance, with canopy-forming brown macroalgae being replaced by less productive turf-forming red algal species. Similarly increased storminess (IPCC 1996) may favour communities dominated by filter feeders, such as barnacles and mussels, rather than grazers and algae (e.g. Bustamante & Branch 1996). Hence warming and increases in storminess may both lead to a reduction in primary productivity.

Increased siltation will also favour turf-forming algae (Airoldi 1998). As described earlier, impacts such as oil spills, eutrophication and exploitation of major space occupiers and grazers lead to increases in the abundance of ephemeral algae and possibly higher primary productivity. Such changes in macroalgal abundance will have implications for mobile species, such as juvenile fish, which use macroalgae as a nursery ground and refuge from predation (e.g. Rangeley & Kramer 1995). Detrital pools derived from large stands of fucoids or kelp would also diminish. Similarly changes in the abundance of filter feeders will affect their mobile predators, such as crabs and wrasse at high tide and birds at low tide (e.g. Coleman *et al.* 1999; Thompson *et al.* 2000*a*) altering flows of energy through ecosystems. There may also be knock on effects on local biodiversity as a consequence of changes in the type and extent of biological habitat provision (Seed 1996; Thompson *et al.* 1996).

## VULNERABILITY AND CONSERVATION

The accessibility of rocky shores means they are vulnerable to a variety of impacts due to the activities of people (collecting, recreation). Their position at the coastal interface means that contaminants can come from the land (e.g. effluents, silt, urban run-off) and the sea (e.g. oil spills, toxic leachates, fish farm effluents). Alternating conditions of submersion and emersion with the tidal cycle also increase the range and provenance of impacts that may affect intertidal communities. Pollutants including excessive nutrient inputs probably have their greatest influence when the tide is in. Collection of organisms and recreation principally act during low tide. Climate change and other large-scale events such as ENSO will probably have effects on intertidal organisms when the tide is out (e.g. extremes of temperature or persistent cloud cover) and also during submersion (changes in mean seawater temperature).

Some impacts are irreversible. An extreme example is 'slagcrete' deposited on the Cumbrian coast of England during the 18th and 19th century, when waste from iron and steel furnaces was poured onto the shore, where it solidified into a conglomerate including lumps of iron, slag, pick handles and even old clogs (Perkins 1977)! Another example is lifting of shores after a nuclear power station explosion (Lebednik 1973). While at a greater spatial scale some of the most concerning irreversible impacts occur as a consequence of the introduction of non-native species (see earlier). These examples aside, rocky shores do not generally suffer persistent residual damage after an impact has ceased. Pollutants rapidly disperse and rocky shores provide few sinks for them, other than the biota themselves and possibly sediment trapped by algal turfs or animal matrices. Most shore communities return to some approximation of their original state(s) within three to five years or so after minor impacts. This process can be more prolonged after severe impacts; for example, shores badly affected by dispersants following the *Torrey Canyon* spill took 10–15 years to recover.

Recovery after physical impacts, such as collection or trampling, generally also occurs rapidly, once the disturbance has stopped. This depends on the species involved. For example, some species of algae and barnacles recolonized plots one year after experimental trampling ceased (Povey & Keough 1991; Schiel & Taylor 1999), whereas mussel populations can take more than ten years to recover (Dye 1992; Brosnan & Crumrine 1994). In slower-growing species such as *Ascophyllum nodosum* and *Hormosira banksii*, recovery can take a very long time following removal or disturbance (Jenkins *et al.* 1999; Schiel & Taylor 1999).

Rapid recovery is aided by recruitment via larvae or algal propagules from unaffected populations (Hawkins *et al.* 1999*a*). Whilst this is true for most species, slower recovery has been noted in animals with direct development, such as high-shore littorinids following the Gulf oil spill (Watt *et al.* 1993) and dogwhelks following TBT pollution (Gibbs *et al.* 1991). For these organisms input from remote sources is much slower, and a case could be made for artificially transplanting individuals to speed up recovery (see Hawkins *et al.* 1999*a* and Howell *et al.* 1999 for fisheries examples). An exception to the general trend of reasonably rapid recovery might occur where a perturbation causes a shift in community structure to an alternative stable state (see Paine *et al.* 1998). Here simply removing the stress may not be sufficient for a community to return, even approximately, to its original composition, although a natural alternative may replace it.

Of all the aquatic systems, rocky shores are likely to be more vulnerable than some of the more extensive offshore and deep-sea habitats (P.A. Tyler, unpublished 2002; Verity *et al.* 2002). They will also be more vulnerable than subtidal (see Steneck *et al.* 2002) and soft bottom (see Hall 2002) seashore habitats. The openness of many rocky shores to recruitment from unimpacted sources reduces their vulnerability compared to more enclosed freshwater and estuarine

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habitats (although this is not the case for shores in semi-enclosed bays with low recruitment). However, rocky shores will be less at risk than habitats with strong biogenic structures such as coral reefs (see McClanahan 2002), saltmarshes (see Adam 2002) and seagrass beds (see Duarte 2002). How rocky shores compare with intertidal sandy beaches (see Brown & McLachlan 2002) is more difficult to judge. Sandy shores are intrinsically dynamic and subjected to disturbance of the sediment by wave action. The organisms living there are well adapted to escaping stresses by burrowing and compared to organisms on rocky shores, most of the species are reasonably mobile and readily recolonize patches after small-scale disturbances. Pollutants can, however, reside in sediments for long periods. Thus rocky shores may be more vulnerable than sandy beaches, but perhaps less vulnerable than mudflats.

## CHANGES IN MANAGEMENT

Infrastructure for management of the marine environment has traditionally lagged behind that for terrestrial ecosystems (e.g. Coleking 1995; Sanderson 1996; Craig *et al.* 2000). The trend for increased public concern about conservation is reflected in increased designation of marine protected areas (Allison *et al.* 1998). If this trend continues, and reserves are chosen using appropriate criteria (Emanuel *et al.* 1992) and restrictions are adequately enforced (see Murray *et al.* 1999), then this may help to conserve rocky shores and decrease degradation (Simberloff 2000). There is also a growing awareness of the need to increase ownership of conservation areas by involving all interested parties from the outset in the development of new management schemes (Baxter 2001). Nevertheless, marine reserves alone do not provide adequate protection from threats such as chemical contamination and invasive species (Allison *et al.* 1998; Simberloff 2000). Such protection is most likely to stem from improvements to the regulatory framework, including legislation, management bodies and enforcement. Clearly, management can only be effective if underpinned by sound understanding of processes and mechanisms affecting marine systems. Such understanding must flow from careful scientific research, rather than well-publicized environmental speculation (Gray 1999). There is an accumulating body of information underpinning marine environmental decision making, some of which is now available via the internet (e.g. *MarLin,* http://www.marlin.ac.uk/ and see Barthel 1995).

Direct contributions of scientists to management include development of improved biomonitoring methods, which can be a considerably more cost-effective and sensitive approach than chemical screening (e.g. Gray 1999; Wells 1999; Aguilera *et al.* 2001). Indicators of ecological status also have the advantage of summarizing complex information for communication to managers, stakeholders and policymakers (Done & Reichelt 1998). Great care must be taken, however, that indices are truly indicative of relevant impacts (Wells 1999; Underwood 2000*b*). To avoid wasting resources, monitoring of any sort must only be embarked upon with clearly defined aims and outputs (Underwood 1991; Risk 1999). Environmental decision-making must also recognize the inherent variability of rocky shores and incorporate analyses of uncertainty into management decisions (see Gray 1999; Ralls & Taylor 2000).

## CONCLUSIONS

### Major problems: present and future

Impacts on rocky shores will range from sublethal effects on individuals through populations to community level responses. Many of these impacts will be localized and stem from point pollution sources and local human usage. Collection of living resources can impact whole coastlines; commercial and recreational usage (including food collection) may also have widespread effects. Creation of new hard substrata as part of sea defence schemes will also occur on a large-scale worldwide. These changes will have direct and indirect effects at all scales of ecological organization: individuals, populations, communities and ecosystems leading to changes in primary and secondary productivity with consequences for both commercially exploited and unexploited species, together with ecosystem goods and services.

Global climate change will have far-reaching effects, but will primarily act to shift species along environmental gradients: up or down the shore with changes in desiccation stress, into shelter with greater wave action and towards the poles on the biogeographic axis. It may also lead to the extinction of some currently isolated relict populations, for example boreal estuarine fauna and flora in southern European estuaries or cold-water pockets in upwelling zones. Some boreal species may have nowhere to go.

One of the greatest potential risks is from introduction of alien species, which could lead to permanent changes in community structure. This is especially so for invasive pathogens which may find hosts lacking natural resistance (see Harvell *et al.* 1999) and high ranking competitors or predators such as *Mytilus galloprovincialis* in South Africa (Griffiths *et al.* 1992) and *Carcinus maenas* in California (Grosholz *et al.* 2000).

### Surprises in store?

In trying to anticipate the future it is interesting to view the past. Many problems already existed in the 1960s (Table 1), but perhaps were not appreciated at the time. Some, such as oil spills, sprang into public consciousness after major events such as the *Torrey Canyon* wreck in the 1960s. Scientific detective work in the 1980s unravelled the effects of TBT on gastropods and oysters in the face of scepticism by industry (Ludgate 1987). Declining yields and concerns about the need for and scope of marine protected areas prompted work

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on intertidal resources in the 1970s and 1980s, which showed the extent and scale of human predation on rocky shores in Southern Africa, Chile (e.g. Castilla & Duran 1985) and New Zealand (Towns & Ballantine 1993)

Looking forward, what will be the surprises? No doubt some new wonder pesticide (as TBT was hailed in the 1970s) will be seen to have a host of unforeseen side effects. An area of current concern is the side effects of various preparations used to treat ectoparasites in aquaculture (e.g. Collier & Pinn 1998). Given the pace of biotechnology, genetically modified organisms could be developed for algal and animal mariculture. Fast growing strains of seaweeds, mussels, oysters, crabs and shrimps could all be developed and escape from culture. These would influence biodiversity at the within-species level in terms of genetic variation but could also influence population and community processes (for fish and shellfish examples see Kapuscinski & Hallerman 1991; Hallerman & Kapuscinski 1995).

An area where coastal development may expand rapidly is the renewable energy sector spanning from offshore wind turbines, through a resurgence of interest in tidal barrages, to wave energy machines. The effects of tidal barrages are well known from experience of the La Rance scheme in France: tidal amplitude was reduced, hydrographic exchange altered and the distribution of sheltered rocky shore organisms changed (see Little & Mettam 1994; Retiere 1994). Offshore wind farms and wave devices will inevitably lead to more artificial hard structures and in the latter case be certain to reduce wave action to the landward side. There will also be the risk of occasional wreckage of structures on the shore causing localized disturbance.

The traditional historical human concerns of war, pestilence and famine will no doubt feature over the next few decades, as in past millennia. The consequences of even quite small regional wars have been illustrated in the Arabian Gulf where oil pollution destroyed many marine communities (e.g. Jones *et al.* 1994). Such conflicts can break out anywhere. Even small-scale insurrections lead to breakdown of law and order and an early casualty is enforcement of conservation legislation.

A theme throughout this review is the near certainty that the majority of the effects described are unlikely to act in isolation (see sections on climate and ecosystem processes). Our ability to predict the consequences of changes in a single impact vary from reasonable certainty in the case of some pollutants on single species to considerable uncertainty, for example in response to changes in global climate or introduction of non-native species (Table 1). Unfortunately, our ability to forecast the combined interactive effects of several environmental factors is at best fairly modest. Hence, we can anticipate that there will be unpleasant surprises ahead, but their nature remains largely unpredictable. The greatest ecological surprises are likely to occur where environmental change induces shifts between alternate stable states (Barkai & McQuaid 1988; Paine *et al.* 1998; but see also Dayton *et al.* 1998 for example of stability in algal communities despite loss of considerable faunal biomass), or where an organism is particularly susceptible to a pollutant (e.g. dogwhelks and TBT), or where an exotic species has a much more prominent role in an invaded community that at home (e.g. *Sargassum muticum*).

## Principal gaps in knowledge

*Basic science*

Small-scale studies focused on individual species or particular communities have greatly enhanced understanding of community regulation. Larger scale approaches to the ecology of rocky shores have started in recent years (e.g. Connolly & Roughgarden 1998; Jenkins *et al.* 2001), but this approach needs encouragement. There is the need to cross-calibrate bioindicators of ecosystem health at different levels of organization from molecular markers, through cells and individuals to those at the population and community level (Hawkins *et al.* 1994, 2002*a*). Further work is also needed on measuring recovery from impacts. Here we highlight some of the gaps we perceive, both in terms of pure scientific understanding, and also applied approaches.

At the individual organism level some species will exhibit marked between-population variation in their physiological tolerances, others will not. Little is known about this phenotypic plasticity and response rate of such plasticity to stress (but see Pakker & Breeman 1996; Gaston & Spicer 1998). There have been few field-based studies of genetic response in marine organisms following pollution events (but see, Hamond & Patarello 1994).

Stepping up to population-level processes, insufficient is known about the sources of recruits, dispersal and the respective roles of pre- and post-settlement processes. Such knowledge is essential to enable prediction about colonization of artificial substrates, recolonization of perturbed areas and to understand the rates of range extension or retraction in response to global change. Species will, as a rule, differ in their response rate; for example a lag of two years occurs before responses to temperature are evident as changes in the abundance of barnacles on the shore (Southward 1991); similar data are needed for other species.

At the assemblage or community level, there has recently been an explicit appreciation of both indirect effects (Wootton 1994; Menge 1995) and weak interactions (Berlow 1999) in the structure and dynamics of rocky shore communities, but much remains to be done on interactions between various physical and biological factors. At the habitat level, research has focused on freely draining open rock. Most ecologists interested in using rocky shores as a tractable system for ecological study tend to select areas of relatively horizontal rock. As a consequence, surprisingly little is known about more diverse and dynamic habitats, such as rock pools (but see Benedetti-Cecchi & Cinelli 1995; Underwood & Skilleter 1996), boulders, crevices, areas with very rough surfaces or areas with episodic sand cover or scour (but see Littler *et al.* 1983; McQuaid & Dower 1990).

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Scaling up to the ecosystem level for whole coastlines, there are several large gaps in knowledge. Ecologists need to become more aware of the geomorphological literature on erosional processes (but see Schoch & Dethier 1996), especially to investigate how projected increases in wave action and sea-level rise will impact coastlines. Anticipated changes over the next few decades need to be put into the context of previous periods of rapid change. In Europe, the English Channel, North Sea and Irish Sea only came into existence in the last 5000–7000 years or so. At that time, some advancing southern species (*Patella depressa, Balanus perforatus*) did not reach Ireland (see Southward *et al.* 1995 for review), although it is likely that they could live there today. On longer timescales, beyond the 25 years of this review, sea-level rise and changes in water currents would be expected to have major influences on the connectivity of some shores. There needs to be greater understanding of these processes in terms of population genetics and demography to make adequate predictions at biogeographic scales of resolution.

Rocky shores have tended to be studied in isolation. There is a need to put them into a broader context. The key physical process that needs to be explored is sediment transport, especially as increased scour and abrasion can be expected on urban and linearized coastlines. We still know very little about the import, export and *in situ* production of living material and nutrients on rocky shores. Work in South Africa (Field & Griffiths 1991; Bustamante *et al.* 1995*a*) has given a tantalising glimpse of some of these processes, but major gaps include the consumption of plankton by filter feeders, *in situ* production by microbial films and the fate of detritus. The growing realization that bottom-up forcing by oceanographic processes is important (Bustamante *et al.* 1995*b*; Menge *et al.* 1997; Menge 2000) is justification in itself for more work of this kind. It needs to be scaled up to include the whole coastline, including depositing shores that are the sinks for much material. We also know surprisingly little about linkages with terrestrial (detritus, vertebrate consumers, especially birds; Bosman & Hockey 1986; Coleman *et al.* 1999) and nearshore or offshore environments (large mobile predators including, crabs, fish, cephalopods; Robles *et al.* 1990).

### *Applying knowledge and research to measuring and predicting change*

A variety of approaches have been used to predict the consequences of environmental change (see Underwood 1999). These include predictions based on comparisons between periods (using both recent and palaeo-data) or locations with differing conditions, on the physiological tolerance of individuals in relation to their distribution (climate envelope), on experiments on the shore or in mesocosms, and use of macroecological approaches.

Each of these approaches has its merits. On a broad temporal scale, using palaeo-data on shifts in abundance, in parallel with independent proxies of changes in the present environment, may provide insight into rates and the extent of biological responses to environmental change. However, it is difficult to obtain predictions on a time scale of decades that would be relevant to planners and legislators. Baseline qualitative (Stephenson & Stephenson 1972; Lewis 1964) and semi-quantitative (Crisp & Southward 1958; Crisp & Fischer-Piette 1959) data are available from the 1930s, 1940s and 1950s in some locations. Useful predictive information could be gained by resurveying these sites to examine patterns of variability in relation to changes in environmental conditions.

In practice it may be difficult to establish causality in resurveys because several environmental variables are likely to have changed in parallel. Hence care must be taken in interpreting any trends observed. For example, see criticism by Denny and Paine (1998) and Underwood (1999) of studies using data collected at Pacific Grove, California, USA, in the 1930s and the 1990s to infer climate-related changes in species composition (Barry *et al.* 1995; Sagarin *et al.* 1999). Greater control over the environmental variables under investigation might be achieved by comparing systems that experience environmental change over much smaller temporal and spatial scales, for example, comparisons between locations (e.g. Cape Cod, USA; Leonard 2000) or between recent periods of differing environmental conditions such as ENSO and non-ENSO years (e.g. Jaksic 1998). Mesocosms and field experiments offer more controlled approaches, but the outcomes of these experiments are restricted to the species or assemblages examined, and it may be difficult to translate outcomes to natural communities.

One area where there has been considerable progress in recent years is the valuable work by Underwood and co-workers in developing survey designs to tease out human impacts from natural temporal and spatial heterogeneity, epitomized by the before–after control–impact, Beyond BACI, approach (see Underwood 1992, 2000*a*). Advanced multivariate methods are under development (Anderson 2001) that will enable statistically more rigorous detection of community level impacts and their interactive effects. These tools can now be deployed for formal testing of management regimes such as rotational closure and marine protected areas (MPAs) to establish their most appropriate size, frequency and interconnectivity. As we scale up to ecosystem scales of resolution it becomes increasingly difficult, however, to obtain sufficient replication for these of approaches; there may only be one upwelling region along a particular coast. The value of basic monitoring programmes should not be underestimated. Data from earlier monitoring work is now proving invaluable as a baseline against which to identify the possible effects of global change on intertidal communities (e.g. Southward *et al.* 1995).

Macroecological comparisons are rapidly evolving as a method to test ecologically relevant hypotheses about broad-scale environmental change (Gaston & Blackburn 2000). Meta-analysis enables broad-scale comparisons of species interactions, or changes in the relative proportions of key species groupings such as grazers and algae. Less common,

https://doi.org/10.1017/S0376892902000115 Published online by Cambridge University Press

but also very informative, are experimental manipulations of key functional groups on broad geographic scales (e.g. Steneck & Dethier 1994; Connolly & Roughgarden 1998; Jenkins *et al.* 2001).

An essential feature of all of these approaches is to identify the most relevant variables to examine. What are the key dependent variables on which ecologists should focus: changes in abundance and distribution patterns, biodiversity, or ecosystem processes such as productivity? What are the most appropriate independent variables to consider in relation to these (see comments in Peterson *et al.* 2000)? Extremes of environmental stressors are probably most appropriate where mortality of individuals is concerned (Gaines & Denny 1993), but mean values may be more appropriate when considering physiological processes such as growth and reproduction.

In conclusion, it appears that despite the volume of research that has been done on rocky shores, it is still difficult to make robust predictions for the future. This deficit can only be addressed by appropriate, statistically rigorous strategic research, targeted at some of the gaps in knowledge identified here. Simulation models of rocky shore communities can be built on the basis of qualitative rules derived from observation (e.g. Burrows & Hawkins 1998) or individual based approaches (e.g. Johnson *et al.* 1998). Such models could be used in a predictive manner to explore future scenarios such as global changes in temperature. Clearly there is also a need for long-term research programmes (monitoring) to inform and complement experimental approaches. If sufficiently long data sets exist, past responses to changes in variables such as temperature, both falls and rises, can be used to enable forecast. Long-term studies can now be designed with *a priori* effect sizes in mind and in such a way as to disentangle local and regional scales of variation. Adequate stratification should ensure that comparisons are made of like with like. We advocate regular monitoring of intertidal communities at vulnerable locations such as oil terminals and major conurbations, together with appropriate reference or control locations, which may include marine protected areas. For global change we advocate monitoring in areas with known biogeographic boundaries as well as areas influenced by upwelling. Areas where there are existing data sets should be regarded as priorities so that the value of archived data can be maximized. In parallel with monitoring, experiments can be used to tease out causal relationships. These can then be fed into models that can be tested and validated using data generated by long-term observations. Hopefully in 25 years time we will be better equipped to make predictions and forecasts of the next 25 years than we are now.

## ACKNOWLEDGEMENTS

We would like to thank Soulein King, Zoe Billinghurst, Susan Kimmance and Stuart Jenkins for their help preparing this manuscript. SJH and RCT would also like to thank the MarClim project supported by The Crown Estate, World Wildlife Fund for Nature, Countryside Council for Wales, Scottish Natural Heritage, The UK Department for the Environment, Food and Rural Affairs, State of Jersey, Joint Nature Conservation Council, English Nature, Environment Agency and Scottish Executive. SJH was also supported by various NERC grants and TPC by an NERC fellowship. We would also like to thank George Branch, Juan Carlos Castilla, Tony Underwood and an anonymous referee for the constructive comments they offered on an earlier version of this manuscript.

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