



Complex interactions in a rapidly changing world: responses of rocky shore communities to recent climate change

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ABSTRACT: Warming of the planet has accelerated in recent years and is predicted to continue over the next 50 to 100 yr. Evidence of responses to present warming in marine ecosystems include shifts in the geographic range of species as well as in the composition of pelagic and demersal fish, benthic and intertidal assemblages. Here we provide a review of the changes in geographic distributions and population abundance of species detected on rocky shores of the NE Atlantic over the last 60 yr. This period encompassed the warm 1950s, a colder period between 1963 and the late 1980s and the recent period of accelerating warming to levels above those of the 1950s. The likely consequences of these responses are then explored. To do this, a summary of the dynamic balance between grazers, macroalgae and barnacles in structuring mid-shore communities is given before outlining experimental work on interactions between key components of rocky shore communities. Modelling and quantitative forecasting were used to predict changes in community composition and dynamics in a warmer world and their consequences for ecosystem functioning discussed. We then identify areas that need further work before making a case for the use of rocky shore species not just as inexpensive indicators of change offshore, but as tractable models to explore the direct and indirect effects of climate change in marine and coastal ecosystems. We also provide a societal perspective emphasising the value of long-term studies in informing adaptation to climate change.

KEY WORDS: Climate change · Rocky shores · Time series · Grazer-algae interactions · Ecological forecasting · Adaptational policy · Europe

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1. INTRODUCTION

Warming of the planet has accelerated in the last few decades (IPCC 2007). Some of the most rapid changes are occurring in the NE Atlantic (IPCC 2007), where increases of up to 1°C have been recorded in areas such as the Western English Channel (Hawkins et al. 2003). Marine ecosystems have responded to this warming with changes in abundance and shifts in geographic ranges of plankton (Beaugrand & Reid 2003, Beau-

grand & Ibanez 2004, Hays et al. 2005), fish (Brander et al. 2003, Beare et al. 2004, Genner et al. 2004), and offshore benthic organisms (Hiscock et al. 2004). Some of the most marked and best-documented changes have been seen on rocky shores in Europe (Herbert et al. 2003, Mieszkowska et al. 2005, Simkanin et al. 2005, Lima et al. 2006, Mieszkowska et al. 2006, Herbert et al. 2007, Lima et al. 2007a), the United States (Barry et al. 1995, Harris et al. 1998, Sagarin et al. 1999, Zacherl et al. 2003, Harley et al. 2006) and South America (Ri-

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vadeneira & Fernandez 2005). In general, coldwater adapted species are decreasing in abundance and retreating polewards while warm water species are increasing in abundance and advancing.

Phenological changes have also been recorded in the NE Atlantic in relation to past climatic fluctuations (Sims et al. 2001, Sims et al. 2004) and phase shifts have been shown as a result of recent change (Edwards & Richardson 2004). These phase shifts may have major consequences throughout food webs including influencing the recruitment of commercially important species (Beau-grand et al. 2003, Edwards & Richardson 2004).

Long-term data sets are particularly valuable in putting recent changes into context. Current abundances and biogeographic distributions of species can be compared to those of previous warm periods such as the end of the 19th century and the middle of the 20th century (Fig. 1). Some of the most comprehensive data sets in terms of species recorded and temporal extent, albeit interrupted, have been collected in the Western English Channel (see Southward 1980, Southward et al. 1995, Hawkins et al. 2003, Southward et al. 2005) where links between climate and ecosystem fluctuation have long been recognised (Southward 1963, Russell et al. 1971, Russell 1973). Charting changes in species abundances, range and assemblage composition is a first step in understanding the influences of climate on community structuring and dynamics and the consequences for ecosystem functioning. While many changes in spatial and temporal patterns have been described, much less work has been done on the consequences for community and ecosystem processes, partly because of the experimental intractability of open offshore ecosystems. Much, however, can be learned from rocky shores, drawing on both the rich heritage of field-based experimentation (Connell

1961a,b, Paine 1966, 1979, Raffaelli & Hawkins 1999, Bertness 2007) as well as extensive long-term data sets and broadscale baselines, particularly in Europe (Fischer-Piette 1936, 1955, Crisp & Southward, 1958). Rocky shores are relatively simple ecosystems; the ecologies of many species are well known; this makes them an excellent model system for understanding the consequences of climate change for community and ecosystem processes.

In this review, stemming from an invitation to give a keynote presentation at the 2007 European Marine Biology Symposium in Kiel, we focus on European rocky shores where extensive long-term datasets spanning cooler and warmer time periods exist. The NE Atlantic region is also experiencing rapid temperature increases above global averages, in response to the recent period of climatic warming. In addition, there is little exploitation (artisanal or commercial) of rocky shore species, particularly in northern Europe, which could make detection of climate-related assemblage responses difficult. We give a brief overview of changes detected over the last 60 yr encompassing the warm 1950s, the colder period between 1963 and the late 1980s and the recent period of accelerating temperature increase (these changes are discussed in more detail in Southward et al. 2005). The likely consequences of accelerating climate warming are then explored at community and ecosystem levels. A summary of changes in mid-shore assemblage composition with latitude is given before outlining experimental work on interactions between key components of the community which are known to be responding to climate change. Modelling and quantitative forecasting are then used to predict community composition and dynamics in a warmer world and what the consequences will be for community structure and ecosystem functioning. A case is made for the use of rocky shore species as inexpensive indicators of change offshore. Rocky shores also provide a tractable model ecosystem in which to explore the likely direct and indirect effects of climate change on marine assemblages. We conclude by providing a societal perspective emphasising the importance of long-term studies in informing adaptational policies.

2. CHANGES IN ABUNDANCE AND DISTRIBUTION OF ROCKY SHORE SPECIES ON EUROPEAN SHORES

Changes in abundance and range limits in response to climatic fluctuations have long been recognised on rocky shores. Yonge (1949) and Wilson (1935) in their classic books on the seashore, report such fluctuations including the appearance and disappearance of the

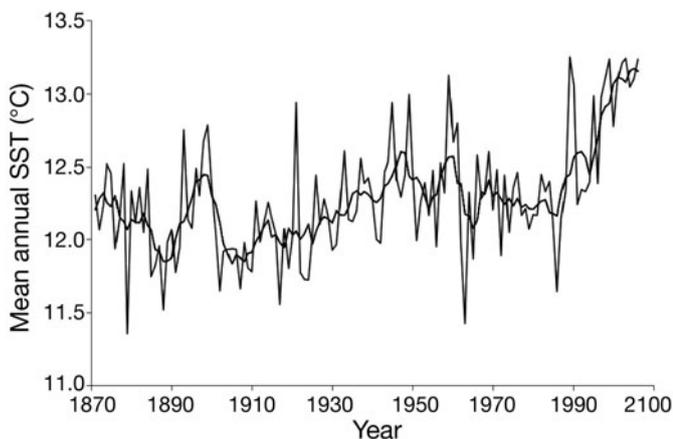


Fig. 1. Mean annual sea surface temperature (SST) for 1871–2006 off Plymouth (grid square 50–51° N, 04–05° W). Data from the UK Meteorological Office Hadley Centre

boreal arctic limpet *Tectura testudinalis* at its southern limit on the northeast coast of England. Southward & Crisp (1954b) observed that the northern species of barnacles *Semibalanus balanoides* was much rarer in the 1950s than in the 1930s in the English Channel. They suggested that this was caused by climate mediated competition with the southern species *Chthamalus stellatus*, which was becoming more abundant. This prompted the initiation of long-term observations which showed that in the southwest of England, the relative proportions of northern and southern barnacles fluctuated with temperature with a 2 yr time lag. *C. stellatus* became rarer in the cooler 1960s (Southward 1967) before increasing in abundance when conditions began to warm in the late 1980s (Southward 1991, Southward et al. 1995, Southward et al. 2005; Fig. 2). These time series were largely interrupted by a lack of funding, but when restarted in the late 1990s showed that the abundance of southern species had increased above levels of the 1950s (Fig. 2). Interestingly, coldwater species persisted despite more frequent failures in recruitment (e.g. Jenkins et al. 2000, Svensson et al. 2005). Resurveys made between 2001 and 2007, largely as part of the Marclim project (www.mba.ac.uk/marclim) and subsequent follow up work, has shown range extensions of several southern species (Mieszkowska et al. 2005). These have occurred at their northern limits in Scotland (e.g. *Gibbula umbilicalis*, Mieszkowska et al. 2006) as well as eastwards into the colder eastern English Channel basin (e.g. *Perforatus perforatus*, Herbert et al. 2003; *Gibbula umbilicalis*, *Patella ulyssiponensis* and *Melaraphe neritoides*, Mieszkowska et al. 2005). These species have breached suspected hydrographic barriers such as Portland Bill, Dorset and St. Catherine's Point, on the Isle of Wight (Crisp & Southward 1958) where

recruitment is low (Herbert et al. 2007), and have jumped across patches of unsuitable habitat, perhaps utilising recently constructed sea defences and marinas as stepping stones (Moschella et al. 2005). Further south in Europe, the southern species of limpet *Patella rustica* has extended its range in northern Portugal past a previous barrier to dispersal as a result of a relaxation of cold water upwelling (Lima et al. 2006), the processes driving this range expansion having been subsequently modelled (Lima et al. 2007a). Other changes have been detected in this region with southern species becoming more persistent (Lima et al. 2006, Lima et al. 2007b).

Other species have made much smaller advances. *Osilinus lineatus* has recolonised areas from which it had disappeared following the cold winter in 1962/63 and has made small advances from these historic range limits in Wales and on the English Channel coast (Mieszkowska et al. 2007). *O. lineatus* has, however, increased in abundance throughout much of its range (Mieszkowska et al. 2007; Fig. 3). *Patella depressa* has made only a small range extension from the Isle of Wight to adjacent sea defences on neighbouring Hayling Island, Hampshire, but again has increased in abundance at many sites on the south and southwest coasts of Britain (Mieszkowska et al. 2005, S. J. Hawkins et al. unpubl. data; Fig. 4). It has, however, not recovered to the levels of the 1950s in North Wales. Limited dispersal capability and suspected specific settlement and nursery ground requirements may be involved in limiting the advances made by these species. Thus, responses are species specific and dependent on life history and other ecological traits.

Although northern species have become less common (e.g. *Semibalanus balanoides* and *Patella vulgata*), major range retractions have not been recorded in the British Isles, except for *Alaria esculenta* in Ireland (Simkanin et al. 2005) and possibly *Tectura testudinalis*, which has not been found on the south coast of the Isle of Man for some years (S. J. Hawkins unpubl. data). Many of these northern species have ranges that extend further south into southern Europe where changes are occurring. Changes in assemblage composition and distribution of macroalgae have been observed with advances of southern species and retraction of northern species (Lima et al. 2007a); *S. balanoides* has also disappeared from the coast of northern Spain (Wetthey & Woodin 2008).

Many of the southern species of animals are able to breed more successfully in warmer years at their northern range limits (Bode et al. 1986, Bowman & Lewis 1986, Lewis 1986, Burrows et al. 1992, O'Riordan et al. 2001, P. J. Moore unpubl.). Warmer, more favourable summers are becoming more frequent and are probably particularly important in the establish-

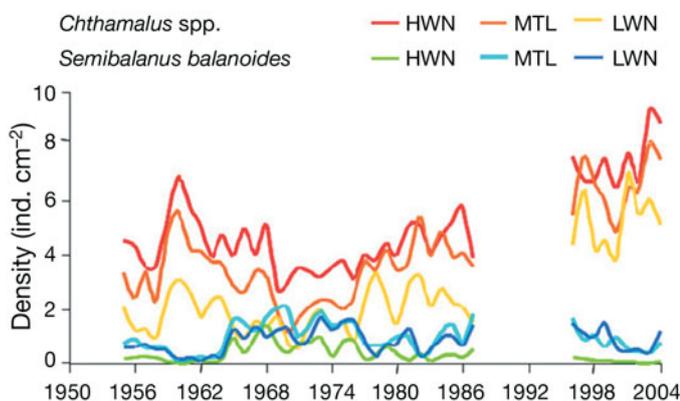


Fig. 2. Long-term changes in northern (*Semibalanus balanoides*) and southern (*Chthamalus* spp.) barnacles averaged for several shores on the south coast of Devon and Cornwall, UK. From Southward et al. (2005). HWN: high water neaps; MTL: mid tide line; LWN: low water neaps

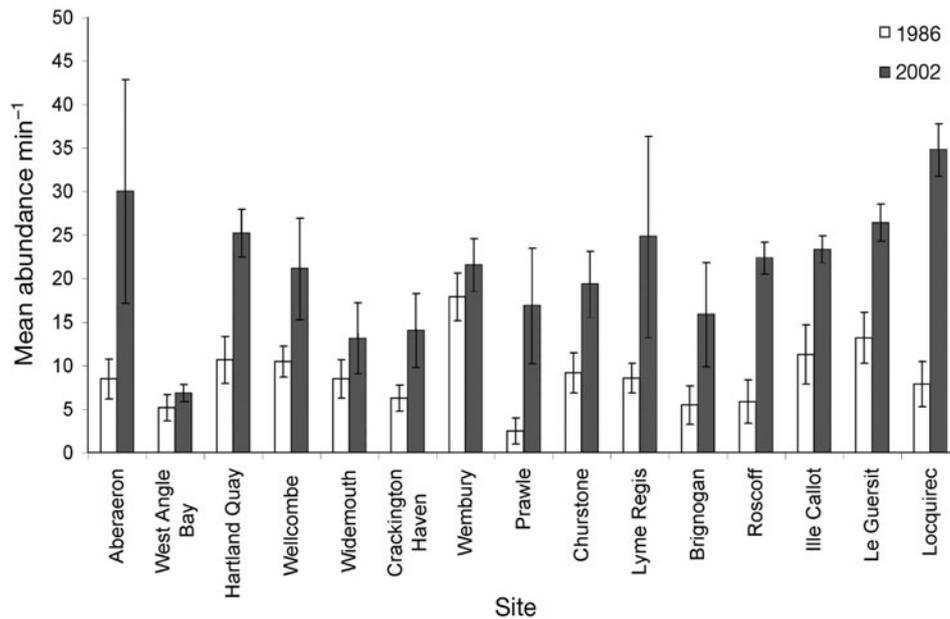


Fig. 3. *Osilinus lineatus*. Mean abundance per minute of timed search at locations in the northern region of its biogeographic distribution immediately prior to the onset of present warming (1986) and 2 decades later (2002). From Mieszkowska et al. (2007)

ment of viable breeding populations and facilitation of range extensions at the northern range limit of southern species. Northern species, however, appear to persist, perhaps because they are better competitors than related southern species (e.g. *Semibalanus balanoides*; Connell 1961b, Poloczanska et al. in press) and occasional massive recruitment events can boost their numbers, especially in species that spawn coincidentally with the spring phytoplankton bloom when good matching can occur (Connell 1961b, Hawkins & Hartnoll 1982, Hansson et al. 2003). Warm springs, however, cause juvenile mortality of *S. balanoides*, releasing *Chthamalus* spp. from competition.

3. COMMUNITY STRUCTURE: LATITUDINAL GRADIENTS IN PATTERN AND PROCESS

In the British Isles, Ireland and northern France, the mid-zone (eulittoral) of sheltered shores is dominated by furoids which give way to barnacles/mussels and grazing limpets on more exposed shores (Lewis 1964). In northern Europe, furoids extend further out onto exposed shores; whereas in southern Europe (Spain and Portugal), furoids are restricted to extreme shelter and estuarine refuges (Ballantine 1961). Classic limpet removal experiments (Jones 1948, Lodge 1948, Southward 1964), follow-up work by Hawkins (1981a,b) and the outcome of major oil spills where all limpets were killed, have all shown that this pattern is directly determined by grazing (Southward & Southward 1978, Hawkins et al. 1992). Subsequent work has confirmed that grazing prevents the establishment of furoids and other algae throughout much of Europe (Jenkins et al. 2005, Coleman et al. 2006), but wave action determines subsequent survival and persistence (Jonsson et al. 2006).

On moderately exposed shores of the Isle of Man and elsewhere in northern Britain, there are complex direct and indirect interactions between limpets (*Patella vulgata*), barnacles (*Semibalanus balanoides*), furoids (*Fucus vesiculosus*) (see Hawkins et al. 1992 for review) and microbial films (Thompson et al. 2004), which are delicately balanced leading to patchy and fluctuating distributions of furoids (Hawkins & Hartnoll 1983b, Hartnoll & Hawkins 1985). The aggregation of *P. vulgata* under adult furoid patches leads to an

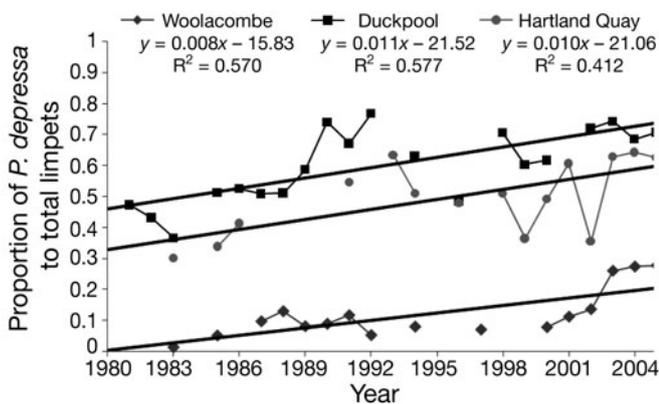


Fig. 4. *Patella depressa*. Proportion of *P. depressa* to total limpets at sites on the north coast of Devon and Cornwall from 1980–2004. Regression analyses are for each site, at $p < 0.01$

uneven grazing field, which can prompt subsequent escapes of juvenile fucoids in areas of reduced *P. vulgata* grazing (Burrows & Hawkins 1998, Thompson et al. 2004; Fig. 5a). Escapes from limpet grazing are crucial to the establishment of patches and are more likely among dense barnacles, in particular *S. balanoides* (Hawkins 1981a, 1983, Hawkins & Hartnoll 1983b). Grazing has also been shown to prevent fucoid and additional macroalgal escapes on barnacle-covered shores throughout Europe (Coleman et al. 2006). In southwest Britain and southern Europe, however, a

reduction in grazing pressure is less likely to lead to algal escapes and dense patches of fucoids as occurs on more northern shores (Jenkins et al. 2005). These patterns have been examined spatial statistics (Johnson et al. 1998b) and process simulated using models (Burrows & Hawkins 1998, Johnson et al. 1998a). These techniques have also highlighted the importance of aggregative behaviour of *P. vulgata* under fucoid patches in the dynamics of the system as well as the role of stochastic events such as barnacle, fucoid and limpet recruitment.

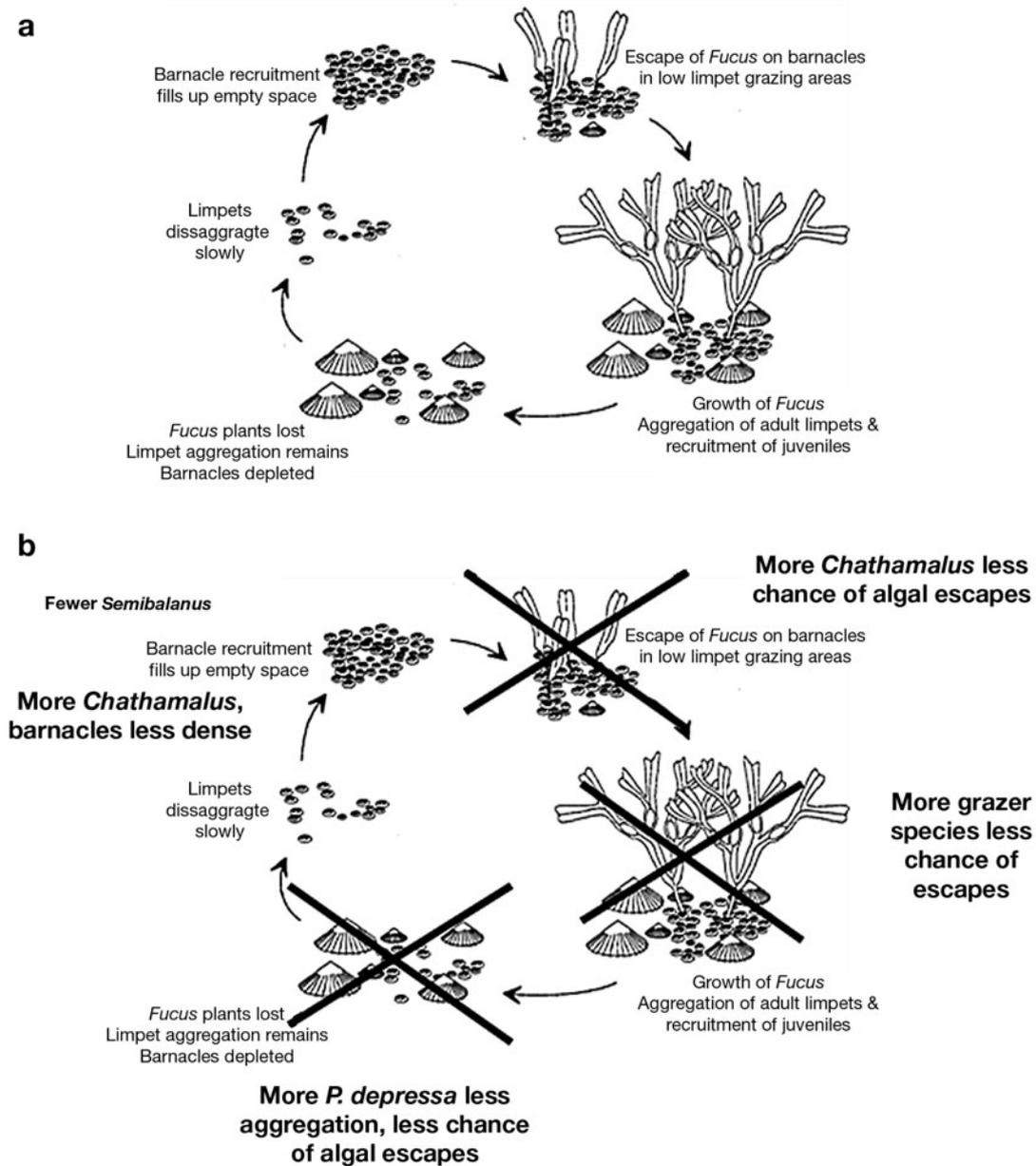


Fig. 5. Sequence of events on patchy, moderately exposed shore over several years. (a) Shores dominated by *Patella vulgata* and *Semibalanus balanoides*, (b) shores dominated by *P. depressa* and *Chathamalus* spp. Adapted from Burrows et al. (1998)

With climate change, the diversity of grazers will increase in northern Europe. Similarly, large barnacles such as *Semibalanus balanoides* capable of extremely dense settlement will be replaced by smaller and less rapidly growing chthamalids (Connell 1961b, Southward 1991, Poloczanska et al. in press). The rates and consequences of such changes are explored in the next section.

4. FORECAST AND PREDICTION: FUTURE STRUCTURE AND FUNCTIONING

Bioclimatic envelope approaches have been used to forecast future distributions of various organisms (see Pearson & Dawson 2003 for a review of different climate envelope methods). These approaches offer a good first-order approximation, giving the likely outer limits of potential distribution through changes in the geographic extent of the potential niche of a species (Pearson & Dawson 2003). These approaches have, however, been criticised because they neglect important factors such as dispersal, habitat quality and connectivity, and biological interactions (Davis et al. 1998, Ibanez et al. 2006). In intertidal systems, experimental approaches have shown that simple models are often unable to predict patterns in species distributions and abundance due to the complex nature of physical and biological interactions across latitudinal gradients (e.g. Helmuth et al. 2002, Sagarin & Somero 2006). We have used a climate envelope approach for intertidal climate indicator species and have found that by using wave exposure (see Burrows et al. 2008) and February isotherms, a reasonable predictive capability is possible (M. T. Burrows et al. unpubl.). The use of long-term data sets can increase the robustness of modelling approaches by testing modelled simulations using hindcast techniques. These techniques allow modelled data to be compared against empirically collected data to test the model fit. Forecasts of future states are also possible using published climate change scenarios and our modelling shows the potential for range extensions of many species. For the English Channel, we predicted range extensions before they were found in the field for *Gibbula umbilicalis*, *Patella ulysiponensis* and *Melaraphe neritoides* (M. T. Burrows et al. unpubl. data, S. J. Hawkins et al. unpubl. data).

A more analytical approach is to build biological interactions into model predictions. The barnacle data set collected by Southward since the 1950s, experiments on the role of competition (e.g. Connell 1961b), and good models of the dynamics of open populations (Roughgarden et al. 1988, Roughgarden et al. 1994, Connolly & Roughgarden 1999, Connolly et al. 2001) have enabled a mechanistic approach to the prediction

of future populations (Poloczanska et al. in press). Detailed path analysis has shown that while temperature in the early summer explains the abundance of the northern barnacle *Semibalanus balanoides* extremely well, it does not explain the abundance of the southern barnacle species *Chthamalus*. This is best explained as an indirect effect mediated by release from competition with *S. balanoides* in warmer years. A variety of models have been constructed, but the best fit to the 40 yr time series involved a space-limited model simulating interference competition between *S. balanoides* and juvenile *Chthamalus* spp. Having constructed a workable model, predictions of future trends have been made using published UKCIP02 (United Kingdom Climate Impact Programme) climate change scenarios. The predictions using both high and low future emissions scenarios suggest that *S. balanoides*, the dominant barnacle in the southwest of England during the 1930s (Moore 1936), will become locally extinct in the next 25 to 50 yr (Poloczanska et al. in press).

Experiments have also been undertaken to explore the consequences of changes in species identity of the major grazers *Patella* spp. (Moore et al. 2007a, Moore et al. 2007b). This work confirms that the northern species of limpet *P. vulgata* preferentially aggregates under furoid patches (Moore et al. 2007a, P. J. Moore unpubl. data, see also Hawkins & Hartnoll 1983a,b). If these patches are removed, significant numbers of *P. vulgata* relocate their home scars beneath new furoid patches or die (Moore et al. 2007a; Fig. 6). In contrast, the southern limpet species *P. depressa* does not preferentially aggregate beneath *Fucus* patches; if found beneath *Fucus*, it does not respond when the canopy is removed (Moore et al. 2007a). Should *P. depressa* continue to increase in abundance, then the cycle of aggregative behaviour typical on shores such as the Isle of Man (Hartnoll & Hawkins 1985) where *P. vulgata* is the only species, will not occur. Thus, the shore is likely to be less patchy (Johnson et al. 1998a) and also less dynamic (Burrows & Hawkins 1998). Furthermore, smaller and slower growing barnacles (*Chthamalus* spp.) are less likely to promote furoid escapes typical on *Semibalanus balanoides* dominated shores (Fig. 5b).

Although so far untested, the addition of extra grazers such as trochids (*Gibbula umbilicalis* and *Osilinus lineatus*) and decapods (*Pachygrapsus marmoratus*) will make escapes of *Fucus* and other algae less likely. Greater physical stress will also slow early growth of furoids reducing the probability of escapes (Thompson et al. 2004). Thus, shores are likely to have less primary producing furoids which will be increasingly restricted to sheltered shores. Mid-latitude shores such as those in southern Britain and Brittany, France may resemble those in Portugal in the foreseeable future. Primary production will decline and there will be less export of

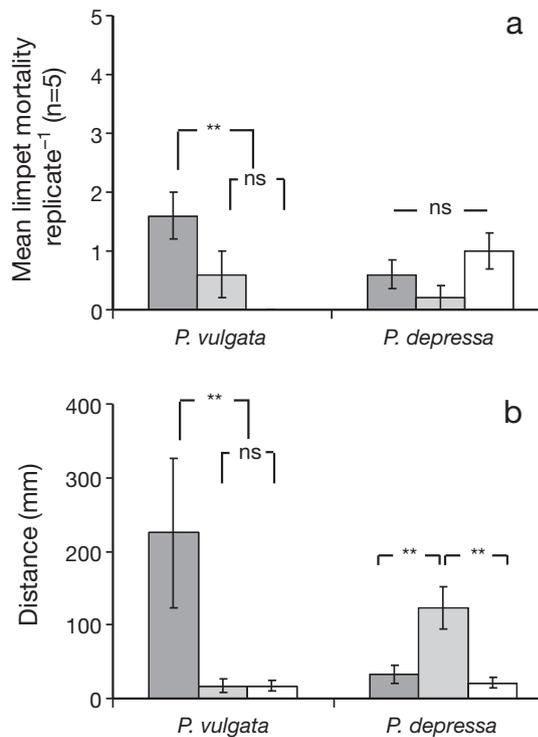


Fig. 6. *Patella vulgata* and *P. depressa*. Response to experimental loss of *Fucus vesiculosus*. (a) Mortality, (b) distance moved to a new home scar. Means ± 1 SE; ** $p < 0.01$, ns: not significant. From Moore et al. (2007a)

macroalgal detritus into coastal ecosystems. Secondary production will also be reduced as *Chthamalus* spp. grows much more slowly than *Semibalanus balanoides*. Thus, climate change is likely to have considerable consequences on the functioning of coastal ecosystems.

There are, however, some surprises in store due to both lags in responses of different species and idiosyncratic trait-dependent differences in the role of species. For example, the southern species of hermit crab *Clibanarius erythropus* that previously colonised Britain during the warm period experienced in the 1950s has yet to return (Southward & Southward 1977, 1988, S. J. Hawkins pers. obs.). The recolonisation and recovery of *C. erythropus* may have been further slowed by interaction with pollution (Southward & Southward 1978). The English Channel has been subjected to repeated pollution incidents (e.g. the tankers 'Torrey Canyon', 'Amoco Cadiz') which not only decimated British populations, but also reduced potential sources of recruits in northern France. Tributyl tin (TBT) pollution also reduced dogwhelk populations with recovery only occurring in the late 1990s, following the ban on TBT-based paints on smaller vessels. Thus, the favoured shell of *C. erythropus* also became rarer. In addition, northern species which retreated in the 1950s such as *Alaria esculenta*, never really recov-

ered during the subsequent cold period of the 1960s, 1970s and early 1980s. Moreover, recent work has shown that the southern species of limpet, *Patella depressa*, does not control macroalgal abundance to the same degree as the northern species *P. vulgata* (Moore et al. 2007b). Fucoïd escapes were able to occur in enclosures containing just *P. depressa* as the grazing activity of this species was significantly reduced during early spring to late summer when their gonads were full. During this time, *Fucus* germlings settled on the shore and were able to grow to a size less vulnerable to the grazing activities of *P. depressa*, which increased in autumn (Moore et al. 2007b). In contrast, in enclosures with only *P. vulgata*, no *Fucus* escapes were found and there was no reduction of grazing activity during the settlement period of *Fucus*. These results were surprising and indicate that as species identities change in response to climate change, there could be considerable impacts on the way species interact due to subtle differences in their behaviour or physiology. Changes in the strength or direction of species interactions could fundamentally alter assemblage composition with consequences for ecosystem functioning. The changes we have described are likely to have consequences for the balance and dynamics of fucoïds on European rocky shores and hence on whether a particular shore is a net importer or exporter of material. Such changes in fucoïd cover will also impact biodiversity given the number of mobile and sessile species that live in and among fucoïds (Thompson et al. 1996).

5. FUTURE WORK: PATTERN, PROCESS AND PREDICTION

Although there is a rich heritage of monitoring responses of species to climate fluctuations in the NE Atlantic, there are still many areas that need further work. The underlying mechanisms driving change that link individual ecophysiology with reproductive success and hence population dynamics are not well understood (but see Sagarin & Somero 2006). Knowledge of the effect of species interactions on species responses to climate change is still limited (but see Helmuth et al. 2006, Moore et al. 2007a, Moore et al. 2007b, Blight & Thompson 2008). Work to date indicates that species interactions will alter under future climate change scenarios, with implications for community structure (Moore et al. 2007a, Moore et al. 2007b, Sanford & Swezey 2008) and ecosystem functioning. In addition, most field and laboratory experiments investigating responses of species to climate change have manipulated mean values in an environmental variable (e.g. temperature) with few studies

manipulating the amount of variability in environmental conditions (Benedetti-Cecchi 2003). This is surprising considering that extreme events are predicted to become more frequent with climate change (IPCC 2007) and that the incorporation of spatial and temporal variance is vital for understanding ecological processes (Benedetti-Cecchi 2000, 2003, Benedetti-Cecchi et al. 2005).

As with many components of marine biodiversity, rocky shore species are showing changing abundance and geographic range in response to climatic warming. At present, more advances than retreats have been recorded. In northern species, this is perhaps due to the greater reproductive output of single brood spring spawners and greater competitive ability. This hypothesis, however, remains to be tested. It must also be remembered that more studies have been made in regions where species reach their northern limits than in lower latitudes where many southern limits are located, potentially skewing evidence. Assemblage-level monitoring needs to be undertaken to measure the effects of changes in the balance of canopy algae and suspension feeders over the next 50 yr and hence the potential contribution of rocky shores to inshore productivity. In addition, experimental studies on population- and community-level processes need to be undertaken to enable modelling techniques that provide better predictions. Better understanding will enable progression from mere forecasts to better predictive modelling and future studies under different climate scenarios. Differences between modelled and actual distributions can then be used to generate testable hypotheses about the processes setting geographic limits, particularly the interaction of ultimate factors such as temperature regime with proximate factors such as habitat quality, connectivity of habitat patches, dispersal capability, the porosity of hydrographic barriers such as major headlands and the role of positive and negative biological interactions.

Rocky shore species have long been known to provide excellent sentinels for detecting changes in biodiversity in other systems that are less accessible and more expensive to survey, such as offshore systems (Lewis 1986, Southward et al. 1995, Southward et al. 2005). Rocky shores also provide a tractable system for field experiments to explore the likely community structuring and ecosystem functioning consequences of changes in species distributions and assemblage composition. Existing time series need to be continued and resurveys made on a European scale to fully exploit the classical baselines provided by Fischer-Piette, Crisp and Southward (e.g. Fischer-Piette 1936, 1955, Fisher 1943, Crisp 1950, 1964, Southward 1951, 1958, 1967, 1980, 1991, Southward & Crisp 1952, 1954a,b, 1956, Crisp & Knight-Jones 1954, Fischer-Piette & Prenant

1956, 1957, Crisp & Southward 1958, Crisp & Fischer-Piette 1959, Fischer-Piette & Gaillard 1959, Southward et al. 1995, Southward et al. 2005).

6. INFORMING ADAPTATION

There are major policy implications of climate change in marine ecosystems from a societal perspective. The inertia of the climate system means that society must live with continuing climate change over the next 50 yr or so (IPCC 2007), until mitigation measures and new technologies enable a switch from a carbon-based economy. Adaptive policies need to be based on real-time monitoring of changes to distinguish actual trends from mere fluctuations. Knowledge of future states would also enable a more precautionary approach to managing the interactions of global change and local- and regional-scale impacts.

Comprehensive, broadscale and long-term observations are essential for a sufficiently accurate knowledge of the state of our seas and coasts to allow adaptive management. Sustained observation/monitoring alone is not enough: integrative experimental studies are required to understand the mechanisms involved in individual and population responses to climate change.

Adapting to climate change requires disentangling human-driven global change of low amplitude and frequency from natural temporal and spatial fluctuations as well as human impacts acting at regional (e.g. overfishing, eutrophication, non-native species) and local scales (aquaculture, habitat loss due to inappropriate coastal development, point-source pollution). Some local impacts can scale up to whole coastlines, such as that of low-crested sea defences (Airoldi et al. 2005) resulting in regional scale habitat alteration and loss. Adaptive policies must focus on managing the interactions of global change (which we cannot slow in the short to medium term, i.e. next 50 yr), with drivers that society can influence and ameliorate, such as overexploitation, pollution and habitat degradation and loss.

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LITERATURE CITED

- Airoidi L, Abbiati M, Beck MW, Hawkins SJ and 6 others (2005) An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. *Coast Eng* 52:1073–1087
- Ballantine WJ (1961) A biologically defined exposure scale for the comparative description of rocky shores. *Field Stud* 1: 73–84
- Barry JP, Baxter CM, Sagarin RD, Gilman SE (1995) Climate-related, long-term faunal changes in a Californian rocky intertidal community. *Science* 267:672–675
- Beare D, Burns F, Jones E, Peach K and others (2004) An increase in the abundance of anchovies and sardines in the northwestern North Sea since 1995. *Glob Change Biol* 10: 1209–1213
- Beaugrand G, Ibanez F (2004) Monitoring marine plankton ecosystems. II. Long-term changes in North Sea calanoid copepods in relation to hydro-climatic variability. *Mar Ecol Prog Ser* 284:35–47
- Beaugrand G, Reid PC (2003) Long-term changes in phytoplankton, zooplankton and salmon linked to climate change. *Glob Change Biol* 9:801–817
- Beaugrand G, Brander K, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. *Nature* 426:661–664
- Benedetti-Cecchi L (2000) Variance in ecological consumer-resource interactions. *Nature* 407:370–373
- Benedetti-Cecchi L (2003) The importance of the variance around the mean effect size of ecological processes. *Ecology* 84:2335–2346
- Benedetti-Cecchi L, Vaselli S, Maggi E, Bertocci I (2005) Interactive effects of spatial variance and mean intensity of grazing on algal cover in rock pools. *Ecology* 86: 2212–2222
- Bertness MD (2007) Atlantic shorelines: natural history and ecology. Princeton University Press, Princeton, NJ, p 446
- Blight AJ, Thompson RC (2008) Epibiont species richness varies between holdfasts of northern and southerly distributed kelp. *J Mar Biol Assoc UK* 88:469–477
- Bode A, Lombas I, Anadon N (1986) Preliminary studies on the reproduction and population dynamics of *Monodonta lineata* and *Gibbula umbilicalis* (Mollusca, Gastropoda) on the central coast of Asturias (N. Spain). *Hydrobiologia* 142: 31–39
- Bowman RS, Lewis JR (1986) Geographical variation in the breeding cycles and recruitment of *Patella* spp. *Hydrobiologia* 142:41–56
- Brander K, Blom G, Borges MF, Erzini K and 6 others (2003) Changes in fish distribution in the eastern North Atlantic: Are we seeing a coherent response to changing temperature? *ICES Mar Sci Symp* 219:261–270
- Burrows MT, Hawkins SJ (1998) Modelling patch dynamics on rocky shores using deterministic cellular automata. *Mar Ecol Prog Ser* 167:1–13
- Burrows MT, Hawkins SJ, Southward AJ (1992) A comparison of reproduction in co-occurring Chthamalid barnacles, *Chthamalus stellatus* (Poli) and *Chthamalus montagui* (Southward). *J Exp Mar Biol Ecol* 160:229–249
- Burrows MT, Harvey R, Robb L (2008) Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Mar Ecol Prog Ser* 353:1–14
- Coleman RA, Underwood AJ, Benedetti-Cecchi L, Aberg P and others (2006) A continental scale evaluation of the role of limpet grazing on rocky shores. *Oecologia* 147:556–564
- Connell JH (1961a) Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol Monogr* 31:61–104
- Connell JH (1961b) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723
- Connolly SR, Roughgarden J (1999) Theory of marine communities: competition, predation, and recruitment-dependent interaction strength. *Ecol Monogr* 69:277–296
- Connolly SR, Menge BA, Roughgarden J (2001) A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology* 82:1799–1813
- Crisp DJ (1950) Breeding and distribution of *Chthamalus stellatus*. *Nature* 166:311–312
- Crisp DJ (1964) The effects of the severe winter of 1962–63 on marine life in Britain. *J Anim Ecol* 33:165–210
- Crisp DJ, Fischer-Piette E (1959) Repartition des principales especes intercotidales de la cote Atlantique Francaise en 1954–1955. *Ann Inst Oceanogr* 36:275–387
- Crisp DJ, Knight-Jones EW (1954) Discontinuities in the distribution of shore animals in North Wales. *Rep Bardsey Observatory* 2:29–34
- Crisp DJ, Southward AJ (1958) The distribution of intertidal organisms along the coasts of the English Channel. *J Mar Biol Assoc UK* 37:157–208
- Davis AJ, Lawton JH, Shorrocks B, Jenkinson LS (1998) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *J Anim Ecol* 67:600–612
- Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430:881–884
- Fischer-Piette E (1936) Études sur la biogéographie intercotidale des deux rives de la Manche. *J Linn Soc Zoology* 40: 181–272
- Fischer-Piette E (1955) Repartition, le long des côtes septentrionales de l'Espagne, des principales especes peuplant les rochers intercotidaux. *Ann Inst Oceanogr* 31:37–124
- Fischer-Piette E, Gaillard JM (1959) Les patelles, au long des côtes atlantiques iberiques et nord-marocaines. *J Conchyliologie* 99:135–200
- Fischer-Piette E, Prenant M (1956) Distribution des Cirripèdes intercotidaux d'Espagne septentrionale. *Bull Cent Etud Rech Sci Biarritz* 1:7–19
- Fischer-Piette E, Prenant M (1957) Quelques donnees ecologiques sur les cirripèdes intercotidaux du Portugal, de l'Espagne du Sud et du Nord du Maroc. *Bull Cent Etud Rech Sci Biarritz* 1:361–368
- Fisher PH (1943) Observations sur les conditions de vie de *Balanus balanoides* dans quelques stations boreales et arctiques. *Bull Lab Marit Dinard* 25:65–72
- Genner MJ, Sims DW, Wearmouth VJ, Southall EJ, Southward AJ, Henderson PA, Hawkins SJ (2004) Regional climatic warming drives long-term community changes of British marine fish. *Proc R Soc Lond B Biol Sci* 271:655–661
- Hansson LJ, Hudson IR, Seddon RJ, Shaw O, Thomason JC (2003) Massive recruitment of the barnacle *Semibalanus balanoides* in the Clyde Sea (Scotland, UK) in the spring of 2000. *J Mar Biol Assoc UK* 83:923–924
- Harley CDG, Hughes AR, Hultgren K, Miner BG and 5 others (2006) The impacts of climate change in coastal marine systems. *Ecol Lett* 9:228–241

- Harris LG, Tyrrell MC, Chester CM (1998) Changing community states in the Gulf of Maine: synergism between invaders, overfishing and climate change. In: Mooi R (ed) Proc 9th Int Echinoderm Conf, AA Balkema, Rotterdam, p 243–248
- Hartnoll RG, Hawkins SJ (1985) Patchiness and fluctuations on moderately exposed rocky shores. *Ophelia* 24:53–63
- Hawkins SJ (1981a) The influence of *Patella* grazing on the fucoid-barnacle mosaic on moderately exposed rocky shores. *Kieler Meeresforsch* 5:537–543
- Hawkins SJ (1981b) The influence of season and barnacles on the algal colonization of *Patella vulgata* exclusion areas. *J Mar Biol Assoc UK* 61:1–15
- Hawkins SJ (1983) Interaction of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). *J Exp Mar Biol Ecol* 71:55–72
- Hawkins SJ, Hartnoll RG (1982) Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977–1981). *J Exp Mar Biol Ecol* 62:271–283
- Hawkins SJ, Hartnoll RG (1983a) Changes in a rocky shore community: an evaluation of monitoring. *Mar Environ Res* 9:131–181
- Hawkins SJ, Hartnoll RG (1983b) Grazing of intertidal algae by marine invertebrates. *Oceanogr Mar Biol Annu Rev* 21: 195–282
- Hawkins SJ, Hartnoll RG, Kain JM, Norton TA (1992) Plant animal interactions on hard substrata in the north-east Atlantic. In: John DM, Hawkins SJ, Price JH (eds) Plant animal interactions in the marine benthos. Systematics Association Special Vol 46. Clarendon Press, Oxford, p 1–32
- Hawkins SJ, Southward AJ, Genner MJ (2003) Detection of environmental change in a marine ecosystem—evidence from the western English Channel. *Sci Total Environ* 310: 245–256
- Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. *Trends Ecol Evol* 20:337–344
- Helmuth B, Harley CD, Halpin PM, O'Donnell M, Hofmann GE, Blanchette CA (2002) Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298: 1015–1017
- Helmuth B, Mieszkowska N, Moore P, Hawkins SJ (2006) Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. *Annu Rev Ecol Evol and Syst* 37:373–404
- Herbert RJH, Hawkins SJ, Shearer M, Southward AJ (2003) Range extension and reproduction of the barnacle *Balanus perforatus* in the eastern English Channel. *J Mar Biol Assoc UK* 83:73–82
- Herbert RJH, Southward AJ, Shearer M, Hawkins SJ (2007) Influence of recruitment and temperature on distribution of intertidal barnacles in the English Channel. *J Mar Biol Assoc UK* 87:487–499
- Hiscock K, Southward AJ, Tittley I, Hawkins SJ (2004) Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquat Conserv: Mar Freshwat Ecosyst* 14: 333–362
- Ibanez I, Clark JS, Dietze MC, Feeley K and 5 others (2006) Predicting biodiversity change: outside the climate envelope, beyond the species-area curve. *Ecology* 87:1896–1906
- IPCC (Intergovernmental Panel on Climate Change) (2007) Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge
- Jenkins SR, Aaburg P, Cervin G, Coleman RA and 9 others (2000) Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *J Exp Mar Biol Ecol* 243:209–225
- Jenkins SJ, Coleman RA, Della Santina P, Hawkins SJ, Burrows MT, Hartnoll RG (2005) Regional scale differences in the determinism of grazing effects in the rocky intertidal. *Mar Ecol Prog Ser* 287:77–86
- Johnson MP, Burrows MT, Hartnoll RG, Hawkins SJ (1998a) Individual-based simulations of the direct and indirect effects of limpets on a rocky shore *Fucus* mosaic. *Mar Ecol Prog Ser* 169:179–188
- Johnson MP, Hawkins SJ, Hartnoll RG, Norton TA (1998b) The establishment of fucoid zonation on algal-dominated rocky shores: hypothesis derived from a simulation model. *Funct Ecol* 12:259–269
- Jones NS (1948) Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. *Proc Trans Liverpool Biol Soc* 56:60–77
- Jonsson PR, Granhag L, Moschella P, Aberg P, Hawkins SJ, Thompson RC (2006) Interactions between wave action and grazing control the distribution of intertidal macroalgae. *Ecology* 87:1169–1178
- Lewis JR (1964) The ecology of rocky shores. English University Press, London
- Lewis JR (1986) Latitudinal trends in reproduction, recruitment and population characteristics of some rocky littoral molluscs and cirripedes. *Hydrobiologia* 142:1–13
- Lima FP, Queiroz N, Ribeiro PA, Hawkins SJ, Santos AM (2006) Geographic expansion of a marine gastropod, *Patella rustica* Linnaeus, 1758, and its relation with unusual climatic events. *J Biogeogr* 33:812–822
- Lima FP, Ribeiro PA, Queiroz N, Hawkins SJ, Santos AM (2007a) Do distributional shifts of northern and southern species of algae match the warming pattern? *Glob Change Biol* 13:2592–2604
- Lima FP, Ribeiro PA, Queiroz N, Xavier R, Tarroso P, Hawkins SJ, Santos AM (2007b) Modelling past and present geographical distribution of the marine gastropod *Patella rustica* as a tool for exploring responses to environmental change. *Glob Change Biol* 13:2065–2077
- Lodge SM (1948) Algal growth in the absence of *Patella* on an experimental strip of foreshore, Port St. Mary, Isle of Man. *Proc Trans Liverpool Biol Soc* 56:78–83
- Mieszkowska N, Leaper R, Moore P, Kendall MA and 10 others (2005) Assessing and predicting the influence of climatic change using intertidal rocky shore biota. *MarClim Final Report Marine Biological Association Occasional Publications* 20
- Mieszkowska N, Kendall MA, Hawkins SJ, Leaper R, Williamson P, Hardman-Mountford NJ, Southward AJ (2006) Changes in the range of some common rocky shore species in Britain—a response to climate change? *Hydrobiologia* 555:241–251
- Mieszkowska N, Hawkins SJ, Burrows MT, Kendall MA (2007) Long-term changes in the geographic distribution and population structures of *Osilinius lineatus* (Gastropoda: Trochidae) in Britain and Ireland. *J Mar Biol Assoc UK* 87:537–545
- Moore HB (1936) The biology of *Balanoides balanoides*. V. Distribution in the Plymouth area. *J Mar Biol Assoc UK* 20: 701–716
- Moore P, Hawkins SJ, Thompson RC (2007a) The role of biological habitat amelioration in altering the relative responses of congeneric species to climate change. *Mar Ecol Prog Ser* 334:11–19
- Moore P, Thompson RC, Hawkins SJ (2007b) Effects of grazer identity on the probability of escapes from canopy-forming macroalgae. *J Exp Mar Biol Ecol* 344:170–180

- Moschella PS, Abbiati M, Aberg P, Airoidi L and 12 others (2005) Low-crested coastal defence structures as artificial habitats for marine life: using ecological criteria in design. *Coast Eng* 52:1053–1071
- O’Riordan RM, Delany J, McGrath D, Myers AA and 7 others (2001) Variation in the sizes of Chthamalid barnacle post-settlement cyprids on European shores. *PSZN I: Mar Ecol* 22:307–322
- Paine RT (1966) Food web complexity and species diversity. *Am Nat* 100:65–75
- Paine RT (1979) Disaster, catastrophe and local persistence of the sea palm *Postelsia palmaeformis*. *Science* 205:685–687
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Glob Ecol Biogeogr* 12: 361–371
- Poloczanska ES, Hawkins SJ, Southward AJ, Burrows MT (in press) Modelling the response of populations of competing species to climate change. *Ecology*
- Raffaelli D, Hawkins SJ (1999) *Intertidal ecology*. Kluwer Academic Publishers, Dordrecht
- Rivadeneira MM, Fernandez M (2005) Shifts in southern endpoints of distribution in rocky intertidal species along the south-eastern Pacific coast. *J Biogeogr* 32:203–209
- Roughgarden J, Gaines S, Possingham H (1988) Recruitment dynamics in complex life cycles. *Science* 241:1460–1466
- Roughgarden J, Pennington T, Alexander S (1994) Dynamics of the rocky intertidal zone with remarks on generalization in ecology. *Philos Trans R Soc Lond B Biol Sci* 343:79–85
- Russell FS (1973) A summary of the observations on the occurrence of planktonic stages of fish off Plymouth. *J Mar Biol Assoc UK* 53:347–355
- Russell FS, Southward AJ, Boalch GT, Butler EI (1971) Changes in biological conditions in the English Channel off Plymouth during the last half century. *Nature* 234:468–470
- Sagarin RD, Somero GN (2006) Complex patterns of expression of heat-shock protein 70 across the southern biogeographical ranges of the intertidal mussel *Mytilus californianus* and the snail *Nucella ostrina*. *J Biogeogr* 33:622–630
- Sagarin RD, Barry JP, Gilman SE, Baxter CH (1999) Climate-related change in an intertidal community over short and long time scales. *Ecol Monogr* 69:465–490
- Sanford E, Swezey DS (2008) Responses of predatory snails to a novel prey following the geographic range expansion of an intertidal barnacle. *J Exp Mar Biol Ecol* 354:220–230
- Simkanin C, Power AM, Myers AA, McGrath D and others (2005) Using historical data to detect temporal changes in the abundances of intertidal species on Irish shores. *J Mar Biol Assoc UK* 85:1329–1340
- Sims DW, Genner MJ, Southward AJ, Hawkins SJ (2001) Timing of squid migration reflects North Atlantic climate variability. *Proc R Soc Lond B Biol Sci* 268:2607–2611
- Sims DW, Wearmouth VJ, Genner MJ, Southward AJ, Hawkins SJ (2004) Low-temperature-driven early spawning migration of a temperate marine fish. *J Anim Ecol* 73: 333–341
- Southward AJ (1951) Distribution of *Chthamalus stellatus* in the Irish Sea. *Nature* 167:410–411
- Southward AJ (1958) Note on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographical distribution. *J Mar Biol Assoc UK* 37:49–66
- Southward AJ (1963) The distribution of some plankton animals in the English Channel and approaches. III. Theories about long-term biological changes, including fish. *J Mar Biol Assoc UK* 43:1–29
- Southward AJ (1964) Limpet grazing and the control of vegetation on rocky shores. In: Crisp DJ (ed) *Grazing in terrestrial and marine environments*. Blackwell Scientific, Oxford, p 265–273
- Southward AJ (1967) Recent changes in abundance of intertidal barnacles in south-west England: a possible effect of climatic deterioration. *J Mar Biol Assoc UK* 47:81–95
- Southward AJ (1980) The western English Channel—An inconsistent ecosystem? *Nature* 285:361–366
- Southward AJ (1991) Forty years of changes in species composition and population density of barnacles on a rocky shore near Plymouth. *J Mar Biol Assoc UK* 71:495–513
- Southward AJ, Crisp DJ (1952) Changes in the distribution of the intertidal barnacles in relation to the environment. *Nature* 170:416–417
- Southward AJ, Crisp DJ (1954a) The distribution of certain intertidal animals around the Irish coast. *Proc R Ir Acad B* 57:1–29
- Southward AJ, Crisp DJ (1954b) Recent changes in the distribution of the intertidal barnacles *Chthamalus stellatus* Poli and *Balanus balanoides* in the British Isles. *J Anim Ecol* 23:163–177
- Southward AJ, Crisp DJ (1956) Fluctuations in the distribution and abundance of intertidal barnacles. *J Mar Biol Assoc UK* 35:211–229
- Southward AJ, Southward EC (1977) Distribution and ecology of the hermit crab *Clibanarius erythropus* in the western Channel. *J Mar Biol Assoc UK* 57:441–452
- Southward AJ, Southward EC (1978) Recolonization of rocky shores in Cornwall after use of toxic dispersants to clean up the *Torrey Canyon* spill. *J Fish Res Board Can* 35: 682–706
- Southward AJ, Southward EC (1988) Disappearance of the warm water hermit crab *Clibanarius erythropus* from south west Britain. *J Mar Biol Assoc UK* 68:409–412
- Southward AJ, Hawkins SJ, Burrows MT (1995) Seventy years’ observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *J Therm Biol* 20:127–155
- Southward AJ, Langmead O, Hardman-Mountford NJ, Aiken J and others (2005) Long-term oceanographic and ecological research in the Western English Channel. *Adv Mar Biol* 47:1–105
- Svensson CJ, Jenkins SR, Hawkins SJ, Aberg P (2005) Population resistance to climate change: modelling the effects of low recruitment in open populations. *Oecologia* 142: 117–126
- Thompson RC, Wilson BJ, Tobin ML, Hill AS, Hawkins SJ (1996) Biologically generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial scales. *J Exp Mar Biol Ecol* 202:73–84
- Thompson RC, Norton TA, Hawkins SJ (2004) Physical stress and biological control regulate the balance between producers and consumers in marine intertidal biofilms. *Ecology* 85:1372–1382
- Wetthey DS, Woodin SA (2008) Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. *Hydrobiologia* 606:139–151
- Wilson DP (1935) *Life of the shore and shallow sea*. Ivor Nicholson and Watson, London
- Yonge CM (1949) *The sea shore*. Bloomsbury Books, London
- Zacherl D, Gaines SD, Lonhart SI (2003) The limits to biogeographical distributions: insights from the northward range extension of the marine snail *Kelletia kelletii* (Forbes, 1852). *J Biogeogr* 30:913–924