Chapter 15

Intertidal Indicators of Climate and Global Change

Nova Mieszkowska

Marine Biological Association of the UK, The Laboratory, Citadel Hill, Plymouth PL1 2PB, United Kingdom

1. INTRODUCTION

The rocky intertidal zone spans the region of the coastline from the highest vertical level reached at high water during spring tides (with associated wave splash) to the lowest level exposed to the air during low water springs. A wide variety of taxa inhabit the rocky intertidal zone, including algae, molluscs, echinoderms, cnidarians and crustaceans. Owing to the accessibility of rocky shores, intertidal species have been studied extensively throughout the nineteenth and twentieth centuries by amateur naturalists [1,2] and professional researchers as model systems for the development of ecological and biological theory [3–15].

Intertidal invertebrates and macroalgae are ectotherms of marine evolutionary origin, but due to the daily regime of emersion and immersion they must contend with both marine and terrestrial regimes. Therefore, they

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provide a unique insight into the impacts of changes in both aquatic and terrestrial climatic environments. Diurnal tidal cycles and seasonal fluctuations in both sea and air temperature mean that intertidal organisms are subject to extremes of temperature with resultant fluctuations in body temperature of over 30 °C frequently experienced [16]. Additional stressors such as desiccation [17], current and wave forces [18], rapid fluctuations in salinity [19–21], oxygen availability [22,23] and nutrient levels [24] mean that organisms are often living close to their physiological tolerance limits [25–32].

Marine ectothermic species often respond faster than terrestrial species to environmental change: the typically short lifespans [33] and sessile or sedentary nature of the adult and juvenile stages prevents escape from changing environmental regimes. The larval stage of most intertidal species is planktonic, and therefore also provides an indication of the impacts of environmental change in the pelagic zone. Changes in distribution and abundance are, therefore, likely to be driven by the direct response of organisms to changes in the environment. Intertidal invertebrates and marine macroalgae are from lower trophic levels, and thus would be expected to respond quicker to alterations in local conditions than species at higher trophic levels, often showing the first response in a cascade of effects up the food chain to tertiary and apex predators [34,35]. Variation in the abundance of keystone structural or functional species can alter the composition and dynamics of entire rocky communities [5,36,37] and these small changes in environmental conditions can lead to major alterations in community structure and functioning [38,39]. Taking all of the above factors into account, the rocky intertidal ecosystem is likely to be one of the most sensitive natural systems and show some of the earliest responses to climate change [40,41].

The geographical ranges of intertidal species are essentially one-dimensional, as they occupy a narrow strip of coastline between the low and high tide levels [42]. In combination with the highly stressful and fluctuating environment in which these species live, the rocky intertidal zone is thus ideal model system in which to study the effects of climate change. Rocky intertidal ecosystems occur all over the globe and thus facilitate spatial and temporal comparisons of the relative impacts of global environmental change. Responses to environmental change can be divided into two categories; proximate ecological responses which depend upon relationships between abiotic factors and organismal-level processes, population dynamics and community structure [43], and direct impacts on individual performance during various life stages through changes in physiology, morphology and behaviour. These impacts scale up to the population level response, which can be additionally affected by climate driven changes in hydrographic processes that affect dispersal of the pelagic larval life-stages and recruitment. All lead to alterations in distributions, biodiversity, productivity and micro-evolutionary processes.

2. CLIMATE CHANGE AND BIOGEOGRAPHY

Biogeographical studies were first introduced by Tournefort [44] in the 1700s, and work undertaken in the early 1900s [24,45–51] is used as the basis for ecological climate change research today. The major marine biogeographic provinces have been defined primarily on where clusters of biogeographic distributional limits occur for taxa of interest. Sea temperature has been assumed to ultimately set biogeographical ranges of marine species (see [24,52] for reviews). Low and high latitude biogeographic limits have been associated with August and February sea surface isotherms, respectively, for fauna and flora across a diverse range of taxonomic groups including marine algae [53–58], cirripedes [59] and molluscs [60,61]. However, the relationship between species' distributions and climate is not simple. Biogeographic studies are often complicated by covarying environmental parameters that prevent cause-and-effect relationships from being understood.

Suitable habitat exists beyond the distributional limits of many species of marine invertebrates [62–65] but the unsuitability of environmental conditions currently prevents their colonisation and therefore the ranges are assumed to be limited by climate. This principle is termed the 'climate envelope' of a species, and is the basis for many bioclimatic models in use today [66,67] but see Refs. [68,69]. Where environmental conditions alter to fall within the physiological tolerance range of a species, range extensions are predicted as organisms are able to colonise new sites of suitable habitat. In practice, however, the range edge may lie some distance inside this fundamental niche 'envelope'. Interactions between species and between organisms and environmental factors, and local influences such as a lack of suitable habitat, poor dispersal and connectivity of suitable habitat space act to set the realised niche for each species. The effects of climatic variability on the distributions of plants and animals and their interactions must, therefore, be measured in order to understand and ultimately forecast changes in marine ecosystems.

2.1. Using Long-Term Datasets to Detect Climate Change

Some of the most spatially and temporally extensive datasets in the world exist for the distribution and abundance of intertidal invertebrates and macroalgae along the coastline of the north east Atlantic. Intensive and wide ranging surveys were made in the 1930s, 1940s and 1950s by Fischer-Piette [70–73] along the Atlantic coastlines of France, Spain, Portugal and North Africa. Crisp and Southward made similar surveys around the coastlines of Britain and Ireland during the 1950s ([74,75], Southward and Crisp, unpublished data). These datasets are particularly valuable within the context of climate change monitoring as they provide extensive baselines from which to measure the rate and extent of changes in distribution and abundance of intertidal species during periods of warming and cooling over the past 70 years [76]. Time-series data for abundance and population structures for barnacles, trochids and limpets also exist for British shores dating back to the 1950s, 1970s and 1980s, respectively [74,75,77–79].

The Marine Biodiversity and Climate Change Project 'MarClim' was established by the Marine Biological Association of the United Kingdom in 2001 to assess and forecast the influence of climate change on rocky intertidal biodiversity in Britain and Ireland. It combined historical data with contemporary re-surveys at over 400 rocky shores (Fig. 1) to provide evidence of changes in abundance, population structure and geographical distribution of intertidal species in relation to recent climate change [64]. MarClim survey protocols were the same as those used in the original surveys made in the 1950s [74,75] to map the distribution and range limits of over 50 species of invertebrates and macroalgae of both cold and warm water origins. In addition, quantitative data on the abundance and population dynamics of key species of barnacles, limpets and trochids were collected. These surveys were carried out at locations spanning sites from the range edges to locations closer to the centers of distribution. These combined datasets have been used to track the changes in abundance and relative dominance of warm and cold water species on shores where they co-exist in response to fluctuating climatic conditions throughout the twentieth century.

2.2. Responses of Intertidal Biota

Contractions and expansions of geographic range edges due to global environmental change are resulting in species both being lost from and introduced to assemblages. Such changes are initially being recorded at the periphery of the geographic range of a species, where organisms are often already experiencing temperatures close to their thermal limits [26]. However, there can also be local or regional heterogeneity within the geographic range of a species as evidenced by environmental hotspots [31,40] or coldspots [79] occurring far from the distributional limits of sessile invertebrates. Such changes in turn influence the outcomes of species interactions for example competition, facilitation and predation, ultimately altering the structure of communities and marine ecosystem processes [41,43,80–82,85].

2.2.1. Europe

Alterations in distributional limits of a wide range of intertidal taxa have already occurred in Britain since rapid warming of the climate began in the mid-1980s. Northern and eastern range edges of warm water trochid gastropods such as *Osilinus lineatus* and *Gibbula umbilicalis*, barnacles including *Chthamalus montagui*, *C. stellatus* and *Perforatus (Balanus) perforatus* and the brown macroalga *Bifurcaria bifurcata* have extended between 85 and 180 km since previous records in the twentieth century [64,65,83] and at rates

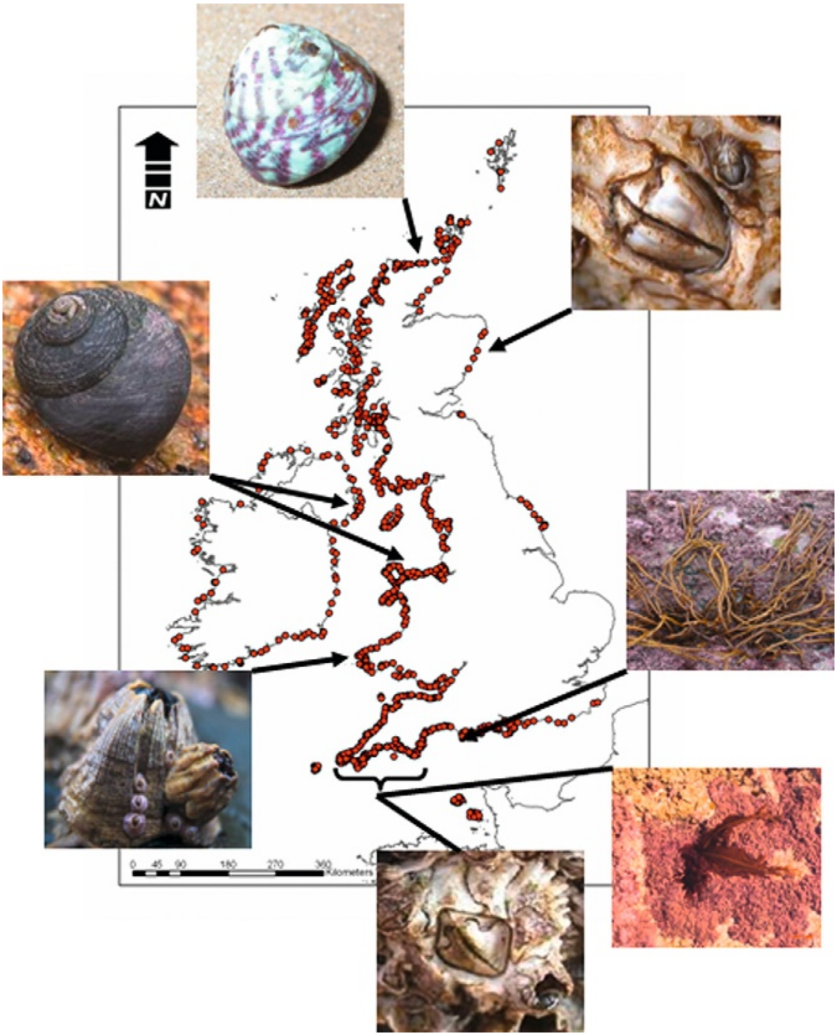

FIGURE 1 Rocky shores in Britain where survey data has been collected in the 1950s and 2000s. Clockwise from bottom left, warm water species which have extended their northern limits; *Perforatus perforatus*, *Osilinus lineatus*, *Gibbula umbilicalis*, *Chthamalus montagui*, *Bifurcaria bifurcata*. Cold water species which have shown contractions in their southern range edge: *Alaria esculenta, Semibalanus balanoides.*

of up to 50 km per decade. This rate is much faster than the average movement of 6.1 km per decade for terrestrial species' ranges [84] and is concordant with northward shifts in plankton recorded in British coastal waters (see Chapter 12 in this volume). The limpet *Patella rustica* has recently bridged a historical gap in its distribution in north Portugal during a period of weakened upwelling in coastal waters [79]. Several factors may be responsible, including increase in sea surface temperature (SST), decrease in upwelling strength in the southern Bay of Biscay and an increase in the strength of the Western Iberian Shelf Current, all of which are driven by the global climate.

Saccharina latissima (*Laminaria saccharina*) has disappeared from large areas across northern Europe during the last decade, with significant losses of populations along the coasts of Scandinavia, Helgoland and southern Brittany. No such decline has been recorded in populations of this macroalga on British coastlines, however [64], suggesting that the causal factor may not be climatic, but potentially disease-related.

In the Mediterranean, influxes of warmer water and propagules of tropical species from the Atlantic, combined with lessepian migration of species from the Red Sea via the Suez canal and human introduction of exotic species are altering ecosystem structure with potential impacts on the trophic web [86]. Marine caves have also been impacted by increases in a warm water mysid and severe declines in an endemic cold water congener [87].

Species of cold water origin including the barnacle *Semibalanus balanoides* [88], tortoiseshell limpet *Tectura testudinalis* and the brown macroalga *Alaria esculenta* [65,89] have shown retractions in the southern range limits and decreases in abundance in Britain and Europe during the last few decades.

Surveys of macroalgal distributions along the coast of Portugal during the 1950s, 1960s [90,91] and the 2000s [92] have identified ~120 conspicuous species that have shown significant alterations in the location of a range edge between these periods. Warm water species have all shifted their high latitude range limits further north, with significant correlations between distributional movement and mean annual inshore SST since 1941 [93]. Species classified as cold water in origin displayed both north and south shifts with no significant change when considered as a group. This alternative response may be in part due to the grouping of these species for this study, some of which are non-native, and others that are widely considered to have a cosmopolitan distribution throughout Europe rather than a warm or cold affinity [76].

2.2.2. Arctic

The blue mussel *Mytilus edulis* extended its distribution from the Norwegian mainland north, by 500 km to Bear Island on the Svalbard archipelago between 1977 and 1994 [94], and was found on the Arctic island of Svalbard itself for the first time in 1000 a after a period of anomalously warm Atlantic seawater influx between 2002 and 2004 [95,96]. This reappearance represented a huge poleward shift in distributional limits of ~1000 km, probably due to transport of pelagic larvae north in the warm water current. However, it is not known whether these populations are sustainable or if the prevailing climate is still too cold for this species to reproduce and survive at such high latitudes.

2.2.3. United States

Studies of rocky shores on both the Atlantic and Pacific coasts of the US date back to the early 1900s, but are mostly limited to recent decades, stemming from the growing awareness of the need for datasets of broad spatial and temporal coverage to track and predict impacts of global environmental change [97,98]. Both geography and oceanography have a large influence on intertidal community structure along the Pacific coast of the USA. In warm-regime years, some species from the Californian biogeographic province of the east Pacific have extended their ranges north into higher latitudes [99,100]. Additional biogeographic shifts have been inferred from increases in the abundance of warm versus decreases in the abundance of cold water gastropods, limpets and anthazoans between the early 1930s and the 1990s at a fixed site in Monterey Bay, California [38,102]. These alterations in the relative dominance of co-occurring species have changed the assemblage composition to a more typically warm-water community. The southern neogastropod *Kelletia kelletii* shifted its biogeographic range northwards in the California region of the northeast Pacific between the late 1970s/early 1980s and the 2000s [103,104]. Fossil records and surveys from the 1830s to the present illustrate that this is the first recorded extension beyond Point Conception, and coincided with strong warming of SST during the late 1900s [104]. *Codium fragile*, a warm water green alga has appeared in the Gulf of Maine on the east coast of the US since the 1970s as summer sea temperatures have increased sufficiently to facilitate successful reproduction [105].

2.2.4. Southern Hemisphere

Both Australia and New Zealand have a very high number of endemics due to their extensive history of geographic isolation from other temperature regions [106,107]. In such regions, reductions in abundance and geographic extent may lead to species becoming globally extinct. In Australia, new research programmes have been initiated to track the rate of biogeographic shifts of rocky intertidal species [108] but data is still sparse for this region. Tropical species of rockpool fishes are already being found at temperate latitude locations on the east coast as coastal water temperatures have increased [109]. Temperate species of kelp that form a dense zone from the low intertidal to shallow subtidal in Tasmania have been continually declining due to the direct impact of rising sea temperatures [110,111]. The decline has been exacerbated by intensive grazing from the spread of the warm water long-spined sea urchin *Centrostephanus rodgersii* from the mainland since the 1960s [112] and increases in abundance of the warm water urchin *Janus edwardsii* and the abalone *Haliotis rubra* [108]. The western rock lobster, *Parulirus cygnus* is the most important single species fishery in Australia [113]. Fisheries landings correlate strongly with the strength of the Leeuwin Current, which drives cross shelf transport of larvae and hence productivity of the stock [113]. The Leeuwin Current strength is highly correlated with ENSO events, with a weakening during El Niño years. Since the 1970s, El Niño events have become more common [114], resulting in more frequent depressions in the size of the lobster fishery.

New Zealand has little quantitative data for intertidal species covering the entire coastline, although extensive time-series exist for individual locations ([115] and Ballantine, unpublished data). Research began in 2008 to quantitatively survey the New Zealand rocky coastline to establish a baseline from which future climate-induced shifts in species distributions and ecosystem-level responses can be measured [116]. Experiments show that the mussel *Perna canaliculus* is less tolerant to warm air temperatures than the co-occurring *Mytilus* spp. on New Zealand shores [117] and exhibits reduced growth and reproductive effort when transplanted to higher intertidal elevations, indicating potentially deleterious effects of climate change. This species typically inhabits the lowshore and damp, shaded regions of the mid-shore and thus may not be subjected to as severe exposures as under experimentally manipulated conditions.

2.2.5. South Africa

Little climate related research has been published from the African continent. Range extensions and population-level changes were reported for warm water rocky intertidal species of limpets (*Patella longicosta*, *P. oculus*) and winkle (*Oxystele variegata*). Recruitment failure was observed in the cold water limpet *P. granatina* in South Africa in response to the unusually warm surface temperatures in the southern Benguela current (around South Africa) in 1982/1983 [118] probably connected to the strong 1982/1983 El Niño event in the Pacific [119]. Whilst there is plenty of evidence for species expanding their northern range limits there is less for contraction of southern limits. This issue stems in part from the lack of knowledge of both past and present locations of southern biological limits of many intertidal species, and the paucity of data collected from southern limit populations, which tend to lie in African or South American coastal waters.

2.3. Extreme Weather Events

The extreme cold winter of 1962/1963 in Britain substantially cut back northern range limits of many intertidal species as a direct result of exposure to sub-zero temperatures. Communities in north Wales were particularly severely impacted due to low water spring tides occurring in the early hours of the morning, when air temperatures are at their lowest. Populations were less affected further south in Wales and England due to low water occurring around mid-day, and northern limits were re-located in these regions [120]. The northern range edge of *O. lineatus* in north Wales did not show much recovery from the retraction caused by the extreme cold winter of 1962/1963 until the 1980s. In the intervening two decades, the range has re-extended by ~100 km around the coastline and multi-age, breeding populations have become established within 15 km of the previous limits [121].

Heatwave events are becoming more common during the current period of rapid global environmental change, and have also caused catastrophic mortalities of intertidal species including the Pacific seastar *Pisaster ochraceus* (Harley, personal communication), the mussel *M. edulis* and macroalgae (Mieszkowska, personal observation) due to exposure to high air temperatures. Interestingly, survival and foraging behavior of *P. ochraceus* does not appear to be negatively influenced by chronic, less severe increases in aerial temperature [122], suggesting that it will cope with global warming over long time periods as long as intense thermal shocks do not occur frequently. Although extreme weather events can cause temporary alterations in range limits of intertidal species, it is the longer-term climatic trends that appear to determine the biogeographic limits and large-scale distributional shifts.

2.4. Interactions

Increasing numbers of species from warm climatic regions are beginning to replace those with colder climate affinities in temporal regions, leading to alterations in the composition of local assemblages [76,101,102,123,124]. These local scale changes will also facilitate the pole-ward spread of species by altering the ratio of extinction to colonisation events within range edge populations. The northern cold water species of barnacle *S. balanoides* and limpet *Patella vulgata* have also declined in abundance relative to southern warm water barnacles (*Chthamalus* species) and limpets (*P. depressa*) in Britain and northern Europe [76,125,126]. Models built and tested using the long-term barnacle time-series for Britain show that this rate is increasing, and *S. balanoides* are predicted to have been completely replaced by *Chthamalus* spp. in south west England between 2060 and 2080. Climate change is also altering facilitative interactions. The cold water limpet, *P. vulgata*, preferentially locates its homescar under the shade of the macroalgae *Fucus vesiculosus*. When *F. vesiculosus* is experimentally removed from shores to simulate the impacts of climate warming, significant mortality is observed in *P. vulgata*, with surviving individuals relocating their homescars. In contrast, the warm water congener *P. depressa* does not suffer increased mortality and does not alter its location [72,127].

3. MECHANISMS

While correlational biogeographic studies can be used to obtain probabilistic maps of species occurrence and generate testable hypotheses, they cannot provide information on cause and effect [84,128]. In order to accurately predict the rate and extent of future biogeographic shifts in species distributions, the biological mechanisms driving these changes need to be better understood. Physical, ecological, evolutionary and physiological factors acting on the processes of reproduction, birth, dispersal, recruitment and mortality are all involved in shaping species' ranges [25,129–131] and must also be considered when studying the effects of a changing environment. Mechanistic responses to climate warming have been detected from the cellular and molecular to the organismal and population levels of biological organisation.

3.1. Thermotolerance

Most species of plants and animals are able to withstand a certain degree of thermal stress due to increased production of heat shock proteins (hsp), which reverse the unfolding of cellular proteins under elevated or reduced temperatures and remove badly damaged proteins from the cell [132]. Geographical trends in increased heat shock protein expression have been shown for intertidal species such as *Nucella canaliculata*, a temperate intertidal whelk occurring along rocky coastlines of the north east Pacific. The increase in hsp expression in southern populations indicates that individuals are more stressed at the southern range edge than in range centre [133]. The purple urchin, *Strongylocentrotus purpuratus* also displays geographic variation in genetic regulation of hsp induction in response to increasing temperatures, which reflects the level of thermal stress experienced at different locations along the biogeographic distribution [134]. hsps may therefore be a sensitive tool with which to monitor the extent of climate-induced stress in intertidal species.

3.2. Reproduction and Recruitment

Variations in sea and air temperatures have also long been known to influence the physiological performance and reproductive success of marine species [14,45,137–141]. Synchronous increases in abundance have been recorded in populations of southern trochids throughout Britain and northern France since the mid-1980s. These increases in abundance are linked to warming in the regional climate since the mid-1908s due to increased frequency of annual recruitment success [65]. The mechanisms behind these changes are earlier onset of annual reproductive cycles of southern trochid gastropods *Osilinus lineatus* and *Gibbula umbilicalis* in response to milder winters and warmer springs, coupled with increased survival of newly settled recruits (often the most sensitive lifestage to environmental stress) exposed to milder, shorter winters on the shore [121]. The annual reproductive cycles of southern limpets are also starting earlier and lasting longer in south-west Britain. In contrast, less than 20% of the population of northern limpets is reaching gonad development stages at which spawning can occur [135]. Recruitment can also be influenced by oceanographic features, which can control dispersal of the pelagic larval phase. Large-scale surveys of the Pacific coast of the USA have demonstrated a tight correlation between SST and recruitment, and large intraspecific differences in recruitment rate along the biogeographic range of keystone barnacle and mussel species [98] demonstrating the potential for alterations in recruitment success in a warming climate.

4. ADDITIONAL IMPACTS OF GLOBAL CHANGE

4.1. Ocean Acidification

Dealt with in Chapter 21, ocean acidification is predicted to impact upon rocky shore species such as barnacles, limpets and topshells during the second half of the twenty-first century. Potential synergistic effects of warming seas and decreases in oceanic pH are as yet unknown, and may also vary depending on the position of the organism within the latitudinal distribution of the species.

4.2. Coastal Zone Development

Other facets of global environmental change are rising sea levels and extreme weather events [142]. Many areas of low-lying coastline are facing greater risk of flooding around the world. This risk has led to proliferation of coastal defences to protect property, agricultural land and infrastructure such as roads and railways. Localised defences can scale up to whole coastlines when multiple structures are built along large sections of the land–sea interface. This has occurred in the Mediterranean [143,144] and on the coasts of the northern Irish Sea and eastern English Channel and North Sea. These developments can have severe impacts with loss of sedimentary habitats and their replacement with artificial rocky shores with an impoverished biota [144]. Such large-scale coastal modification can also influence biogeographic processes. Recent range extensions of rocky shore species in the eastern English Channel are probably the result of a combination of increased reproductive success and the provision of artificial habitat (sea defenses, marinas, seaside piers) as stepping stones for advance across patches of unfavourable habitat [145].

4.3. Climate Change and Non-Native Species

Introductions of non-native species are increasing globally due to increases in maritime shipping, aquaculture, mariculture, the aquarium trade and imported live bait. Ballast water, hull fouling and intensive culture practices have been identified as high risk vectors for the introduction of invasive non-native species into the marine environment. There is also evidence that such introductions are more likely in a warmer world [146]. The importation of shellfish species for aquaculture and mariculture businesses in the United Kingdom (e.g., the Pacific oyster *Crassostrea gigas*, the Mediterranean blue mussel

M. galloprovinicialis) have facilitated the spread of these species into natural ecosystems in Britain, Europe and the USA. Inshore sea temperatures are now warm enough to allow successful reproduction of these introduced species, resulting in aggressive colonisation of areas outside their site of cultivation, often to the detriment of native congeners which are outcompeted by the non-native species. Once non-natives become established in the natural environment there are few barriers to prevent further spread. The introduction of non-native species from different biogeographical realms can be considered as a facet of global environmental change with the potential for global homogenisation of biotas and hence decreased biodiversity.

5. CONCLUSIONS

Intertidal invertebrates and algae are already responding to global climate warming, with shifts in biogeographic distributions away from warmer low latitude regions towards the cooler poles. In general, the rate of recession of northern species is not as fast as the rate of advance of southern species. The rate and extent of change is also species specific, leading to alterations in community composition with knock-on effects for ecosystem structure and functioning and likely declines in biodiversity in temperate-tropical regions. These shifts are ultimately being driven by physiological responses to temperature, with additional indirect impacts from species interactions, oceanographic processes, coastal zone development and habitat availability. There is still a paucity of data with long temporal and wide spatial coverage, which is hampering the detection of environmentally driven changes in coastal ecosystems, especially in the southern hemisphere. It is of vital importance that research focuses on the combination of maintaining these valuable datasets with the development of experimental research to determine the mechanisms underpinning the observed responses, so that we may be better placed to predict the future impacts on intertidal systems from our rapidly changing environment.

ACKNOWLEDGEMENTS

The author wish to thank K. Richardson for comments and advice which helped to improve this chapter; the MarClim project www.mba.ac.uk/marclim and MarClim funding consortium; and B.T. Helmuth, B.R. Broitman and E.S. Poloczanska for assistance with publications.

REFERENCES

1. P.H. Gosse, Tenby: A Seaside Holiday, John van Voorst, Paternoster Row, London, 1856, pp. 1–397.
2. C. Kingsley, Glaucus; or, the Wonders of the Shore, Macmillan and Company, Cambridge, 1856, pp. 1–168.
3. J.H. Orton, Nature 123 (1929) 14–15.

4. M.S. Doty, Ecology 27 (1946) 315–328.
5. J.H. Connell, Ecology 42 (1961) 710–723.
6. R.T. Paine, Am. Nat. 100 (1966) 65–75.
7. R.T. Paine, Oecologia 15 (1974) 93–120.
8. T. Carefoot, Pacific Seashores, J.J. Douglas, Vancouver (1977) 1–208.
9. R.T. Paine, J.M. Levine, Ecol. Monogr. 51 (1981) 145–178.
10. J.R. Lewis, The Ecology of Rocky Shores, English Universities Press, London, 1964, pp. 1–323.
11. P.K Dayton, Ecol. Monogr. 41 (1971) 351–389.
12. B.A. Menge, Ecol. Monogr. 46 (1976) 355–393.
13. A.J. Southward, Nature 175 (1955) 1124–1125.
14. A.J. Southward, J. Mar. Biol. Assoc. UK 36 (1957) 323–334.
15. R.T. Paine, JAE 64 (1994) 425–427.
16. B.T. Helmuth, M.W. Denny, Limnol. Oceanogr. 48 (2003) 1338–1345.
17. B.A. Foster, Mar. Biol. 8 (1971) 12–29.
18. J.A. Kitzes, M.W. Denny, Biol. Bull. 8 (2005) 114–119.
19. J. Davenport, H. Macalister, J. Exp. Mar. Biol. Ecol. 76 (1996) 985–1002.
20. R. Li, S.H. Brawley, Mar. Biol. 144 (2004) 205–213.
21. L.E. Burnett, Am. Zool. 37 (1997) 633–640.
22. R.F. Service, Science 305 (2004) 1099.
23. E.P. Dahlhoff, B.A. Menge, Mar. Ecol. Prog. Ser. 144 (1996) 97–107.
24. L.W. Hutchins, Ecol. Monogr. 17 (3) (1947) 325–335.
25. R.M. MacArthur, Geographical Ecology: patterns in the distribution of species, Harper & Rowe, New York. pp. 269.
26. J.R. Lewis, Hydrobiologia 142 (1986) 1–13.
27. J.H. Brown, G.C. Stevens, D.M. Kaufman, Annu. Rev. Ecol. Syst. 27 (1996) 597–623.
28. J.H. Brown, Am. Nat. 124 (1984) 255–279.
29. J.H. Stillman, G.N. Somero, JEB. 199 (1996) 1845–55.
30. A.A. Hoffmann, P.A. Parsons, Extreme Environmental Change and Evolution, Cambridge University Press, Cambridge, 1997, p. 235.
31. B. Helmuth, C.D. Harley, P.M. Halpin, M. O'Donnell, G.E. Hofmann, C.A. Blanchette, Science 298 (2002) 1015–1017.
32. J.H. Stillman, Integr. Comp. Biol. 42 (2002) 790–796.
33. M.H. Carr, J.E. Neigel, J.A. Estes, S. Andelman, R.R. Warner, J.L. Largier, Ecol. Appl. 13, S90–S107.
34. P.E. Smith, Can. J. Fish. Aquat. Sci. 42 (1985) 69–82.
35. S. Jenouvrier, C. Barbraud, H. Weimerskirch, JAE 72 (2003) 576–587.
36. J.R. Lewis, Mar. Biol. Ann. Rev. 14 (1976) 371–390.
37. S.J. Hawkins, R.G. Hartnoll, J. Exp. Mar. Biol. Ecol. 62 (1982) 271–283.
38. J.P. Barry, C.H. Baxter, R.D. Sagarin, S.E. Gilman Science 267 (1995) 672–674.
39. J.R. Lewis, R.S. Bowman, M.A. Kendall, P. Williamson, Neth. J. Sea Res. 16 (1982) 18–28.
40. B. Helmuth, N. Mieszkowska, P. Moore, S.J. Hawkins, Annu. Rev. Ecol. Evol. Syst. 37 (2006) 373–404.
41. M.D. Bertness, G.H. Leonard, J.M. Levine, J.F. Bruno, Oecologia 120 (1999) 446–450.
42. R.D. Sagarin, S.D. Gaines, J. Biogeogr. 29 (2002) 985–997.
43. C.D.G. Harley, A.R. Hughes, K. Hultgren, B.G. Miner, C.J.B. Sorte, C.S. Thornber, L.F. Rodriguez, L. Tomanek, S.L. Williams, Ecol. Lett. 9 (2006) 228–241.
44. J.P. de Tournefort, Relation d'un voyage du Levant (1717). Paris. pp. 288.
45. J. Grinnell, Am. Nat. 51 (1917) 115–128.

46. J.H. Orton, J. Mar. Biol. Assoc. UK 2 (1920) 299–366.
47. W.A. Setchell, The temperature interval in the geographical distribution of marine algae (1920). Science 187–190.
48. S.A. Cain, Foundations of Plant Geography, Harper Brothers, New York, London, 1944.
49. L.W. Hutchins, Ecol. Monogr. 17 (1947) 325–335.
50. E.V. Wulff, An Introduction to Historical Plant Geography (translated from the Russian by E. Brissenden), Waltham, MA, 1950.
51. H.G. Andrewartha, L.C. Birch, The Distribution and Abundance of Animals, University of Chicago Press, Chicago, 1954.
52. E.C. Pielou, Biogeography, Wiley-Interscience, Chichester, 1979.
53. A.M. Breeman, Helgoland Marine Research 42 (1988) 199–241.
54. G. Michanek, Bot. Mar. 22 (1979) 375–391.
55. K. Luhning, Seaweeds their environment, biogeography and ecophysiology (1990) John Wiley & Sons, London, 1–61.
56. G.M. Voskoboinikov, A.M. Breeman, C. van den Hoek, V.N. Makarov, E.V. Shoshina, Bot. Mar. 39 (1996) 341–346.
57. F.J. Molenaar, A.M. Breeman, J. Phycol. 33 (1997) 330–343.
58. S. Orfanidis, A.M. Breeman, J. Phycol. 35 (1999) 919–930.
59. A.J. Southward, Nature 165 (1950) 408.
60. D.R. Franz, A.S. Merrill, Malacologia 19 (1980) 209–225.
61. G.J. Vermeij, Evolution 36 (1982) 561–580.
62. J.R. Lewis, The Ecology of Rocky Shores, English Universities Press, London, 1964.
63. M.A. Kendall, J.R. Lewis, Hydrobiologia 142 (1986) 15–22.
64. N. Mieszkowska, R. Leaper, P. Moore, M.A. Kendall, M.T. Burrows, D. Lear, E. Poloczanska, K. Hiscock, P.S. Moschella, R.C. Thompson, R.J. Herbert, D. Laffoley, J. Baxter, A.J. Southward, S.J. Hawkins, J. Mar. Biol. Assoc. UK Occasional Publ. 20 (2005) 1–55.
65. N. Mieszkowska, M.A. Kendall, S.J. Hawkins, R. Leaper, P. Williamson, N.J. Hardman-Mountford, A.J. Southward, Hydrobiologia 555 (2006) 241–251.
66. R.G. Pearson, T.P. Dawson, Glob. Ecol. Biogeogr. 12 (2003) 361–371.
67. G.R. Walther, E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, T.J.C. Fromentin, O.H. Guldberg, F. Bairlein, Nature 416 (2002) 389–395.
68. A.J. Davies, L.S. Jenkinson, J.H. Lawton, B. Shorrocks, S. Wood, Nature 391 (1998) 783–786.
69. R.W. Brooker, R.W. Travis, E.J. Clark, C. Dytham, J. Theor. Biol. 245 (2007) 59–65.
70. E. Fischer-Piette, J. Conch. Paris 79 (1935) 5–66.
71. E. Fischer-Piette, J. Linn. Soc. Zool. 40 (1936) 181–272.
72. E. Fischer-Piette, Ann. Insitut. Ocen. Monaco 31 (1955) 37–124.
73. D.J. Crisp, E. Fischer-Piette, Ann. Insitut. Ocen. Monaco 36 (1959) 276–381.
74. A.J. Southward, D.J. Crisp, Proc. R. Ir. Acad. 57 (1954) 1–29.
75. D.J. Crisp, A.J. Southward, J. Mar. Biol. Assoc. UK 37 (1958) 157–208.
76. A.J. Southward, S.J. Hawkins, M.T. Burrows, J. Therm. Biol. 20 (1995) 127–155.
77. M.A. Kendall, J.R. Lewis, Hydrobiologia 142 (1986) 15–22.
78. M.A. Kendall, J. Moll. Stud. 53 (1987) 213–222.
79. F.P. Lima, N. Queiroz, P.A. Ribeiro, S.J. Hawkins, A.M. Santos, J. Biogeogr. 33 (2006) 812–822.
80. B. Helmuth, J.G. Kingsolver, E. Carrington, Ann. Rev. Phys. 67 (2005) 177–201.
81. C. Parmesan, S. Gaines, L. Gonzales, D.M. Kaufman, J. Kingsolver, A.T. Peterson, R. Sagarin, Oikos 108 (2005) 58–75.
82. P. Moore, S.J. Hawkins, R.C. Thompson, Mar. Ecol. Prog. Ser. 334 (2007) 11–19.

83. R.J.H. Herbert, S.J. Hawkins, M. Sheader, A.J. Southward, J. Mar. Biol. Assoc. UK 83 (2003) 73–82.
84. C. Parmesan, G. Yohe, Nature 421 (2003) 37–42.
85. I. Bartsch, C. Wiencke, K. Bischof, C.M. Buchholz, B.H. Buck, A. Eggert, P. Feuerpfeil, D. Hanelt, S. Jacobsen, R. Karez, U. Karsten, M. Molis, M.Y. Roleda, H. Schubert, R. Schumann, K. Valentin, F. Weinberger, J. Wiese. The genus Laminaria sensu lato: recent insights and developments, European Journal of Phycology, 43(1) (2008) 1–86, doi:10.1080/09670260701711376.
86. C.N. Bianchi, Hydrobiologia 580 (2007) 7–21.
87. P. Chevaldonné, C. Lejeusne, Ecol. Lett. 6 (2003) 371–379.
88. D.S. Wethey, S.A. Woodin, Hydrobiologia 606 (2008) 139–151.
89. T. Vance, MRes Thesis, University of Plymouth, 2005.
90. F. Ardré, Port. Acta Biol. 10 (1970) 1–423.
91. F. Ardré, Bull. Centre d'Etudes Rech.Sci. Biarritz 8 (1971) 359–574.
92. F.P. Lima, P.A. Ribeiro, N. Queiroz, S.J. Hawkins, A.M. Santos, Glob. Change Biol. 13(12) (2007) 2592–2604.
93. R.T. Lemos, H.O. Pires, Intern. J. Clim. 24 (2004) 511–524.
94. J.M. Wesławski, M. Zajączkowski, J. Wiktor, M. Szymelfenig, Polar Biol. 18 (1997) 45–52.
95. O. Salvigsen, Nor. Geogr. Tidsskr. 56 (2002) 56–61.
96. J. Berge, G. Johnsen, F. Nilsen, B. Gulliksen, D. Slagstad, Mar. Ecol. Prog. Ser. 303 (2005) 167–175.
97. C.A. Blanchette, C.M. Miner, P.T. Raimondi, D. Lohse, K.E.K. Heady, B.R. Broitman, J. Biogeogr. (2008) in press.
98. B.R. Broitman, C.A. Blanchette, B.A. Menge, J. Lubchenco, P.A. Raimondi, C. Krenz, M. Foley, D. Lohse, S.D. Gaines, Ecol.Monogr. 78(3) (2008) 403–421.
99. R.S. Burton, Evolution 52 (1998) 734–745.
100. M.E. Hellberg, D.P. Balch, K. Roy, Science 292 (2001) 1707–1710.
101. J.P. Barry, C.H. Baxter, R.D. Sagarin, S.E. Gilman, Science 267 (1995) 672–674.
102. R.D. Sagarin, J.P. Barry, S.E. Gilman, C.H. Baxter, Ecol. Monogr. 69 (1999) 465–490.
103. T.J. Herrlinger, Veliger 24 (1981) 78.
104. D. Zacherl, S.D. Gaines, S.I. Lonhart, J. Biogeogr. 30 (2003) 913–924.
105. L.G. Harris, M.C. Tyrrell, Biol. Invasions 3 (2001) 9–21.
106. G.C.B. Poore, State of the Marine Environment Report for Australia: The Marine Environment - Technical Annex: 1 Compiled by Leon P. Zann Great Barrier Reef Marine Park Authority, Townsville Queensland, Ocean Rescue 2000 Program, Department of the Environment, Sport and Territories, Canberra, 1995 ISBN 0 642 17399 0.
107. R. Tsuchi, S. Nishimura, A.G. Beu, Tectonophysics 281 (1997) 83–97.
108. E.S. Poloczanska, R.C. Bobcock, A. Butler, A.J. Hobday, O. Hoegh-Guldberg, T.J. Kunz, R. Matear, D.A. Milton, T.A. Okey, A.J. Richardson, Oceanogr. Mar. Biol. Ann. Rev. 45 (2008) 407–478.
109. S.P. Griffiths, Est. Coast. Shelf Sci. 58 (2003) 173–186.
110. K.S. Edyvane, Final Report for Environment Australia, Department of Primary Industries, Water and Environment, Hobart, 2003.
111. G.J. Edgar, C.R. Samson, N.S. Barrett, Conserv. Biol. 19 (2005) 1294–1300.
112. C. Johnson, S. Ling, J. Ross, S. Shepherd, K. Miller, Tasmanian Aquaculture and Fisheries Institute, Australia, FRDC Project No. 2001/004, 2005.
113. N. Caputi, C. Chubb, A. Pearce, Mar. Freshw. Res. 52 (2001) 1167–1174.
114. K.E. Trenberth, Bull. Am. Met. Soc. 78 (12) (1997) 2771–2777.

115. J.E. Morton, V.J. Chapman, Rocky Shore Ecology of The Leigh Area, North Auckland, University of Auckland Press, Auckland, 1968, 44pp.
116. N. Mieszkowska, C. Lundquist, N. Z. J. Mar. Freshw. Res. in review.
117. L.E. Petes, B.A. Menge, G.D. Murphy, J. Exp. Mar. Biol. Ecol. 351 (2007) 83–91.
118. G.M. Branch, S.A. J. Sci. 80 (1984) 61–65.
119. R.T. Barber, F.P. Chavez, Science 222 (1983) 1203–2110.
120. D.J. Crisp, JAE 33 (1964) 165–210.
121. N. Mieszkowska, S.J. Hawkins, M.T. Burrows, M.A. Kendall, J. Mar. Biol. Assoc. UK 87 (2007) 537–545.
122. E. Sanford, J. Exp. Mar. Biol. Ecol. 273 (2002) 199–218.
123. J.A. McGowan, D.B. Chelton, A. Conversi, CalCOFI Report, 37 (1996).
124. S.J. Holbrook, R.J. Schmitt, J.S.J. Stevens, Ecol. Appl. 7 (1997). pp. 1299–1310.
125. A.J. Southward, J. Mar. Biol. Assoc. UK 71 (1991) 495–513.
126. S.J. Hawkins, P. Moore, M. Burrows, E. Poloczanska, N. Mieszkowska, S.R. Jenkins, R.C. Thompson, M. Genner, A.J. Southward, Hydrobiologia, Climate Research, 37 (2/3), (2008) pp. 123–133.
127. P. Moore, R.C. Thompson, S.J. Hawkins, J. Exp. Mar. Biol. Ecol. 344 (2007) 170–180.
128. M.J. Fortin, T.H. Keitt, B.A. Maurer, M.L. Taper, D.M. Kaufman, T.M. Blackburn, Oikos 108 (2005) 7–17.
129. R.N. Carter, S.D. Prince, Nature 293 (1981) 644–645.
130. D.M. Lodge, in: P.M. Karieva, J.G. Kingsolver, R.B. Huey (Eds.), Biotic Interactions and Global Change, Sinauer, Sunderland, MA, 1993, pp. 367–387.
131. J.J. Lennon, J.R.G. Turner, D. Connell, Oikos 78 (1997) 486–502.
132. S. Lindquist, Ann. Rev. Biochem. 55 (1986) 1151–1191.
133. C.J.B. Sorte, G.E. Hofmann, Mar. Ecol. Prog. Ser. 274 (2004) 263–268.
134. C.J. Osovitz, G.E. Hofmann, J. Exp. Mar. Biol. Ecol. 327 (2005) 134–143.
135. P. Moore, PhD Thesis, University of Plymouth, 2005.
136. V.L. Loosanoff, Science 102 (1945) 124–125.
137. R.A. Boolootian, in: R.A. Boolootian (Ed.), Physiology of Echinodermata, Wiley, New York, 1966, pp. 561–614.
138. B. Cocanour, K. Allen, Comp. Biochem. Physiol. 20 (1967) 327–331.
139. R.E. Stephens, Biol. Bull. 142 (1972) 132–134.
140. P.W. Frank, Mar. Biol. 31 (1975) 181–192.
141. B.T. Helmuth, G.E. Hofmann, Biol. Bull. 201 (2001) 371–381.
142. IPCC, Climate Change 2007: The Scientific Basis, IPCC 2007 1–996.
143. L. Airoldi, M. Abbiati, M.W. Beck, S.J. Hawkins, P.R. Jonsson, D. Martin, P.S. Moschella, A. Sundelöf, R.C. Thompson, P. Åberg, Coast. Eng. 52 (2005) 1073–1087.
144. P.M. Moschella, M. Abbiati, P. Åberg, L. Airoldi, J. Anderson, J.M. Bacchiocchi, F. Bulleri, G.E. Dinesen, M. Frost, E. Gacia, L. Granhag, P.R. Jonssonn, M.P. Satta, A. Sundelöf, R.C. Thompson, S.J. Hawkins, Coast. Eng. 52 (2005) 1053–1071.
145. S.J. Hawkins, N. Mieszkowska, P. Moschella, unpublished data.
146. J.J. Stachowicz, J.R. Terwin, R.B. Whitlatch, R.W. Osman, PNAS 99 (2002) 15497–15500.