



Explaining Ocean Warming:

Causes, scale, effects and consequences

Edited by D. Laffoley and J. M. Baxter

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3.7 Impacts and effects of ocean warming on intertidal rocky habitats

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Summary

- Intertidal rocky habitats comprise over 50% of the shorelines of the world, supporting a diversity of marine life and providing extensive ecosystem services worth in the region of US\$ 5-10 trillion per year.
- They are valuable indicators of the impacts of climate change on the wider marine environment and ecosystems.
- Changes in species distributions, abundance and phenology have already been observed around the world in response to recent rapid climate change.
- Species-level responses will have considerable ramifications for the structure of communities and trophic interactions, leading to eventual changes in ecosystem functioning (e.g. less primary producing canopy-forming algae in the North-east Atlantic).
- Whilst progress is made on the mitigation¹ required to achieve goals of a lower-carbon world, much can be done to enhance resilience to climate change. Managing the multitude of other interactive impacts on the marine environment, over which society has greater potential control (e.g. overfishing, invasive non-native species, coastal development, and pollution), will enable adaptation¹ in the short and medium term of the next 5-50 years.

¹ See IPCC Assessment Reports (2005 onwards) for usage.

Ocean warming effect	Consequences
Species range extensions and retractions	Changes in composition and structure of intertidal communities Reduced primary production and supply of detritus to inshore food webs Some reduction in provisioning and regulating services
Changes in vertical shore distributions	Changes in composition and structure of intertidal communities Reduced extent of suitable habitat for intertidal organisms Some reduction in provisioning and regulating services
Shifts in phenology	Promotion of multi-brooding warm-water species Increased reproductive failure of single-brooding cold-water species Changes in composition and structure of intertidal communities Trophic mismatches may have ramifications for commercial fisheries
Species invasions	Promotion of nuisance and fouling species Reduced diversity of native species Changes in composition and structure of intertidal communities Potential positive and negative effects on commercial fisheries and regulatory and cultural services
Proliferation of sea defences (adaptation to rising and stormier seas)	Loss and disturbance of natural sedimentary habitats and species Changes in connectivity as a result of ocean sprawl Assisted spread (via stepping stones) of non-native species Assisted range shifts (via stepping stones) of native species Potential positive and negative effects on primary production and cultural services
Range extension, species invasion and proliferation of sea defences combined	Promotion of biotic homogenization with negative implications for all ecosystem service provision

3.7.1 Introduction

The intertidal zone is the most accessible part of the ocean. Shoreline habitats have been heavily-exploited since the time of hunter-gatherers and increasingly used for recreation by modern societies. It is also the best-studied part of the ocean with formal scientific investigation going back to the time of Aristotle (Hawkins *et al.*, 2016). We focus here on rocky shores for three main reasons. Firstly, they have been subject to extensive broad-scale and long-term studies in many parts of the world – particularly in the North-east Atlantic and North-east Pacific. They have also been the focus

of considerable field experimentation because of their ease and tractability for manipulative study (Connell, 1972; Paine, 1994; Hawkins *et al.*, 2016). Thus, the link between pattern and process in these systems is well-established, enabling better interpretation of the direct and indirect effects of climate change. Secondly, rocky intertidal organisms must contend regularly with both marine and atmospheric (at low tide) conditions on a daily basis, and so are subject to challenges posed by both aquatic and aerial environmental regimes, which are amplified by climate change. Thirdly, fluctuations in intertidal species have been found to mirror changes

in other species further offshore (Southward, 1980; Helmuth *et al.*, 2006b; Mieszkowska *et al.*, 2014a). Rocky shores have, therefore, long been used as easily-observed indicators of the influence of climate fluctuations on the wider marine environment (e.g. Southward and Crisp, 1954; Southward, 1963, 1980, 1991; Southward *et al.*, 1995). They have proved valuable sentinel systems in early detection of recent rapid climate change (Barry *et al.*, 1995; Sagarin *et al.*, 1999; Mieszkowska *et al.*, 2006, 2014b; Hawkins *et al.*, 2009), as well as for forecasting and predicting future trends (Helmuth *et al.*, 2006b; Poloczanska *et al.*, 2008; Hawkins *et al.*, 2009; Wetthey *et al.*, 2011).

Intertidal rocky habitats are directly and indirectly affected by the global environmental changes associated with current climate warming and ocean acidification. In addition they are subject to frequent invasions by non-native species, which has contributed to the global homogenization of biota (e.g. Trowbridge, 1995; Streftaris *et al.*, 2005; Allen *et al.*, 2006; García Molinos *et al.*, 2016). Global-scale influences are often, however, less obvious than acute regional- and local-scale impacts from both land and sea (see Thompson *et al.* (2002) for review). Regional-scale impacts can include the consequences of overfishing on mobile fish and shellfish using the intertidal as feeding or nursery grounds, and eutrophication of enclosed seas. Local-scale impacts can include eutrophication at the scale of enclosed bays or inlets, point-source pollution, coastal development, over-harvesting for food, curios and bait, trampling due to recreational activity, and sedimentary input. Some of these local impacts can scale up to have regional-scale effects (Huston, 1999; Airolidi *et al.*, 2005a). For example, urban coastlines are frequently modified by engineered developments such as port, road and rail infrastructure, industry and housing, as well as sea defences built to reduce erosion or flood risk. This has led to additive effects in terms of hardening and linearization of long stretches of coastlines, and replacement of natural sedimentary habitats by artificial rocky shores, which often support impoverished biodiversity compared with natural shores (discussed further below).

In this section, we discuss rocky intertidal habitats and the observed and predicted effects of climate change on the species and communities that inhabit them. We first summarize the biodiversity and ecosystem services supported by rocky shores, along with the

major factors determining the distribution of species at global, regional and local scales (drawing largely on Raffaelli and Hawkins (1996) and Thompson *et al.* (2002)). The responses of rocky shore species to past climate fluctuations and recent rapid change are then presented, with consideration of the consequences for communities and ecosystem functioning. We focus largely on the North-east Atlantic biogeographic region because of the wealth of broad-scale and long-term studies that provide a baseline, although other global examples are presented. To inform adaptive management to climate change, we then explore the mechanisms and drivers of change, and consider potential interactions with other impacts acting at regional and local scales. Some positive suggestions for adaptation are proposed, including ecologically-sensitive design of sea defences that are built in response to rising and stormier seas.

3.7.2 Intertidal rocky shores and their global and regional significance

3.7.2.1 Definition and extent

At the interface between land and sea, intertidal rocky habitats connect the marine environment with terrestrial habitats beyond the influence of sea spray. The seaward transition towards the subtidal zone is part of a continuum from rocky shore to submerged reef, but the lower intertidal boundary may be considered the lowest level exposed to the air during lowest tides. Shore platforms and reefs often give way, both horizontally and vertically, to depositing boulder and cobble fields, gravel or sand.

Intertidal rocky habitats occur extensively along both open and sheltered coasts globally, comprising well over 50% of the shorelines of the world (Emery and Kuhn, 1982; Davis and Fitzgerald, 2004). The extent of intertidal hard substrata is increasing due to the proliferation of engineered coastal structures such as breakwaters, groynes and sea walls, built to protect people, property and infrastructure from rising and stormier seas (Thompson *et al.*, 2002; Firth *et al.*, 2013a, 2016a). These artificial rocky habitats are not, however, the same as natural rocky shores. Although they are often colonized by common rocky shore organisms, they are frequently found to support less diverse communities (Moschella *et al.*, 2005; Pinn *et al.*, 2005; Firth *et al.*, 2013b, 2016b; Aguilera *et al.*, 2014), with opportunistic and invasive species taking advantage of the novel habitat (Bulleri and Airolidi, 2005;

Glasby *et al.*, 2007; Vaselli *et al.*, 2008; Bracewell *et al.*, 2012; Firth *et al.*, 2015). Nevertheless, in light of the predicted reduction in spatial extent, through loss of natural intertidal rocky habitats as sea levels rise (“coastal squeeze”, e.g. Jackson and McIlvenny (2011)), these artificial structures may provide surrogate habitats for rocky shore organisms (see Para. 3.7.5).

3.7.2.2 Biodiversity and ecosystem services

Rocky shores are home to a wide variety of marine flora and fauna that have upwardly colonized the intertidal zone from fully marine conditions. Thus, they host far fewer organisms of terrestrial evolutionary origin. Seaweeds and sessile animals (e.g. barnacles, sea anemones, bivalves and sponges) find secure attachment on the hard substratum. Mobile animals (e.g. snails, crustaceans and fish) forage for food over the reef at high tide, some taking refuge in abundant pits, pools and crevices when the tide is out (Silva *et al.*, 2008, 2010, 2014; Taylor and Schiel, 2010). Some rocky shore species are considered of particular conservation concern on account of their rarity, for example the highly endangered limpet *Patella ferruginea* and *Scutellastra mexicana* (García-Gómez *et al.*, 2011, 2015). Others are of conservation value due to their importance in ecosystem functioning, for example the reef-building worm *Sabellaria alveolata* (Dubois *et al.*, 2002; Frost *et al.*, 2004).

Intertidal rocky habitats support a number of important ecosystem services for human well-being (The Economics of Ecosystems and Biodiversity: TEEB, 2010). Based on an interpolation of figures presented in a recent valuation of global ecosystem services (Costanza *et al.*, 2014), the estimated value of services supported by intertidal rocky habitats globally may be somewhere in the realm of US\$ 5-10 trillion per year. In terms of *production services*, marine photosynthesis accounts for 50% of total global primary production, of which a considerable proportion is attributable to marine macrophytes in the coastal zone where seaweeds and seagrass detritus drive food webs (Beardall and Raven, 2004; Chung *et al.*, 2011). Highly productive macroalgae are common on rocky shores; the overall productivity of rocky habitats tends to be an order of magnitude higher than sedimentary ones (Bourget and Ricciardi, 1999). Habitat amelioration by seaweed canopies (Thompson *et al.*, 1996; Moore *et al.*, 2007; Teagle *et al.*, 2016; Walls *et al.*, 2016) and trophic exchange (Menge *et al.*, 1997) can lead to successional development of diverse benthic and pelagic marine communities. Detached macroalgae can even subsidise low productivity of

terrestrial ecosystems by export through strandlines (Ince *et al.*, 2007). In terms of *provisioning services*, rocky shores are inhabited by a number of edible species that can be exploited as a food or bait resource, for example seaweeds, mussels, winkles, oysters and limpets (Keough *et al.*, 1993; Kyle *et al.*, 1997; Airolidi *et al.*, 2005b; Martins *et al.*, 2010). They can further provide nursery habitat for juvenile commercial fish and shellfish (Rangeley and Kramer, 1995; Silva *et al.*, 2010). Common and abundant macroalgal species may also be harvested for biofuel production (Maceiras *et al.*, 2011) and for biochemical derivatives used for additives to food, cosmetics and pharmaceuticals (Pereira *et al.*, 2013). Both harvested seaweeds and those collected from strandlines are also used as fertilizer or soil conditioners. In terms of *regulatory services*, intertidal communities can take an important role in regulating environmental conditions. For example, macroalgae (Figure 3.7.1) are important for carbon sequestration and macro-nutrient (nitrogen and phosphorus) removal (Chung *et al.*, 2011), while bivalves and macrophytes are important for water purification (Kohata *et al.*, 2003). Biofiltration is particularly important for regulating water chemistry and controlling potentially-harmful phytoplankton blooms (Hily, 1991; Allen *et al.*, 1992; Newell, 2004; Foullaron *et al.*, 2007). Water filtration by diverse rocky-reef assemblages can therefore be linked to societal benefits for coastal communities (Lamberti and Zanuttigh, 2005). Biogenic reef-forming species and kelp beds also provide regulatory services in terms of natural coastal protection, by attenuating wave energy and stabilizing sediments (Mork, 1996; Naylor and Viles, 2000; Borsje *et al.*, 2011). Finally, in terms of *cultural services*, where rocky shores are close to, and easily-accessed by, coastal communities and tourists, they can support a number of direct and indirect uses. They are highly valued for recreational uses such as rock-pooling, angling, snorkelling and



Figure 3.7.1 *Laminaria digitata*. © John M Baxter.

environmental education (Firth *et al.*, 2013a). As coastal habitats become increasingly threatened by a number of interacting pressures (Thompson *et al.*, 2002; Knights *et al.*, 2013), and canopy algae are suffering widespread declines in many parts of the world (Airoldi and Beck, 2007; Connell *et al.*, 2008; Mangialajo *et al.*, 2008; Mineur *et al.*, 2015), conservation of rocky shores becomes increasingly important to ensure maintenance of these essential ecosystem services.

3.7.2.3 Factors influencing biodiversity in intertidal rocky habitats

The distribution of species on rocky shores around the world is largely driven by broad-scale climatic regimes, associated with latitude and modified by ocean currents and upwelling regimes (Hutchins, 1947; Helmuth *et al.*, 2006b; Fenberg *et al.*, 2015). There are warm- and cold-water adapted species, leading to different species pools able to live in different biogeographic areas. The species pool is ultimately determined by phylogeographic processes associated with the evolutionary origin of species and their subsequent spread in response to tectonic and climatic processes over long geological timescales, including opening and closing of ocean basins (Rivadeneira *et al.*, 2015). Natural biogeographical processes have been altered, however, by human-mediated transport of species around the world. In the ocean this has occurred via transport of organisms fouling ships and in ballast water, and also via accidental and deliberate introductions associated with aquaculture and the ornamental aquarium trade. Marine canals can also enable species to take short-cuts between biogeographic regions. For example, the Suez Canal has acted as a conduit of numerous species from the Indo-Pacific biogeographic realm of the Red Sea to the Mediterranean (so-called Lessepsian migration: Por (1978)). This has had a profound effect on the eastern and wider Mediterranean. Expansions and contractions of glaciation have also had a strong influence on species pools. For example, during the trans-Arctic interchange which occurred approximately 3.8 million years ago, groups of organisms migrated into the North-east Atlantic from the North Pacific (Cunningham and Collins, 1994). Recent changes in ice cover in the Arctic, opening up the North-west Passage, have again led to species entering or re-entering the Atlantic from the Pacific (e.g. Reid *et al.*, 2007). This is likely to accelerate if warming continues (Wisn *et al.*, 2015).

Within broad biogeographic constraints, the biological communities that develop on rocky shores are ultimately

determined by the ability of different species to first recruit, and then to tolerate local environmental stress gradients acting at different spatial and temporal scales, and by biological interactions with neighbouring organisms (see reviews by Hutchins, 1947; Lewis, 1964; Little and Kitching, 1996; Raffaelli and Hawkins, 1996). Regional-scale variation in salinity, pollution, and nutrient and sediment loads influence species distributions, particularly around estuaries and near to human settlements. At local scales, rocky shores are characterized by steep and largely-predictable environmental gradients, both vertically (low to high shore) and horizontally (sheltered bays to exposed headlands). Intertidal organisms experience desiccation stress and temperature fluctuations during emersion. These stressors increase unidirectionally along the vertical gradient, from low to high shore, as emersion time increases (Foster, 1971; Raffaelli and Hawkins, 1996). Since some organisms are more tolerant to desiccation and temperature fluctuations than others (e.g. Connell, 1961a; Schonbeck and Norton, 1978; Dring and Brown, 1982), species distributions are limited along this vertical gradient. Along horizontal wave exposure gradients, physical disturbance regimes (e.g. from wave energy and scouring by suspended sediments) change, but the influence of wave action on organisms is not unidirectional. Some species thrive in wave-swept conditions, for example suspension feeders such as mussels (*Moschella et al.*, 2005; Vaselli *et al.*, 2008). Others favour shelter, for example intertidal canopy-forming macroalgae in the North-east Atlantic (Lewis, 1964; Jonsson *et al.*, 2006). Some kelp canopy species, however, prosper in wave-exposed conditions (e.g. *Postelsia palmaeformis* in the North-west Pacific: Blanchette (1996), and *Laminaria* species in Europe: Hawkins and Harkin (1985), Smale *et al.* (2015)). Biological interactions such as grazing can also set distribution limits along wave exposure gradients (Hawkins, 1981; Harley, 2003; Jenkins *et al.*, 2005; Taylor and Schiel, 2010). For example, establishment of large brown algae on European shores is prevented by grazing, but persistence is determined by wave action (Jonsson *et al.*, 2006). Microhabitats such as rock pools, crevices and gullies modify and provide refuge from physical stressors, creating a mosaic of environmental conditions and enabling rocky shores to support diverse communities of marine life. These microhabitats further shape spatial patterning on shores as they provide shelters from and in which grazers (Noël *et al.*, 2009; Skov *et al.*, 2011) and predators (Fairweather, 1988a; Johnson *et al.*, 1998b) forage, sometimes creating

“haloes” of bare rock (Fairweather, 1988b). Where larger consumers are present, they are also important for providing refuge from predation and grazing pressure (Menge and Lubchenco, 1981), influencing the potential for species to co-exist.

Environmental conditions experienced by rocky shore communities vary, relatively predictably, on short (tidally and daily) and medium (seasonally) time scales. For example, tidal cycles, and diurnal and seasonal weather

patterns lead to variation in stresses experienced during low tide windows and disturbance from wave energy and scouring. Occasional natural catastrophic events occur, however, such as extreme cold winters (Crisp, 1964; Todd and Lewis, 1984) or hot springs and summers (Hawkins and Hartnoll, 1985; Harley, 2008; Smale and Wernberg, 2013), extreme storms (Perkol-Finkel and Airoldi, 2010; Benedetti-Cecchi *et al.*, 2015) and toxic algal blooms (Southgate *et al.*, 1984), which are less predictable in their occurrence and effects. Superimposed on local

Box 3.7.1 Shifting ranges

In recent years, range extensions have been recorded for a number of rocky intertidal species in the North-east Atlantic. Around the UK, a number of southern warm-adapted species have shown northwards and eastwards extensions along the Welsh and Scottish coastlines, and eastwards extensions into the cooler Eastern English Channel basin (Figure 1). In some cases, artificial structures (e.g. piers, breakwaters) have probably aided range extensions by acting as stepping stones between previously-isolated rocky intertidal habitats.

Likewise, in California, the northern limits of a number of rocky intertidal species have expanded up the coast in recent years (Figure 2). For *Mexacanthina l. lugubris*, the expansion is thought to be due to a combination of factors, including the spatial availability of habitat and food, high abundances near their historical range limit, and increasing sea surface temperatures. Other species, however, such as the limpet *Lottia gigantea*, have experienced a range contraction, presumably due to sporadic recruitment success and naturally low abundances towards its northern limit.

Responses to climate change are species-specific and dependent on coastal context, with the same species responding differently in different locations.

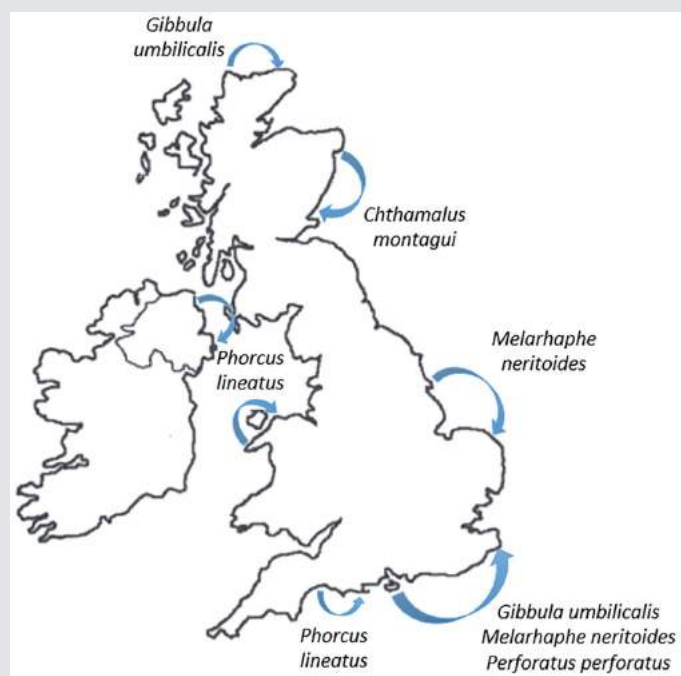


Figure 1 Some examples of range extensions in rocky intertidal species around the UK. Arrows indicate the limit to which each of the species ranges have reached and the direction of extension (Herbert *et al.*, 2003, 2009; Mieszkowska *et al.*, 2005, 2006, 2007; Hawkins *et al.*, 2009).

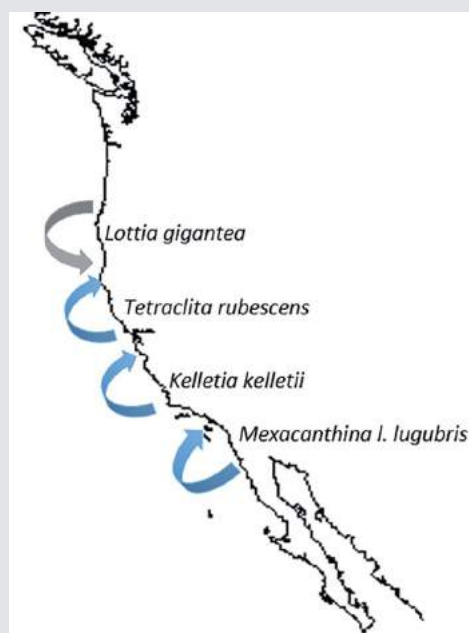


Figure 2 Some examples of range extensions and contractions in rocky intertidal species along the Californian coast. Arrows indicate the limit to which each of the species ranges have reached and the direction of shift (Zacherl *et al.*, 2003; Dawson *et al.*, 2010; Fenberg and Rivadeneira, 2011; Fenberg *et al.*, 2014).

gradients are broad-scale (with geographic setting) and longer-term climate fluctuations, and more recent rapid anthropogenic climate change. The signal of climate fluctuations and change is of low amplitude and long wavelength compared to the noise of weather and tidal cycles. The ‘openness’ of intertidal populations, because larvae and propagules are often recruited from outside sources, can often lead to unpredictable variability and patchiness of species distributions both spatially and temporally (Underwood and Fairweather, 1989; Burrows *et al.*, 2010). Disentangling the effects of climate change from species responses to shorter-term fluctuations and natural variability is a challenging, yet key, task for predicting impacts and their subsequent mitigation (Southward *et al.*, 1995; Hawkins *et al.*, 2008, 2009; Mieszkowska *et al.*, 2014b).

3.7.3 Climate change: trends and impacts

IPCC Assessment Reports (2007, 2014) have briefly reported some of the responses to climate change observed in rocky intertidal habitats. Here we summarize the main trends and impacts on species, assemblages and communities recorded in the literature, and outline the key drivers and mechanisms of change.

3.7.3.1 Geographical distribution and abundance of species

One of the global “fingerprints” of climate change, recorded consistently across natural systems, is the steady shift of the geographical ranges of species towards the poles as the climate warms (Walther *et al.*, 2002; Parmesan and Yohe, 2003; Root *et al.*, 2003; Burrows *et al.*, 2011; Sunday *et al.*, 2012; Bates *et al.*, 2014). Range extensions occur over time as a result of increasing abundance in populations towards the leading (often poleward) range limits, leading to expansions into previously uncolonized habitat. For example, the predatory gastropod *Mexacanthina lugubris lugubris* recently expanded its northern range limit into southern California, which was likely facilitated by high abundances and a wealth of habitat availability and food resources at its historical northern range limit (in northern Baja California Mexico; Box 3.7.1 Figure 2, Fenberg *et al.* (2014)). Conversely, retractions at the trailing (often equatorward) edge are a result of declining abundance, leading to local extinctions of populations due to lack of recruitment. However, range contractions associated with lack of recruitment and low abundances toward poleward limits have also been observed (Box 3.7.1 Figure 2, Fenberg and Rivadeneira (2011)). Changes in abundances are often driven by

altered survivorship and reproductive success under fluctuating ambient conditions, punctuated by advances and retreats caused by extreme events (Hutchins, 1947; Crisp, 1964; Southward, 1980; Southward *et al.*, 1995; Wetthey *et al.*, 2011; Poloczanska *et al.*, 2013; Smale and Wernberg, 2013; Spinuzzi *et al.*, 2013; Bates *et al.*, 2014; Firth *et al.*, 2016a).

In the North-east Atlantic biogeographic region, long-term and broad-scale study of intertidal rocky habitats has revealed clear patterns of ecological change in response to climate fluctuations. In particular, building on early time series studies (Southward and Crisp, 1954, 1956; Southward, 1963, 1967, 1991), there is growing evidence of changes in the abundances and distributions of species in the English Channel (Southward, 1991; Southward *et al.*, 1995; Hawkins *et al.*, 2008, 2009; Mieszkowska *et al.*, 2014a). Barnacles are valuable “model systems” in rocky intertidal ecology. They are easily quantified and compete for clearly definable resource space (Connell, 1961a). In recent decades, fluctuations have been recorded in the relative abundances of warm- and cold-water barnacle species on North-east Atlantic rocky shores, with warm-water species (*Chthamalus stellatus* and *C. montagui*) flourishing in the warmer 1950s (Southward and Crisp, 1954) and the colder-water species (*Semibalanus balanoides*) doing well in the cooler 1930s, 1960s and 1970s (Moore and Kitching, 1939; Southward, 1967, 1991; Hawkins *et al.*, 2003). Consistent warming since the late 1980s, which has exceeded previous levels (Box 3.7.2 Figure 1, Hawkins *et al.* (2008, 2009), Firth *et al.* (2015)), has led to a subsequent decline in *S. balanoides* and an increase in the warm-water *Chthamalus* species, which are now more abundant than in the 1950s (Box 3.7.3 Figure 1, Mieszkowska *et al.* (2014a)). Poloczanska *et al.* (2008) used a 40-year time series to develop models involving interactions between the two species to investigate the processes explaining past fluctuations and predicting future shifts. They showed that, although *S. balanoides* is the faster-growing dominant competitor (Connell, 1961a), warm years negatively affected its recruitment, thereby releasing *Chthamalus* species from competition. Using future climate predictions under alternative emissions scenarios (low, medium-low, medium-high and high future scenarios as defined by the UK Climate Impacts Programme: Hulme *et al.* (2002)), they predicted that *S. balanoides* would eventually go extinct in south-west Britain, and that barnacle populations in the British Isles would eventually resemble those in Portugal and Spain

Box 3.7.2 Sea surface temperature (SST) – long-term trends, short-term fluctuations & species responses

Long-term records of sea surface temperature (SST) such as those off Plymouth, UK (Figure 1) show considerable fluctuations over the last 140 years, with warmer periods (1890s, 1950s) alternating with colder spells (1900–20, 1962–87) before the recent period of accelerated warming. The record is punctuated by extremely cold winters such as 1962–63 associated with North Atlantic oscillation negative index years. More recently there were cold winters in 2008–09 and 2010–11. These broad-scale oceanographic patterns of temperature are modulated by local micro-environmental variation – especially in the intertidal when exposed to air at low tide. Figure 2 illustrates this in intertidal mussels which are much warmer than their predator the starfish, *Pisaster ochraceous*. *In situ* temperatures can be logged by deploying sensors within limpet shells (“robolimpets”). Figure 3 shows that differences due to microhabitat and shore level can be as important as geographic setting.

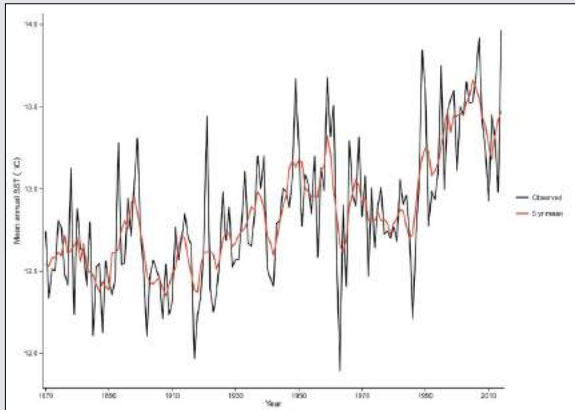


Figure 1 Mean annual sea surface temperature (SST) 1870–2014 off Plymouth, UK (Met Office Hadley Centre). Black line indicates annual mean temperature; red line indicates 5-year running average.



Figure 2 Thermal imagery of the seastar *Pisaster ochraceous* feeding on a bed of *Mytilus californianus* mussels illustrates how intertidal animals can experience different body temperatures when exposed to identical ambient temperature (Helmuth, 2002).

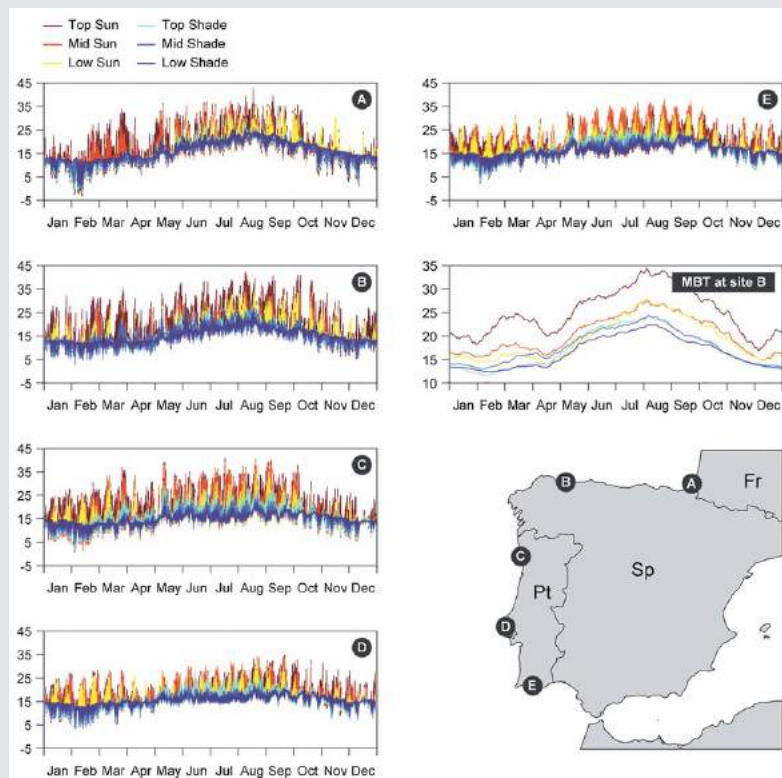


Figure 3 Body temperature profiles obtained by “robolimpets” deployed in different microhabitats (depicted by different line colours): (A–E) profiles recorded at 5 sites along the Atlantic coast of the Iberian Peninsula; (MBT at site B) 30-day rolling average of daily maxima at La Caridad (adapted from Seabra *et al.*, 2011).

Box 3.7.3 Long-term monitoring & historical data reveal community and phenological responses in rocky intertidal indicator species

Barnacles are good indicators of climate change responses. Long-term monitoring at Cellar Beach, UK, shows that the warm-water Chthamalid barnacles predominated in the warm 1950s; in the cooler 1960s, 1970s and early 1980s the more northerly-distributed *Semibalanus balanoides* was generally more abundant. From the 1990s onwards, the warm-water *Chthamalus* increased in abundance whilst *Semibalanus* became much rarer (Figure 1). Changes in barnacles mirror changes offshore in plankton and fish in the Western English Channel. Fluctuations in warm-water pilchards and cold-water herring have been reconstructed back to the middle ages using historical methods. Over the last 60 years such fluctuations broadly match those in barnacles (Figure 2). In addition to shifts in distribution and changes in abundance, phenological shifts have occurred. A southern species of limpet, *Patella depressa*, is now reproductively active for most of the summer in the UK, whereas it used to only reproduce once at most. Conversely the northern species, *Patella vulgata*, has shown failure years recently as its reproductive season has been pushed later (Figure 3).

Figure 1 Abundance per cm² of the warm-adapted *Chthamalus* spp. and cool-adapted *Semibalanus balanoides* in the mid-shore region at Cellar Beach, Southwest UK, 1950s–2000s (Mieszkowska *et al.*, 2014a).

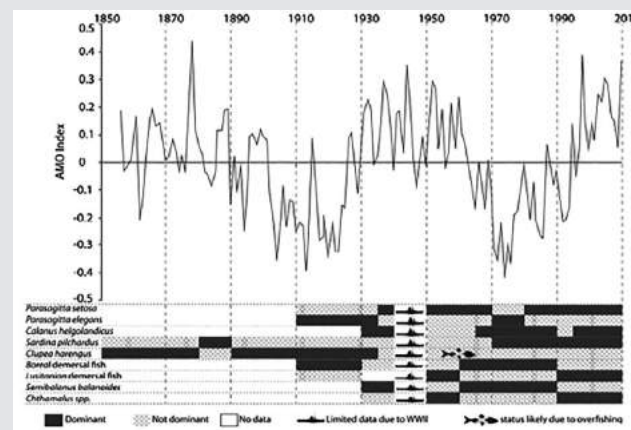
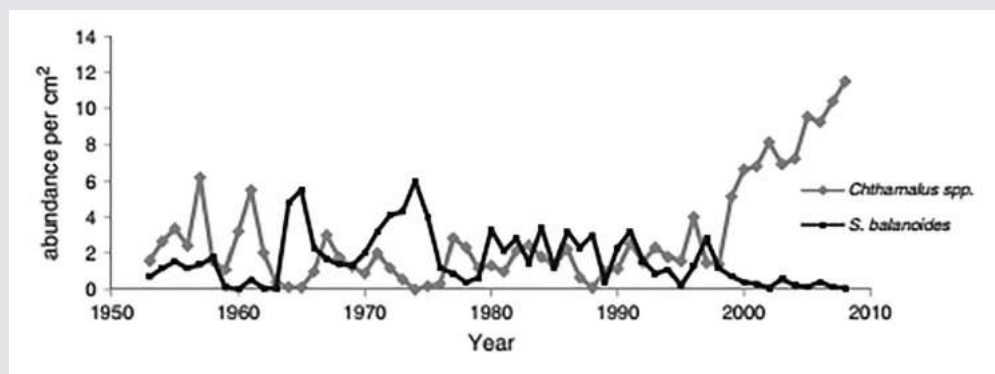


Figure 2 Annual Atlantic Multidecadal Oscillation (AMO) with phases of key taxa of warm- and cold-water biogeographic origins in the western English Channel (Mieszkowska *et al.*, 2014a).

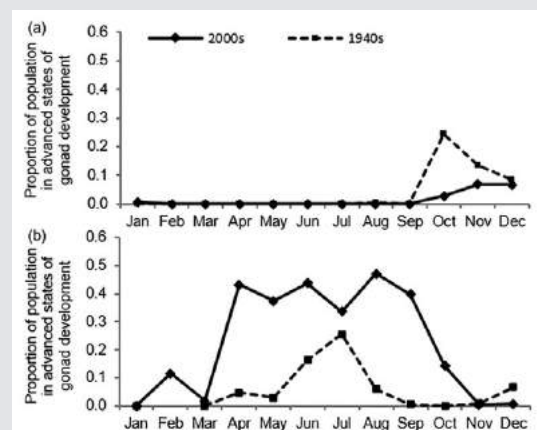


Figure 3 Mean monthly proportion of limpets in the SW of England in advanced states of gonad development in the 1940s (1946–1949) and the 2000s (2003–2007): (a) northern cool-adapted species *Patella vulgata* and (b) southern warm-adapted species *P. depressa* (adapted from Moore *et al.*, 2011).

(Box 3.7.4 Figure 1, see also Hawkins *et al.* (2008, 2009)). Wetthey *et al.* (2011) have already shown that *S. balanoides* has fluctuated between abundant and absent at its current southern limit in Galicia over the last 50 years, which they suggest is a precursor of local extinction and hence range contraction.

Importantly, the fluctuations in barnacle species described here have long been known to mirror wider changes in the Western English Channel ecosystem (Box 3.7.3 Figure 2, Southward, 1980; Southward *et al.*, 1995; Hawkins *et al.*, 2003; Mieszkowska *et al.*, 2014a). Thus they provide easily-sampled indicators of change

offshore in the English Channel in plankton (Genner *et al.*, 2009), fish (Genner *et al.*, 2004, 2009) and squid (Sims *et al.*, 2001). Similar fluctuations in warm- and cold-water species have also been reflected in other intertidal taxa of the North-east Atlantic, including algae (Lima *et al.*, 2007; Yesson *et al.*, 2015), other barnacle species (Herbert *et al.*, 2007), trochids (Mieszkowska *et al.*, 2007) and limpets (Southward *et al.*, 1995; Kendall *et al.*, 2004; Hawkins *et al.*, 2008). It must be stressed, however, that whilst southern warm-water species have generally increased in abundance beyond baselines established in the warm 1950s and cooler 1960s, the responses are often species-specific, reflecting life history characteristics, and dependent on coastline context. Some species have exhibited range extensions in the English Channel, including *Perforatus perforatus* (Herbert *et al.*, 2003), *Patella ulyssiponensis* (Hawkins *et al.*, 2009), *Gibbula umbilicalis* (Mieszkowska *et al.*, 2006; Herbert and Hawkins, *pers. obs.*), *Melarhaphie neritoides* (Hawkins *et al.*, 2009) and *Phorcus lineatus* (Mieszkowska *et al.*, 2005, 2007) (Box 3.7.1 Figure 1). Meanwhile other species have not, including both *Chthamalus* spp. (Herbert *et al.*, 2007, 2009). The lack of range expansion in these species is thought to be due to a combination of hydrographic barriers, habitat limitation and dispersal capability of different species (Herbert *et al.*, 2009; Keith *et al.*, 2011). In contrast to the English Channel, Chthamalid barnacles have, for example, shown range shifts in the Irish Sea and the North Sea along more continuous coastlines (Hawkins *et al.*, 2009). *Patella depressa* has made very small advances along the English Channel coast, primarily on artificial structures such as sea defences (Hawkins *et al.*, 2008). It is highly likely that several range extensions along the English Channel coast have been assisted by artificial structures acting as stepping stones (Moschella *et al.*, 2005; Firth *et al.*, 2013a), for example range extensions recorded in *Gibbula umbilicalis*, *Perforatus perforatus*, *Melarhaphie neritoides*, and *Patella ulyssiponensis*. This has also been seen in the recovery of the reef-building worm *Sabellaria alveolata* (Figure 3.7.2) in the northern Irish Sea and its spread southwards toward North Wales; on the Wirral it colonized sea defences as a novel habitat interfacing with sand (Firth *et al.*, 2015). Hence, the continued proliferation of artificial structures, both as a mitigational (e.g. marine renewable energy infrastructure) and adaptational (e.g. sea defences) response to climate change, is likely to have an additive effect, aiding shifts in species distributions with climate warming (Firth *et al.*, 2016a). It has been suggested that artificial structures may even provide opportunities for

assisted migration of species at risk from climate change (Hoegh-Guldberg *et al.*, 2008). The negative implications of urban sprawl becoming an additional driver of biological homogenization by facilitating the spread of non-native species at local, regional and global scales (Airoldi *et al.*, 2015), however, may outweigh potential positive effects (Kühn and Klotz, 2006; McKinney, 2006; Bishop *et al.*, 2016; Firth *et al.*, 2016a).

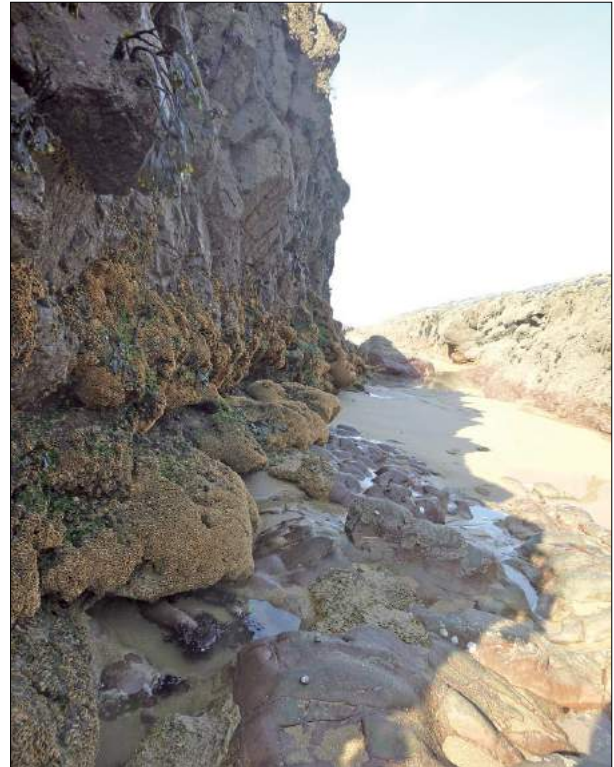


Figure 3.7.2 The honeycomb worm (*Sabellaria alveolata*) is a species of conservation interest in the UK. The worms build networks of sandy tubes to live in, which provide habitat for other intertidal animals and algae. On boulder shores, the worms perform an important function by cementing mobile boulders into stable reef habitats, which allows more mature intertidal communities to develop. © Ally Evans.

3.7.3.2 Vertical shore distribution: climate-driven changes in zonation

In addition to predicted effects on geographical species distributions, climate change is likely to promote changes in vertical shore distribution patterns in intertidal rocky habitats. Evidence of this to date is, however, limited (but see Harley and Paine, 2009; Harley, 2011). Upper distributional limits of species on rocky shores, especially those at upper- and mid-shore levels, are often set directly by physical factors, such as temperature and desiccation (Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985; Harley, 2003). Biological interactions, such as competition, grazing and predation, become more important controlling factors lower down the shore,

generally setting lower distributional limits (Connell, 1972; Lubchenco, 1980; Hawkins and Hartnoll, 1985; Harley, 2003), and also setting upper limits of some mid- and low-shore species (Hawkins and Hartnoll, 1985; Jenkins *et al.*, 1999, 2005; Boaventura *et al.*, 2002a).

Organisms inhabiting intertidal shores must withstand prolonged emersion, which may become increasingly stressful with rising air and sea surface temperatures. Although the effects of temperature on the survival and physiological performance of invertebrates and algae are relatively well-understood (Somero, 2002, 2005; also discussed further below in *para.* 3.7.3.4), it is evident that different organisms experience different body temperatures when exposed to identical climates (Box 3.7.2 Figure 2, Helmuth (2002)). Non-lethal effects of heat stress (e.g. tissue damage, alteration of metabolic rates, activation of heat-shock responses) which carry considerable energetic costs, can lead to changes in activity and reproductive output, and hence influence population dynamics and community structure on rocky shores. Hot weather has also been observed to cause mortality at the upper limits of many intertidal species, particularly seaweeds (Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985), but also invertebrates (Harley, 2008; Firth and Williams, 2009). The upper intertidal limits of the canopy-forming alga *Fucus serratus* (Figure 3.7.3), for example, have been “pruned back” at its southern range edge along the Iberian Peninsula (Pearson *et al.*, 2009). This appears to be a result of reduced resilience to desiccation from extreme temperatures compared to populations in cooler regions further north. Since canopy algae provide important refuge habitat for other intertidal organisms, this is likely to have implications for overall community composition and structure. Warmer summers, with more frequent warm events and rising sea levels, may therefore be expected to truncate shore zones, reducing the extent of suitable habitat for intertidal species. It is important to note, however, that the temperatures experienced by organisms on rocky shores can be ameliorated by wave splash, which may reach different distances up the shore depending on the exposure of the coastline as well as localized weather and larger-scale climatic conditions (Harley and Helmuth, 2003; Helmuth *et al.*, 2006a). With predicted increasing storminess, greater wave splash may enable species to persist higher on the shore in certain locations. To complicate things further, biological interactions, such as competition between overlapping species and predator-prey interactions, are likely to be modulated by climate change (Sanford, 1999, 2002; Poloczanska *et al.*, 2008;



Figure 3.7.3 *Fucus serratus*. © John M Baxter.

Kordas *et al.*, 2011). As an example, Harley (2011) found that climate warming substantially reduced predator-free space in intertidal rocky habitats in the North-east Pacific region over a 52-year period of warming. Upper shore limits of mussels (*Mytilus californianus* and *M. trossulus*) and barnacles (*Semibalanus balanoides* and *Balanus glandula*) shifted down the shore, whereas the foraging limit of the predatory sea star *Pisaster ochraceus* was unaffected by thermal stress. This led to a thermally-forced reduction in predator-free space. Consequently, the vertical extent of mussel beds was reduced by approximately half in some locations, and several local extinction events were recorded. Thus, a complexity of interacting factors may lead to unexpected changes in vertical species distribution patterns into the future. It is likely that species will be pushed further down the shore and may need to rely on subtidal refuges.

3.7.3.3 Phenological shifts

Changes to the synchronous timing of ecological events in response to interannual changes in temperature are now well known in the marine environment (Poloczanska *et al.*, 2013). Recurring life cycle events responding to changing environmental cues include the timing of reproduction and migrations (e.g. Sims *et al.*, 2001; Edwards and Richardson, 2004; Moore *et al.*, 2011; Pankhurst and Munday, 2011). In addition to direct spatial and temporal distributional effects, this may lead to mismatches in the timing of ecological interactions between species and their prey. There may therefore be considerable ramifications for populations of higher trophic-level species, including commercial fishery species, which often depend on synchronized planktonic production (Edwards and Richardson, 2004; Beaugrand and Kirby, 2010; Sumaila *et al.*, 2011).

In rocky intertidal habitats, phenological shifts have been observed in the congeneric limpets *Patella depressa*

and *P. vulgata* in the North-east Atlantic region (Box 3.7.3 Figure 3, Moore *et al.* (2011)). *Patella depressa* is a warm-water Lusitanian species that occurs between Spain and North Wales, while *P. vulgata* is a more cold-water species extending from the Algarve as far north as northern Norway. The two species inhabit the same shore zone and habitat type, and co-occur and compete where their ranges overlap (Boaventura *et al.*, 2002b; Firth *et al.*, 2009). Peak spawning time in the southern species, *P. depressa*, has shifted from mid-July in the 1940s to mid-April by the warmer early 2000s, with links to sea surface temperature (Moore *et al.*, 2011). The advance in peak reproductive development of this species is double the average observed for terrestrial and freshwater systems (Root *et al.*, 2003), indicating that marine species may be responding faster to climate warming (see also Poloczanska *et al.*, 2013). In addition to this temporal shift in reproductive development, the duration of the reproductive season of *P. depressa* has also lengthened over time and a much higher proportion of the population is reaching advanced stages of gonad development than previously. Concurrently, *P. vulgata* populations have experienced more frequent failure years due to delayed periods of development and spawning (Moore *et al.*, 2011). This is thought to be the first observation of a cool-adapted species showing a delayed reproductive season as a response to warming. This delay may lead to trophic mismatches if larvae are spawned into the plankton when there is little planktonic food available, particularly given observed advances in the phenology of a number of other autumn-blooming plankton species (Edwards and Richardson, 2004). Increased larval mortality may lead to recruitment failures and local extinctions at southern range edges (Connell, 1961b; Svensson *et al.*, 2005).

3.7.3.4 Mechanisms of change

Most organisms inhabiting intertidal rocky habitats, such as algae and invertebrates, are ectothermic and their metabolic processes are driven by temperature. In algae, both respiration and photosynthesis are temperature-dependent. Thus, warmer temperatures generally lead to faster growth and productivity (Oh and Koh, 1996), although greater respiration can reduce any benefits of faster photosynthesis (Fortes and Lfining, 1980; Terrados and Ros, 1992). In invertebrates, warmer seawater temperatures tend to promote greater activity, such as increased filtering rates in suspension-feeders (Schulte, 1975; Riisgård *et al.*, 1993) and increased foraging in mobile grazers (Thompson *et al.*, 2004), detritivores and predators (Sanford, 1999). This in turn

can lead to faster growth and greater reproductive output. For many intertidal organisms, the majority of physiological processes function better when the tide is in, although there are some exceptions (e.g. some algae photosynthesize when the tide is out provided desiccation is not extreme; Dring and Brown (1982)). Thus, during the *tide-in* phase, warmer temperatures resulting from climate change may drive metabolism and be beneficial for many organisms in temperate regions, in terms of activity, growth and reproductive output. This is only beneficial, however, up until respective optima are reached, beyond which sub-lethal effects, heat comas and mortality will occur. Some species are also active when the tide is out, often at night (e.g. limpets, *Patella* spp.: Santini *et al.* (2004)) and provided conditions are humid (e.g. dogwhelks, *Nucella lapillus* (Figure 3.7.4): Burrows and Hughes (1989)). Low tide windows can present highly stressful conditions, such as extreme high (especially at lower latitudes and during the day) or extreme low (especially at higher latitudes and during the night) atmospheric temperatures. Such extremes cause stress, slowing metabolism, activity, food intake and hence growth, and in some cases leading to damage or death (e.g. Somero, 2002; Firth and Williams, 2009; Firth *et al.*, 2015). The increased likelihood of more extreme hot weather in the future, therefore, may be expected to cause more costly stress levels during the *tide-out* phase – in essence putting a brake on metabolism, growth and occasionally causing mortality events.



Figure 3.7.4 *Nucella lapillus* © John M Baxter.

In certain circumstances, temperature may be a contributor, but not the direct mechanism of organism damage or death. For example, in 2013, massive die-offs were documented in populations of the sea star *Pisaster ochraceus* at many rocky intertidal sites along North-east Pacific coastlines (Stokstad, 2014; Jurgens

Box 3.7.4 Modelling the future

Long-term data and in-parallel experimentation can be used for statistically-based population modelling and for validating and calibrating mechanistic models. These approaches can be used to both understand past changes and forecast future status of populations. Long-term barnacle data (similar to that in Box 3.7.3) has been used to create models incorporating competition between the competitively superior cold-water northern species *Semibalanus balanoides* and the warm-water Chthamalids. During warm springs, the warm-water species were released from competition with the cold-water species. Using future climate scenarios, predictions for the future status of these populations indicate that Chthamalids will replace *S. balanoides* as the dominant barnacles on intertidal rocky shores (Figure 1).

Statistical modelling has also been used to predict how warmer and windier conditions will influence the abundance of the dominant canopy-forming seaweed *Ascophyllum nodosum* ("eggwrack") (Figure 2). Increased wave exposure and warmer temperatures were predicted to lead to fewer shores being dominated by this seaweed.

Shores in northern Europe (UK, Ireland), therefore, will increasingly resemble those further south in Europe (Spain, Portugal), with more southern species of barnacles and less seaweed cover.

Figure 1 Competition-based model simulating future populations of the northern barnacle species *Semibalanus balanoides* and the southern species *Chthamalus* spp. under high and low emissions scenarios (Hawkins *et al.*, 2009, adapted from Poloczanska *et al.*, 2008).

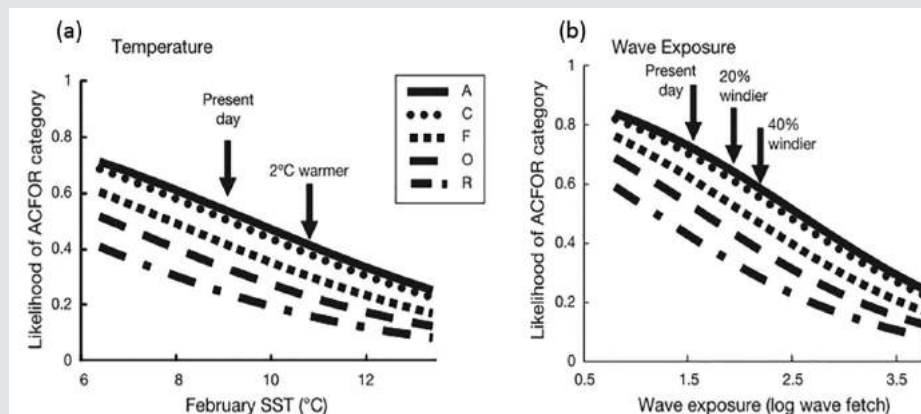
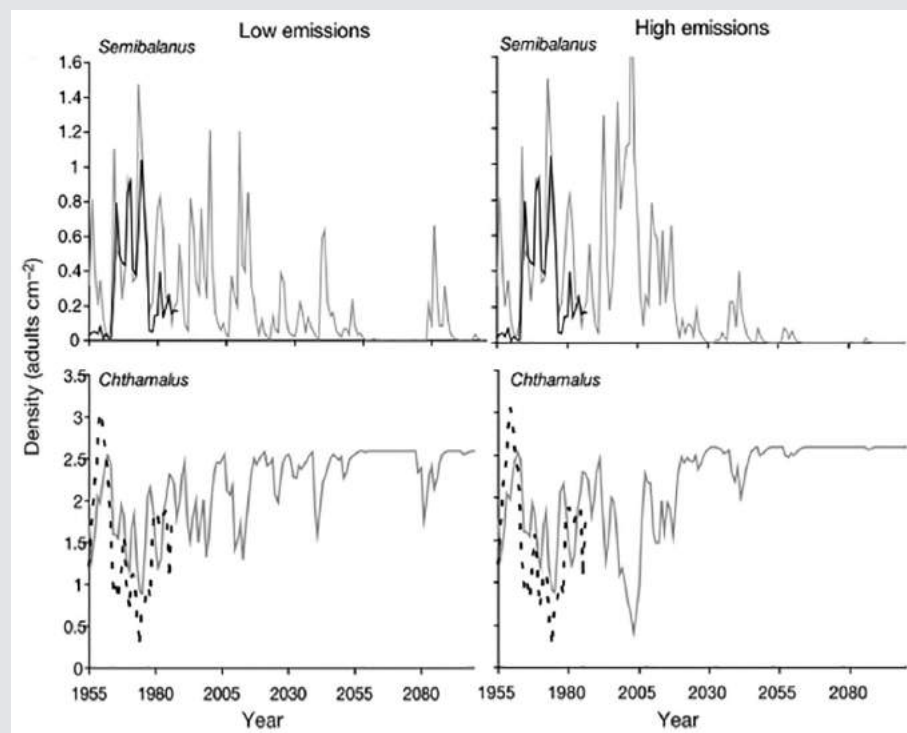


Figure 2 Outputs of multinomial logistic regression modelling of present-day distributions of *Ascophyllum nodosum* versus winter sea surface temperature (SST; February) and wave fetch. The predicted shifts along the ACFOR category (Abundant, Common, Frequent, Occasional and Rare) with (a) increased SST of 2°C and (b) wind speeds of 120 and 140 % are highlighted, showing subsequent decreases in this key species (Hawkins *et al.*, 2009).

et al., 2015). In as little as three days, individual sea stars developed lesions, lost structural integrity and limbs, changed in behaviour, and ultimately died. Hewson *et al.* (2014) suggested that this “sea star wasting syndrome” was likely to be caused by a virus called Sea Star Associated Densovirus (SSaDV). Although the ultimate trigger for the viral outbreak has not yet been established, many sites, especially where earlier and more recent outbreaks were recorded in southern California and Washington, had been associated with warming events (e.g. the 1997 El Niño event: Stokstad (2014)). However, sites in Oregon had cooler water temperatures during recent observations of wasting, making predictions of whether temperature is a driver of the die-offs more difficult to confirm (Menge *et al.*, 2016). Regardless of the ultimate cause of these mortality events, *Pisaster ochraceus* has long been known to significantly affect the structure and functioning of intertidal communities as an important predator of mussels and other invertebrates. Indeed, it was one of the species for which the term “keystone species” was first coined (Paine, 1969). Furthermore, sea star wasting syndrome is not restricted to *P. ochraceus*; outbreaks in several sub-tidal sea star species have also been observed (pacificrockyintertidal.org). If the spread of SSaDV is indeed facilitated (at least in part) by warmer temperatures, then climate warming can be expected to lead to further outbreaks in the future. The potential mass depletion of these voracious predators would have cascading effects on local ecological communities. It is not yet clear whether new cohorts recently recruited along the Oregon coast (Menge *et al.*, 2016) will be affected or whether they will be able to restore depleted populations and local ecological balance.

At the other end of the spectrum of temperature-induced responses, warmer climatic conditions have enhanced performance and facilitated range extensions in many warm-water species at their poleward limits (see Para. 3.7.3.1). Range shifts and population expansions tend to be driven by increased reproductive output and recruitment (Wetthey *et al.*, 2011; Bates *et al.*, 2014). Warm-temperate, sub-tropical and tropical species are often capable of multiple broods (e.g. Lewis, 1986; Ribeiro *et al.*, 2009). In animals that are direct-developers, population expansions stem directly from brood size and frequency leading to more juveniles being born and surviving initial developmental stages. In animals with a planktonic phase, increased brood number and size, larval development, survival and

metamorphosis can all be enhanced under warmer conditions. Earlier timing of recruitment can mean juveniles can grow and thus be less susceptible to winter mortality, which may already be reduced due to milder winters (Helmuth *et al.*, 2006b). Moreover, greater numbers of planktonic larvae at range edges can increase the probability of crossing hydrographic boundaries such as headlands (Gaylord and Gaines, 2000; Keith *et al.*, 2011), thereby enabling range shifts to occur (Herbert *et al.*, 2003; Keith *et al.*, 2011). The rocky intertidal species that have exhibited the greatest extension in range in the North-east Atlantic region are those with quite short-lived larvae, such as the trochid *Gibbula umbilicalis* in the English Channel (Box 3.7.1 Figure 1; Mieszkowska *et al.* (2006), Hawkins *et al.* (2009)). These shifts seem to have occurred via a series of small steps, with populations consolidating once hydrographic barriers had been breached. In contrast, some animals with longer larval duration, such as barnacles, seem to have been less able to make and consolidate range extensions (Herbert *et al.*, 2007, 2009). This may be because breeding populations require high adult population densities, because to reproduce, adults need to be within penis range of each other (Kent *et al.*, 2003). Such circumstances will only arise when cues for gregarious settlement have been successful. This so-called “Allee effect” (Kent *et al.*, 2003) may be important at range edges for both externally and internally fertilizing species.

3.7.3.5 Predicted community and ecosystem consequences

Distributional and phenological responses of individual species to climate change have considerable ramifications for the structure of communities and trophic interactions, leading to eventual changes in ecosystem functioning (Hawkins *et al.*, 2009). There is limited evidence for such changes in intertidal rocky habitats, but inferences can be made on the basis of localized observations and theory. For example, temperature-induced mortality events in important keystone species (such as *Pisaster ochraceus* in the North-east Pacific region; see para. 3.7.3.4) would be likely to have cascading effects on local and regional community structure. Similarly, contraction of vertical shore distributions of canopy-forming algae (such as *Fucus serratus* along the Iberian Peninsula; see para. 3.7.3.2) would effectively reduce the extent of suitable habitat for a number of intertidal species, again with implications for overall community structure and ecosystem functioning.



Figure 3.7.5 Very sheltered boulder shore with dense *Fucus* spp. and *Ascophyllum nodosum* cover. © John M Baxter.

Fucoid canopies are dense stands of *Fucus* and/or *Ascophyllum* seaweeds (Figure 3.7.5). They are important ecosystem engineers in temperate intertidal rocky habitats, providing food and habitat for a number of other species (Thompson *et al.*, 1996). Their abundance and density can, therefore, considerably influence the overall structure and functioning of rocky shore communities. In northern Europe, fucoid canopies are common and abundant features of most sheltered, and some more exposed, rocky shores (Ballantine, 1961; Hawkins and Harkin, 1985). At mid-latitudes, such as in Northern France, the British Isles and Ireland, and in moderately-exposed locations, patchy shores are typical (Lewis, 1964; Hartnoll and Hawkins, 1985). Further south in warmer parts of Europe, however, rocky shores tend to be devoid of large canopy-forming algae (Ballantine, 1961; Boaventura *et al.*, 2002c). Fucoid abundance is largely determined by the success rate of propagules “escaping” from grazers such as limpets, which is more likely among dense cover of *Semibalanus balanoides* barnacles as they restrict gastropod movement and provide refuges for juvenile plants (Hawkins, 1981; Hartnoll and Hawkins, 1985; Johnson *et al.*, 1997, 1998a; Burrows and Hawkins, 1998). Fucoid canopy cover is predicted to decline in response to climate change (Box 3.7.4 Figure 2) due to a combination of greater physiological stress (Pearson *et al.*, 2009; Martínez *et al.*, 2012; Ferreira *et al.*, 2014; Zardi *et al.*, 2015) and increased grazing pressure (Jenkins *et al.*, 2001, 2005; Ferreira *et al.*, 2015). At mid-latitudes in particular, escape rates are predicted to decline due to a combination of reduced recruitment in drier summers (Ferreira *et al.*, 2015), greater grazing pressure as southern species of limpets and trochids increase in abundance and ranges extend further north (Southward *et al.*, 1995; Mieszkowska *et al.*, 2006), and reduced barnacle density as populations

of *Semibalanus balanoides* are replaced by slower-growing *Chthamalus* species (Hawkins *et al.*, 2008, 2009; Poloczanska *et al.*, 2008). Predicted stormier weather is also likely to contribute to declines in algal canopies because of increased dislodgement and the likelihood of higher limpet abundances with elevated wave exposure (Jonsson *et al.*, 2006). There is evidence that the canopy-algae *Ascophyllum nodosum* is already being denuded by limpet grazing towards its southern range limit (Lorenzen, 2007), as well as in sheltered locations such as Strangford Lough further north, where local increases in wave action have interacted with limpet grazing to reduce cover (Davies *et al.*, 2007). No conclusive pattern is yet clear (Yesson *et al.*, 2015), but going forward, intertidal rocky ecosystems in northern Europe are likely to become increasingly like those further south. Fucoid canopies may even become restricted to refuges such as estuaries, as has been observed in southern Europe (Lorenzen, 2007; Neiva *et al.*, 2012). This, in turn, would have implications for the diverse array of species that shelter in and under canopies (Thompson *et al.*, 1996; Moore *et al.*, 2007). There would also be reduced primary production and supply of detritus to the food chain in inshore waters.

Production and nutrient cycling are probably the most important ecosystem services supported by functioning intertidal rocky habitat communities (Costanza *et al.*, 1997; see para. 3.7.2.2). Loss of macroalgal canopies is not the only reason that productivity of rocky shore systems is predicted to decline with climate change. In the North-east Atlantic it is well known that northern species of invertebrates grow faster and outcompete slower-growing, but more physiologically-hardy, southern species. For example, *Semibalanus balanoides* outcompetes *Chthamalus stellatus* (Connell, 1961a; Poloczanska *et al.*, 2008). Thus, as southern species advance northwards, secondary production is likely to be reduced. In areas where upwelling occurs, however, upwelling processes are likely to intensify in response to climate change, thus additional nutrients brought up from deeper waters may supplement productivity in intertidal and nearshore communities (discussed further in Para. 3.7.4). In any case, on the basis of available evidence, we can be confident that community structure and ecosystem functioning of rocky intertidal habitats will change into the future. It remains to be seen whether they will continue to support current levels of important ecosystem services we rely upon as species and communities modify and adapt to the changes they face.

3.7.4 Drivers of change

As highlighted throughout this section, temperature is a key driver of observed and predicted ecological responses to climate change in intertidal rocky habitats, in part because temperature drives metabolic processes in ectothermic intertidal organisms. During the *tide-in* phase, warmer water temperatures may boost metabolism with some physiological benefits for certain species, for example by promoting increased foraging activity, growth and reproductive output. In contrast, increased *tide-out* temperatures are likely to cause stress in some species, with sublethal and/or lethal consequences. Milder winters may, on the other hand, reduce the incidence of winter mortality. Superimposed upon long-term warming, however, are shorter-term weather fluctuations, often influenced by hemispheric-scale processes such as the El Niño Southern Oscillation (ENSO) events and the North Atlantic Oscillation (NAO). Certainly, the last few years in the North-east Atlantic have shown extreme NAO index “negative” winters, such as 2010/11 – the coldest since 1962/63, which was a 300-year cold event (Wetthey *et al.*, 2011). There have also been NAO “positive” winters, such as 2013/14, which was extremely stormy (Matthews *et al.*, 2014). Here we emphasize two important points. Firstly, climate change is not just about temperature; the intertidal zone will be very strongly influenced by changes in storminess and the return-time of extreme events influencing wave action gradients and disturbance regimes (Perkol-Finkel and Airoldi, 2010; Walsh *et al.*, 2014; Benedetti-Cecchi *et al.*, 2015), as well as sea-level rise on a centennial scale (Jackson and McIlvenny, 2011; Church *et al.*, 2013) (Box 3.7.5 Figures 1 and 2). Secondly, whilst temperature (including aerial temperature) is undoubtedly extremely important, it is necessary to consider, not only average temperatures (warming), but also the frequency and extent of extreme events (Wetthey *et al.*, 2011; Smale and Wernberg, 2013).

For rocky shore species and communities under threat from climate change, there are several sources of refuge that can ameliorate stressful conditions at a variety of spatial scales. These can, in some sense, be considered indirect drivers of change, as they additively or interactively modulate direct ecological responses. At the small scale (<1 m), shores with variable topography and aspect can provide shading and moisture in a mosaic of different microhabitats. These features modify species abundances and distributions in relation to the sharp vertical (temperature, desiccation) and horizontal

(wave action) environmental gradients. Such small-scale processes can often over-ride the very gentle geographical gradients of climate change with latitude (Box 3.7.2 Figure 3; Seabra *et al.*, (2011); Lima *et al.*, (2016)). On top of this are mesoscale (100-1000 km) processes, driven by upwelling systems and coastal topography, which can further modulate the effects of climate change. For example, estuarine regions can provide refuge for cold-water species at lower latitudes. This has been well-demonstrated along the Iberian Peninsula for a variety of intertidal species, including fucoids (Lorenzen, 2007; Neiva *et al.*, 2012), *Carcinus maenas* (Silva *et al.*, 2006) and *Patella vulgata* (Fischer-Piette, 1955), although the underlying processes are not clear. Enclosed seas (e.g. Irish Sea, North Sea), meanwhile, can lead to counter-intuitive species distributions. For example, warm-water species such as *Sabellaria alveolata* have expanded southwards in the Irish Sea (Frost *et al.*, 2004), and several warm-adapted intertidal species have spread southwards into the Southern North Sea (Mieszkowska *et al.*, 2005; Philippart *et al.*, 2011). This is because enclosed seas, whilst often warmer in the summer, are also colder in the winter. This emphasizes the importance of coastline context for identifying and predicting ecological responses to climate change in different places.

Upwelling is a phenomenon caused by winds blowing along the coast, pushing surface waters offshore, while bringing nutrients and cold water from the deeper ocean to the surface. Upwelling systems strongly influence rocky intertidal communities along the eastern boundaries of the world's oceans. These systems, known as Eastern Boundary Upwelling Systems (EBUS) include the California, Humboldt, Benguela and Canary upwelling zones. In these regions, nutrient-rich water is brought to the surface and fuels production within intertidal and nearshore communities. Where upwelling is particularly intense, for example around headlands, reductions in sea-surface temperature can also be important in structuring species distribution and abundance patterns at regional scales (Blanchette *et al.*, 2008; Fenberg *et al.*, 2015; Reddin *et al.*, 2015). Under future climate change projections, it is predicted that land temperatures will increase faster than coastal waters, creating a scenario favouring stronger upwelling-producing winds (Bakun *et al.*, 2010; Di Lorenzo, 2015; Wang *et al.*, 2015). Increased cold-water upwelling may, therefore, provide refuge from climate warming in some locations. Effects, however, are unlikely to be consistent across latitudes. Models predict that upwelling intensification will be

Box 3.7.5 Beyond warming – ecologically-sensitive adaptation to rising and stormier seas

Engineered coastal structures (such as breakwaters, seawalls and groynes) are proliferating around coastlines globally as a societal response to rising (Figure 1) and stormier (Figure 2) seas. Their construction can cause loss of and disturbance to sensitive natural habitats and species. They tend to provide poor-quality habitat themselves, supporting low biodiversity and non-natural communities of marine life. They are often colonized by weedy and opportunistic species. Therefore, where structures act as stepping stones between previously-isolated rocky habitats (Figure 3), they can facilitate the spread of non-native species and contribute to biotic homogenisation over large geographical areas.

In light of this, it is becoming increasingly necessary to incorporate ecologically-sensitive design into

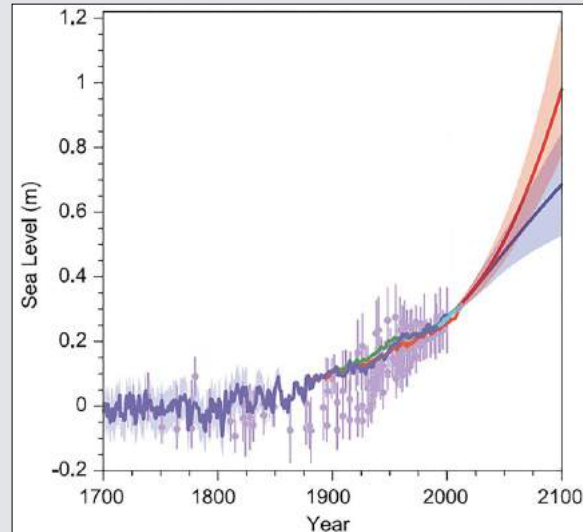


Figure 1 Past and future sea-level rise. For the past, proxy data are shown in light purple and tide gauge data in blue. For the future the IPCC projections for very high emissions (red) and very low emissions (blue) are shown (Church *et al.*, 2013; IPCC AR5 Figure 13.27).

Variation of Storm Frequency and Intensity during the Cold Season (Nov-Mar)

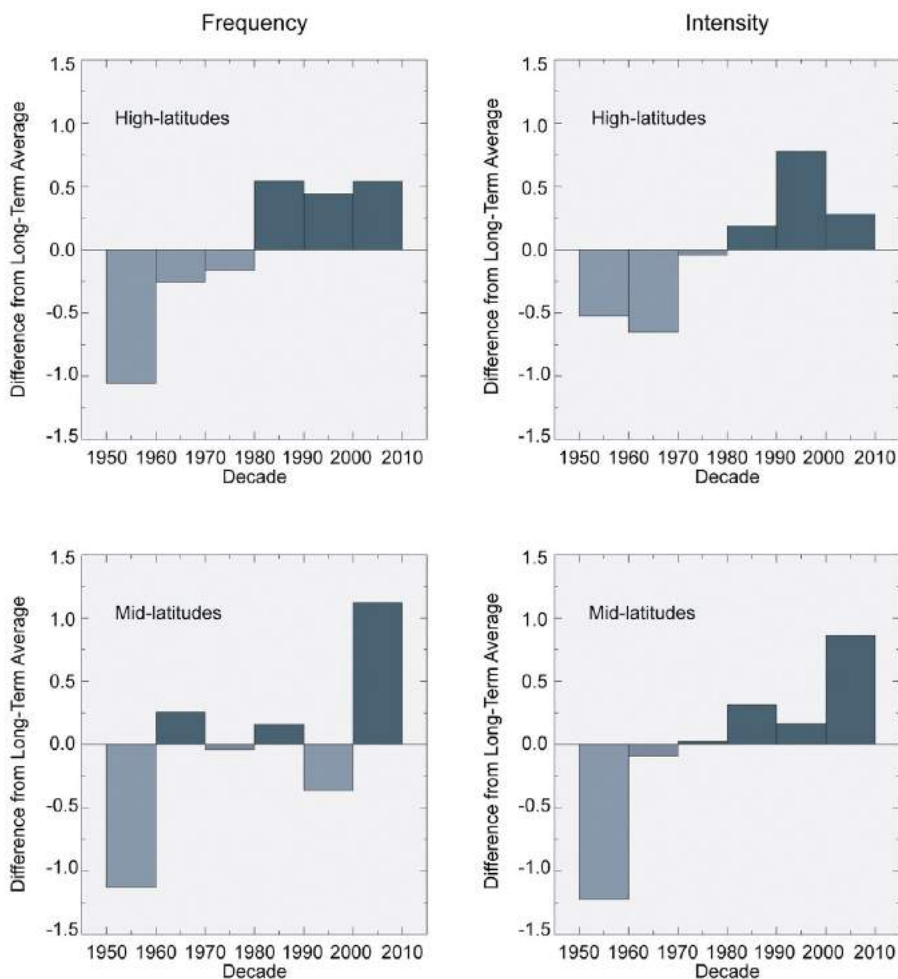


Figure 2 Variation of storm frequency and intensity during the cold season (November – March) for high latitudes (60–90° N) and mid latitudes (30–60° N) of the Northern Hemisphere over the period 1949–2010. The bar for each decade represents the difference from the long-term average. Storm frequencies have increased in middle and high latitudes, and storm intensities have increased in middle latitudes (updated from CCSP, 2008).

Box 3.7.5 Cont.

coastal developments, not only to minimize their environmental impacts, but also to maximize potential ecological and socio-economic benefits. By *eco-engineering* additional microhabitats (e.g. artificial rock pools; Figure 4) into coastal structures, it is possible to enhance their biodiversity and support similar ecosystem functions to natural rocky shores. A number of different eco-engineering designs have been tried-and-tested in different parts of the world. It is essential that this potential good practice is communicated to end-users to ensure every opportunity is taken to deliver environmentally-desirable outcomes of coastal and marine developments.

Figure 3 Elmer coastal defence scheme: structures can act as stepping stones and facilitate dispersal of species. © Arun District Council.



Figure 4 Artificial rock pools installed in an intertidal breakwater in Wales, UK, provided important habitat for marine life and performed a similar function to natural rock pools on nearby rocky shores (Evans *et al.*, 2016). © Ally Evans.

particularly marked at higher latitudes, where coastal upwelling is generally less intense. This, in turn, may cause homogenization of upwelling-influenced habitats across latitudes (but notably not in the California EBUS), and have cascading effects on the abundance and distribution of intertidal and nearshore flora and fauna (Wang *et al.*, 2015). There is evidence that upwelling has already intensified in most of the EBUS (Sydeman *et al.*, 2014; Varela *et al.*, 2015). While this may potentially be beneficial in terms of marine food production as the EBUS already produce >20% of global fisheries, there are a number of other biological consequences of a net increase in upwelling. For example, deeper waters have lower pH and oxygen levels than at the surface. Thus, an increase in upwelling may exacerbate emerging threats to coastal ecosystems, such as acidification and anoxic events (Chan *et al.*, 2008; Bakun *et al.*, 2015). Reduced pH can affect metabolism and energy budgets in marine organisms, particularly in organisms that produce calcium carbonate for shells or skeletons (Kroeker *et al.*, 2010; Harvey *et al.*, 2013, 2016). For example, calcification rates in *Mytilus californianus* mussels in Washington State, USA, have decreased significantly, probably due to declining pH (Pfister *et al.*, 2016). Mussel beds are the dominant space occupier of many temperate rocky shore coastlines around the planet. They provide habitat for other species (particularly for juveniles; Lohse (1993)), are an important food source for intertidal predators (e.g. whelks and sea stars), and have been harvested by humans for food for millennia (Rick and Erlandson, 2008). If this trend of shell thinning continues, the ability for *M. californianus* (and other mussel species) to play an important role in shaping the structure, functioning, and diversity of temperate rocky coastlines in the future may be in doubt.

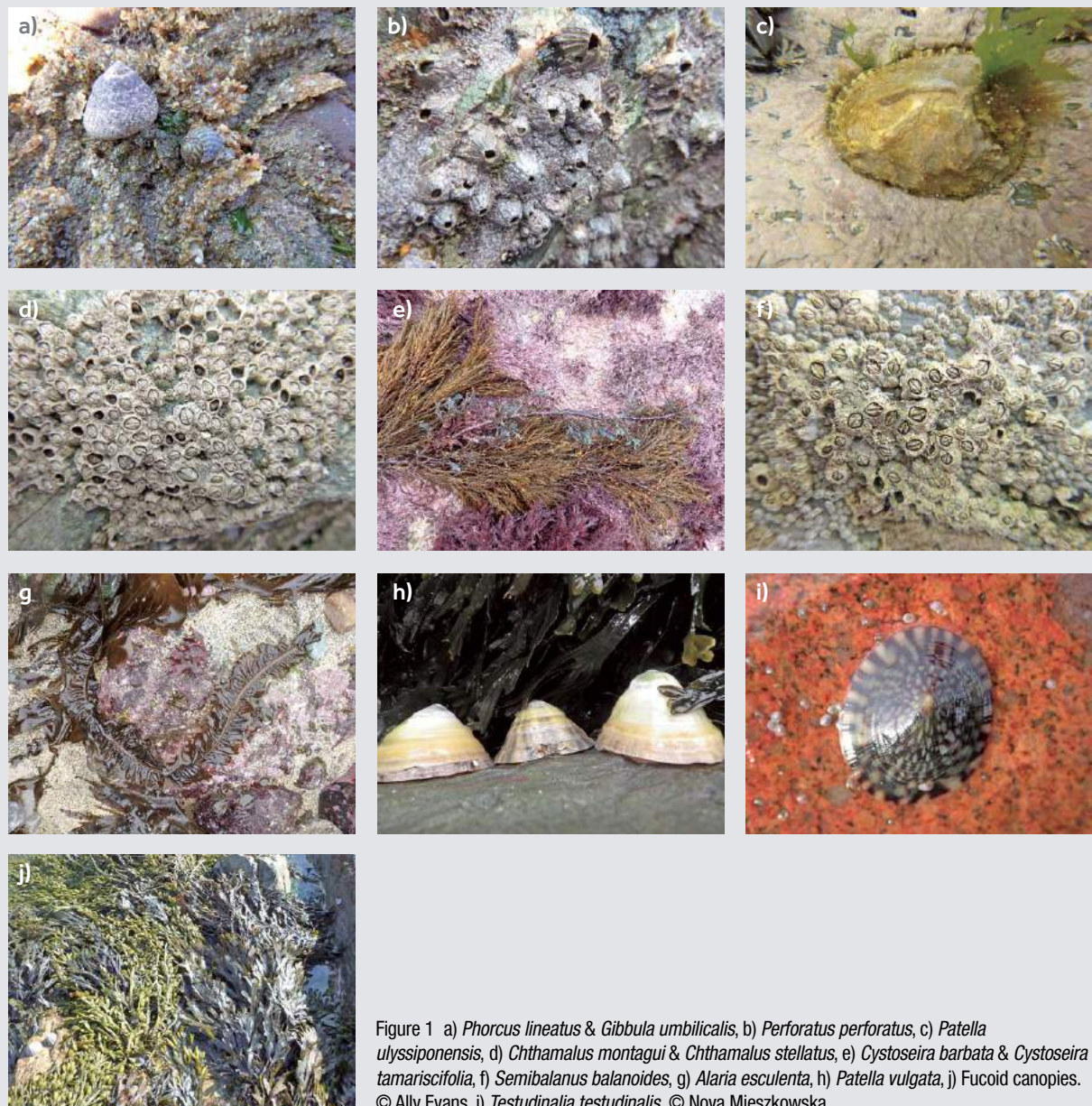
Although these various drivers of change are relatively well-understood in isolation, it is difficult to predict how each will interact to shape intertidal rocky habitats in different parts of a rapidly-changing world (but see Crain *et al.*, 2008; Harvey *et al.*, 2013; Lemasson *et al.*, 2016). Species are likely to be affected variably at different locations within and at the edge of their geographic ranges, at different positions along vertical and horizontal shore gradients, and differently during the *tide-in* and *tide-out* phases. The balance of processes will also vary with regional modulation by upwelling or enclosure of seas/bays, and by other local environmental gradients and microhabitat variation. Furthermore, the region of evolutionary origin of species may predetermine their responses to interacting climate-driven processes

(Rivadeneira *et al.*, 2015). Long-term contextual monitoring of natural systems (Hawkins *et al.*, 2013; Mieszkowska *et al.*, 2014b), coupled with experimental investigation of multi-stressor effects on species and communities (e.g. Przeslawski *et al.*, 2005; Firth and Williams, 2009; Atalah and Crowe, 2010; O’Gorman *et al.*, 2012), will be essential for disentangling the drivers and mechanisms of past, present and predicted future trends.

3.7.5 Concluding remarks – the need for adaptive management

There is now irrefutable evidence that climate-driven changes are occurring in intertidal rocky habitats, with important implications for the species and communities that inhabit them and the ecosystem services they support. Many of the examples described in this section are from the North-east Atlantic region, partly because of the extent of long-term and broad scale data available from this part of the world, but also because there is evidence that it has experienced faster warming than other regions (Burrows *et al.*, 2011). Climate-driven changes similar to those recorded in the North-east Atlantic have been observed elsewhere, along the Pacific coasts of North and South America (Barry *et al.*, 1995; Rivadeneira and Fernández, 2005; Harley *et al.*, 2006), Australia (Lathlean *et al.*, 2015), and New Zealand (Schiel *et al.*, 2016). Such shifts are occurring worldwide. In general, more species are advancing poleward than are retreating (Parmesan and Yohe, 2003), with some evidence from the northern hemisphere that cold-water species can persist in the face of climate change, if they outcompete southern species (e.g. Poloczanska *et al.*, 2008). Nevertheless, the composition, structure and functioning of communities on intertidal rocky shores is certain to change (Box 3.7.6).

Climate-driven changes interact with other global phenomena, such as ocean acidification, and also with regional- and local-scale impacts. In intertidal rocky habitats, these can include eutrophication, sedimentation, over-exploitation of seaweeds and shellfish, trampling from recreational use, and coastal development (Thompson *et al.*, 2002). This combination of impacts is already having considerable negative impacts on rocky shore communities, particularly by causing declines of canopy-forming algae, and instead favouring proliferation of fast-growing ephemeral algae and invasive species (Airoldi, 2003; Connell *et al.*, 2008; Perkol-Finkel and Airoldi, 2010; Airoldi and Bulleri, 2011). Algal canopies confer resilience to climate change for other organisms

Box 3.7.6 Rocky intertidal winners & losers in the North-east Atlantic

by providing refuge habitat and ameliorating local ambient conditions (Thompson *et al.*, 1996; Moore *et al.*, 2007; Teagle *et al.*, 2016; Walls *et al.*, 2016). Their loss, therefore, increases stress on more delicate understorey algae and invertebrates with community- and ecosystem-level implications. As a temperate phenomenon, these habitat engineers are likely to be under particular pressure from continued warming, with added physiological stress and increased grazing pressure (see para. 3.7.3.5). Thus direct (physiological stress) and indirect (more grazing or predation) effects of climate change may potentially be exacerbated in intertidal rocky habitats by a plethora of interactions with other impacts.

Through the complex localized and regional-scale responses described in this section, climate change is ultimately contributing to global homogenization of biodiversity, as vulnerable species become extinct and “non-native” species from different biogeographic regions spread, overlap, and become established across the world’s ocean. Invasive species have been particularly successful during the spell of recent warming (Dukes and Mooney, 1999; Stachowicz *et al.*, 2002; Sorte *et al.*, 2010), and the likelihood of further successful invasions will increase with projected climate change (Walther *et al.*, 2009; Bellard *et al.*, 2013; Rius *et al.*, 2014), in particular with increased frequency and intensity of

disturbance events (Perkol-Finkel and Airoldi, 2010; Airoldi and Bulleri, 2011; Benedetti-Cecchi *et al.*, 2015). This is not a surprise, since invasive species tend to be fast-growing opportunistic species, able to withstand variable conditions (e.g. *Undaria pinnatifida*: Dean and Hurd (2007), *Austrominius modestus*: Harms (1999), *Carcinus maenas*: Naylor (1962), *Mytilus* spp.: Pollard and Hodgson (2016), which have all been involved in invasions worldwide). There is growing evidence that the proliferation of artificial hard structures in the marine environment has had an additive effect with climate warming, and facilitated range shifts in non-native species (Ruiz *et al.*, 2009; Bracewell *et al.*, 2012; Mineur *et al.*, 2012; Spinuzzi *et al.*, 2013; Airoldi *et al.*, 2015). Artificial structures essentially act as stepping stones to aid the spread of species responding to climate-driven change. There is strong evidence for this already in the Eastern English Channel (Mieszkowska *et al.*, 2005; Moschella *et al.*, 2005; Hawkins *et al.*, 2008, 2009; Firth *et al.*, 2013a) and Irish Sea (Firth *et al.*, 2015). Much of this “ocean sprawl” has come about as a mitigational response to climate change (e.g. wind, wave and tidal energy generation infrastructure), and also as a societal adaptation to rising and stormier seas (e.g. coastal defences). There is growing interest in the concept of *ecological engineering* to design artificial structures with ecological implications in mind (Chapman and Underwood, 2011; Firth *et al.*, 2013a, 2014; Dafforn *et al.*, 2015; Dyson and Yocom, 2015). By incorporating physical engineered features, their habitat quality may be enhanced, thus enabling them to support more diverse and more natural communities of marine life. For example, artificial rock pools can be retro-fitted by drilling holes in breakwater units (Box 3.7.5 Figure 4; Evans *et al.* (2016)) or appending “flower pots” to seawalls (Browne and Chapman, 2011, 2014), and large habitat units can be cast in concrete to incorporate different microhabitats whilst also contributing to the body of structures (Firth *et al.*, 2014; Perkol-Finkel and Sella, 2014, 2016; Sella and Perkol-Finkel, 2015). Such interventions can be targeted for specific management outcomes, and can confer resilience to climate change by providing refuge for intertidal organisms during the *tide-out* phase. Ecologically-sensitive design of artificial structures may become increasingly important as natural intertidal rocky habitats are “squeezed” by sea-level rise (Jackson and McIlvenny, 2011); artificial habitats may eventually become important surrogate habitats for rocky shore organisms (e.g. Perkol-Finkel *et al.*, 2012).

The mitigation essential to achieve goals of a lower-carbon world will take time. The inertia of the climate

system is such that even should emissions be reduced, there will be a phase-lag of at least 50 years over which warming will flatten out. In the meantime, much can be done to enhance resilience to climate change, by managing those impacts and interactions over which society has greater potential control in the short to medium term of the next 5–50 years (Knights *et al.*, 2013). In general, climate change exacerbates other impacts, and reducing these other impacts confers resilience to climate change. For example, the likelihood of non-native species invasions appears greater in a warmer, more disturbed world; over-exploited populations are susceptible to climate change, and climate change can increase vulnerability to over-exploitation; and harmful algal blooms are more likely in warmer and more stratified eutrophic seas. In mitigating (e.g. developing marine renewable energy generation) and adapting to (e.g. building sea defences) climate change, care must be taken to ensure ecological consequences are taken into consideration at both local and regional scales.

3.7.6 References

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