Intertidal species and habitats

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1. INTRODUCTION

Intertidal areas are the most accessible of marine habitats and because of this ready access offer a significant opportunity to observe and document the effects of climate change in the ocean at minimal cost. Rocky coasts were the focus of much effort in the second half of 20th Century to assess patterns of distributions along gradients of temperature, and to measure the effects of variability in temperature on populations and species distributions over time. This early work by researchers including Alan Southward in Plymouth (Southward and Crisp, 1954), Dennis Crisp in Bangor (Crisp and Southward, 1958) and Jack Lewis from Leeds (Lewis, 1964; Lewis et al., 1982) forms a solid basis for assessment of change over the last half century and more. Methods developed for quantifying patterns have been developed and extended into present-day efforts. The ongoing MarClim programme over the past 15 years has surveyed annually a number of representative
sites across a wide swath of the rocky coastline in SW Britain and, less regularly, has assessed the complete distribution of intertidal species across the whole of the UK coast. The resulting data on patterns of distributions and changes over time are revealing much about how, for example, climate-sensitive species such as barnacles are fluctuating over years and decades (Mieszkowska et al., 2014) and how environmental conditions like wave action play an important role in structuring communities (Burrows et al., 2008). High quality ecological information combined with strong natural history and a long history of experimental work in the intertidal has allowed models to be built of the mechanisms that produce climate change responses, such as competition (Poloczanska et al., 2008) and the potential for species to shift their distributions to track shifts in temperature over time (Burrows et al., 2011).

2. TOPIC UPDATE

Changes in distributions and fluctuations in abundance of intertidal species have formed a central basis of confirmed reports of the effects of climate change on intertidal ecosystems in the UK over the last decade. While the most dramatic of these changes have been reported as occurring over the decades preceding the MCCIP Report Cards, and corresponding to recent regional warming, some have been reported as happening between subsequent Report Cards. On this timescale, it is difficult to attribute changes to climate change. Short-term responses that are consistent with the short-term fluctuation in environmental conditions linked to climate are, however, useful corroborative evidence for the likely sensitivity to longer term anthropogenic changes in climate.

In Scotland, recent resurveys in 2014 and 2015 (Burrows et al., 2016) showed little evidence for climate-related changes in species distributions and abundance at the northern limits of climate-sensitive species since the last major survey period in 2002-2006. The areas resurveyed covered the northern limits of two intertidal barnacles (Chthamalus montagui and Chthamalus stellatus) and the purple topshell (Gibbula umbilicalis). The two species of barnacles are most abundant on the west coast of Scotland but appear sporadically in low population densities and as isolated individuals on the east coast as far south as East Fife on the north coast of the Firth of Forth. The east coast was surveyed more intensively in 2014 and 2015 than in previous years and did yield more sites with populations of Chthamalus, but not significantly more abundant than in the previous decade. Evidence from another long-term monitoring study of rocky shores in Sullom Voe, by the Shetland Oil Terminal Environmental Advisory Group (SOTEAG) (Moore and Howson, 2013), does suggest that the warm-water barnacle Chthamalus stellatus is becoming more prevalent in Shetland. The 2015 MarClim survey found the species at 19 out of 22 sites around the coastline of Shetland, the northern limit of the species, compared to only 1 site of 42 in surveys in the late 1970s (Hiscock, 1981), albeit focussed on more sheltered locations. Most populations of C. stellatus on Shetland in 2015 included individuals less than two years old, indicating successful reproduction even at the range edge (Fig. 1). Expansion of the species may have reached a physical barrier in this region with the next nearest coast to Shetland being 280km NW and 1°C colder in Faroe and 300km E in Norway at the same temperature. Similarly, the purple topshell Gibbula umbilicalis was found in more places towards its ultimate geographical limit in 2014 and 2015, particularly in on the west coast of Orkney, but this may reflect the increased survey effort in these two years compared to efforts in the preceding decade. Other widespread changes were found to have

Figure 1: (a) Old adults of the warm-water barnacle Chthamalus stellatus (arrowed red) on the high shore in North Yell at 5/7/2015, amongst adults and juveniles of the cold-water species Semibalanus balanoides (arrowed blue). (b) A recruit Chthamalus stellatus (arrowed green) at the mid shore at the same site.
occurred in Scotland since 2002-2006, most notably the coast-wide decline of the blue mussel *Mytilus edulis* and the general increase in large brown intertidal seaweeds including serrated wrack (*Fucus serratus*), spiral wrack (*Fucus spiralis*) and bladder wrack (*Fucus vesiculosus*). None of these changes are easily attributable to changes in climate over the period. Similar ongoing surveys of intertidal rock species in south west England also showed no evident large changes in distributions since the last MCCIP report in 2013 (Mieszkowska et al., 2013a).

Resurveys and reassessments of geographical ranges have continued to reveal climate-related changes in other intertidal habitats, albeit relative to earlier decades. The distribution of the honeycomb worm *Sabellaria alveolata* has been recently re-assessed towards its limit in the northern Irish Sea (Firth et al., 2015). Distribution limits did not change but abundance did change in line with temperatures. The northern limit for the species remains at Luce Bay in the Solway Firth as observed in the early 1980s, but return surveys to these locations showed increases in abundance from the 1980s to the early 2000s and the 2010s, following declines since the 1960s. Similarly, in the shallow subtidal, a range expansion and increase in abundance of the golden kelp *Laminaria ochrolueca* has been found in the English Channel at the northern edge of its range (Smale et al., 2015). Across whole taxa, reanalysis of historical data has shown a general decline of brown seaweeds in southern UK but not in the north (Yesson et al., 2015). Most species examined (10 of 14) showed a significant association of abundance with temperature change, implicating climate change as a driver. This decline in seaweeds in the south of the UK may be part of a wider regional decline, with cold-temperate canopy species also declining strongly in Spain since the 1970s (Fernández, 2016).

2.1 Recent sea temperature trends explain why so few changes have been reported recently

This lack of observed effects of climate on rocky shore species since 2000 is not surprising given the small and, along most UK coasts, downward change in temperature from 2000 to 2015 (Figure 2). Despite the continued global upward trend in temperature (Figure 2a) (Karl et al., 2015), the sea surface temperature trend in south west England from 2000 to 2015 has been level or slightly downwards (-0.011 °C/yr, Figure. 2b) following two decades of warming (+0.033 °C/yr, 1980-2015 +0.018 °C/yr). Most of the important range changes reported since the turn of the Millennium appear to have occurred before the commencement of more intense efforts to document change, and are associated with the period of rapid warming between 1980 and 1999, and little change has occurred since that date. Elsewhere in the UK, the contrast between the pre- and post-Millennium decades is less strong: in W Scotland for example the trend before and after 2000 was similar (Figure. 2b: 1980-1999, +0.010 °C/yr; 2000-2015, +0.010 °C/yr; 1980-2015 +0.021°C/yr). With such little change in temperature over the past 15 years in the western part of Britain, changes in UK intertidal species distributions reported as occurring since 2000 are unlikely to have been driven by an upward shift in temperature.

Over the longer-term from 1980 to 2015 the rate of increase in temperature was similar in both regions at 0.02°C/yr, or a 0.7°C absolute increase over 35 years. Maps of the trends in temperature over the shorter and longer periods show that trends in temperature are more regionally variable over the two shorter periods (Figure. 3a, 3b), but more consistently upwards over the longer term (Figure. 3c).

The pattern since 1980 has been dominated by greatest warming in the southern North Sea and least warming in the west (Figure. 3c). This rapid warming on the east coast of the UK occurred mainly from 1980-1999 (Figure. 3a), and was followed by a period of cooling from 2000-2015, somewhat but not entirely reversing the trends of the previous two decades (Figure 3b). The net long-term climate change effect was a warming trend all around the UK since 1980. Cooling during the 2000-2015 period occurred across the North Atlantic at around 40-60 °N (Figure. 4), suggesting that a lack of climate-related changes may also be evident in other datasets in the region, such that from the Continuous Plankton Recorder (Reid et al., 2003) and the European International Bottom Trawl Survey (IBTS) and Database Trawl Survey (DATRAS) datasets for bottom-living fishes.
3. HOW HAS OUR UNDERSTANDING DEVELOPED OVER THE PAST DECADE?

Understanding and predicting the effects of climate change on the ecosystems of the world has been a major focus of research effort, summarised in 2014 by the Fifth Assessment of the Intergovernmental Panel on Climate Change (IPCC) (IPCC, 2014a; b), including chapters on global and regional oceans. More recently, the International Union for the Conservation of Nature (IUCN) produced a report on the effects of ocean warming on ocean ecosystems (Laffoley and Baxter, 2016), with reviews on the effects of climate change on rocky shore communities (Hawkins et al., 2016), on seaweeds (Wernberg and Straub, 2016), seagrasses (Koch, 2016), tidal marshes (Megonigal et al., 2016) and on the effects of climate change on coastal protection offered by intertidal habitats (Burrows, 2016). The magnitude of effects of climate change in intertidal systems that have been published in the scientific literature over the last 50 years has been assessed alongside changes in other ecosystems globally (Poloczanska et al., 2013; 2016), with intertidal species showing responses that include changes in abundance, shifts in distributions and changes in seasonal timing of events. Observed changes have mostly been in the same direction as those expected from the direction of climate change, and mostly in line with the size of climate change in different regions.

3.1 Observing and predicting range shifts

Developing better predictions of how intertidal ecosystems might change in the future and improving our understanding of current responses benefits much from the recent efforts to compile and assess evidence of recent climate-related change. The need to develop expectations for responses to climate change has led to new methods for predicting distribution shifts. Climate-based predictions of distribution shifts allow benchmarks to be set against which observed changes can be measured, and combined with climate prediction scenarios providing forecasts of the way intertidal species and communities might respond to future change.
Predictions of distribution shifts of UK intertidal species based on isotherm shifts (Hiscock et al., 2001) have yet to be observed during the first two decades of the 21st century, despite the close association of distribution limits and temperatures and an intensification of survey efforts (Mieszkowska et al., 2005). While this lack of effect of climate is associated with a lack of change in temperature since 2000, it is nonetheless difficult to generate explicit expectations of shifts from plots alone. The pattern in sea temperature around the UK is not simply poleward, and combined with differences in the rates of warming around the UK over time (Figure 5) further obscure how distributions might be expected to shift during a period of temperature change. One approach that solves this problem is the scaling of the rate of change in temperature over time (°C/yr) to the spatial gradient in temperature (°C/km). This measure gives the rate of spatial shifts in isotherms in km per year, also known as the velocity of climate change. Climate velocity multiplied by the time over which the change occurs gives the expected distance shifted by isotherms: a useful first-principles expectation for the rate of shift in species distributions, if distributions follow the changing temperatures (Loarie et al., 2009; Burrows et al., 2011). The approach is generally becoming useful across all ecosystems as a way of gauging the likely effects of climate change on species biogeography (Poloczanska et al., 2014).

Velocity-of-climate/isotherm-based predictions of the rate magnitude of shifts of species around the UK coast (Fig. 5) are for considerable shifts of considerable magnitude since 1980, especially where high rates of large changes in temperature over time coincide with shallow spatial gradients as in the northern part of the North Sea (Figure. 3c, 5a and 5d). Given that the rate of increase in temperature between 1980 and 2015 gives a median increase of 0.78°C (25%ile, 0.61°C; 75%ile, 1.23°C) between 1980 and 2015, this means that species should have shifted by 240km (median value, 170-550km interquartile range, 2-2.5 degrees of latitude) to keep pace with the changing climate. Visually, the expected shift corresponds to roughly 80% of the distance between isotherms at 1°C intervals (Figure. 5a).

This expected magnitude of range expansions of warm water species and contractions of cold water ones is generally much faster than the reported shifts, and is large enough to have been detected by the current sampling intensity of the MarClim programme of sites every 30-50km of shoreline at decadal intervals. On land, the discrepancy between the expected distance of shifts from isotherms and the observed shifts is termed climatic debt (Devictor et al., 2008). Birds in Europe had a climatic debt of 212km over the period from 1990 to 2008, while butterflies were more responsive and had a lesser debt of 135km over the same period (Devictor et al., 2012). Species in the UK intertidal appear to have accumulated the same or larger climatic debts from 1980 to 2015. The actual sizes of the debts in terms of species range shifts are not currently estimated but are likely to be in the order of 100s of km.

3.2 Advances in understanding biological responses to climate-related changes

Ocean acidification poses a growing threat to marine life, with generally negative effects on shallow water organisms, particularly if shell-building, and sometimes positive as for macroalgae (Kroeker et al., 2013). Year-long mesocosm studies on effects of ocean acidification on rocky intertidal species, including Nucella lapillus, have proved useful in showing how acidification may affect the biology of the species over ecologically relevant timescales (Queirós et al., 2014). Complex effects including increased feeding rates but greater distances covered while feeding have been included in models that scale up to population abundance by the end of the 21st century, predicting widespread declines with knock-on impacts on rocky intertidal communities. Similar studies involving both short- and long-term experiments on other intertidal organisms continue to produce positive and negative effects on traits related to ecological performance. The edible winkle Littorina littorea (Melatunan et al., 2013) shows reduced shell growth in response to elevated temperatures and CO₂, with less thickened shell margins and potential for greater susceptibility to predation. Greater clarity as to the likely effects of OA is likely to emerge as this body of work grows.

Figure 5: (a) Average annual SST around the UK with 0.5°C contours. Shifts in isotherms in km predicted from velocity of climate change for UK annual sea surface temperatures: larger shifts in the direction of cooler waters (b) for the period 1980-1999, associated with greater warming; (c) slowing and reversal of previous shifts during 2000-2015; and (d) shifts over the whole period 1980-2015. Axes show longitude and latitude, inset panel shows the magnitude of shifts (red towards cooler areas and blue towards warmer areas).
Field evidence for acidification-related change in the UK intertidal remains lacking in 2016, despite reports from other parts of the world where changes in the intertidal have matched changes in coastal pH. In the north-west Pacific (Wootton et al., 2008), a decade-long series of pH measurements showed a steady decline in annual values, at the same time as a shift from mussel-dominated to algae-dominated communities. The change in pH may have been associated with upwelling of deep water onto the coast in the region (Feely et al., 2008), an event highly unlikely in the UK continental shelf but possible further south.

4. KNOWLEDGE GAPS / KEY CHALLENGES / EMERGING ISSUES

4.1 The problems of assessing change in distributions

Distribution shifts are very hard to detect (Bates et al., 2015) and may be limited by sampling intensity when species are less abundant and have patchy populations. Considering the probability of presence separately from the probability of detection (Tingley and Beissinger, 2009) helps to distinguish non-detection from true absences of species near range edges. Non-detection is a problem for historical data, especially at advancing range edges since the conclusion of a range shift depends critically on confidence in the species being truly absent in the past from the newly occupied portions of the range. Many past records are presence-only, further reducing the usefulness of the past data in inferences of range advancement. Range contractions may be easier to conclude when a species that had been previously extensively recorded from an area is now no longer found occupied on resurvey. Range contractions may be easier to conclude when a species, being lost from parts of their range following cold-water events, is only detectable by the earlier workers in the field, and so do not suffer from the problems of the difficulties of detection of shifts. Sparse and inconsistent recordings of species other than those initially identified as sentinel of climate change, do however make comparisons with subsequent surveys difficult. The problem may benefit considerably from detailed statistical modelling (Mieszkowska et al., 2013b) that specifically addresses the separate issues of detection and presence of species at their range edges.

Range contractions are seldom reported, with the only major contractions occurring in warm water species after a cold event. The extremely cold winter of 1963 in the west and south of Britain (Crisp, 1964) was associated with some species, being lost from parts of their range following cold-induced mortality (Lewis et al., 1982) such as the toothed topshell Phorbus lineatus. Recovery of these populations in subsequent warmer years was evident from their state when resurveyed at the beginning of the 2000s, with breeding populations of toplshells Phorbus lineatus and Gibbula umbilicalis being found up to and beyond their limits before the cold spell (Mieszkowska et al., 2006). While negative effects in south west Britain were dramatic in some cases, with 30-100% mortality in Gibbula umbilicalis, Phorbus lineatus, Perforatus perforatus, and Sabellaria alveolata (Crisp, 1964), many other taxa suffered no adverse effects of extreme cold. Macroalgae and several warm-water species near their northern limits such as the black sea urchin Paracentrotus lividus were not affected, suggesting that these taxa may not be limited by minimum temperatures. Range contractions due to warming have never been reported in the UK. Few species reach their equatorward/warm range edges here. These species tend to be rare and living in hard-to-sample (the kelp Alaria esculenta and brown seaweed Fucus distichus in extreme wave exposure) or cryptic habitats (Tectura testudinalis under boulders, and the northern starfish Leptasterias muelleri under seaweed canopies), making it hard to draw firm conclusions about range changes. Solutions to the problems of understanding the consequences of the complexities of hard-to-detect and varied responses to climate among species are likely to emerge from the continued survey and analysis of spatial and temporal patterns of change.

4.2 Linking change to temperatures experienced in the field: direct effects of heat waves

Responses to extreme heat events in UK intertidal systems are likely to characterise the short-term response to climate change. Trends in frequency of extreme temperature events, (Hobday et al., 2016) tend to follow trends in means. Marine heatwaves and their impacts are being increasingly reported, such as the large-scale event off Western Australia in 2011 where sea temperatures were 2-4°C above seasonal averages for a period of ten weeks, associated with a major die back of macroalgae and an ingress of tropical fish species (Wernberg et al., 2013). By measuring temperatures experienced by intertidal organisms directly alongside high frequency monitoring of shore populations, it is possible to detect the effects of heatwaves on intertidal rock systems. Advances in technology have enabled the direct measurement of the temperatures experienced by intertidal organisms. In situ recording of temperatures, using biomimetic sensors based on mussels and barnacles (Helmuth et al., 2016) or limpets (Lima et al., 2015; Seabra et al., 2015) are making it possible to link observed ecological changes to actual climatic events such as heatwaves, and to link these events to short-term physiological responses, such as the expression of heat shock proteins (Tomanek, 2010). Thermal stress shown by limpets Patella vulgata, for example, across its geographical range are directly linked to the temperatures experienced while in water (Seabra et al., 2016). The association between stress and temperature at the equatorward limit of this species is such that small changes in upwelling along the Iberian coast may be enough to cause large changes in the distribution and abundance of the species.

Continued monitoring of populations alongside logging in situ temperatures may show whether thermal extremes play an important role in setting geographical limits. Intertidal temperature loggers deployed near Oban since 2006 (data in Helmuth et al., 2016) show surprisingly high values at the top of the shore, with temperatures exceeding 40°C on occasions in 7 of the 11 years observed. Extremely high temperatures (>45°C) recorded by loggers are often accompanied by noticeable mortality events in adjacent barnacle populations. These temperatures exceed the upper lethal temperatures of 44°C for the cold-water species Semibalanus balanoides but are within the lethal temperature range for the warm water barnacle Chthamalus montagui (Foster, 1969). On the high shore at least, the ability to survive transient heat stress events may be a major determinant of geographical distributions and the response of intertidal species to climate. New technology such as these should allow a fuller exploration of the links between ecological responses to climate and the thermal physiology, genetics, and gene expression in relation to heat and cold stress. Understanding these links should help distinguish the likely contributions of local adaptation to changed conditions experienced by staying in place versus responses through dynamic changes in populations and distributions.
Non-temperature-related extremes are associated with storms, particularly the impact of extreme wave action. Swell wave heights have been increasing across the North Atlantic (1958-2002, Gulev and Grigorieva, 2006) and this may result in more frequent and more severe wave stress on intertidal shorelines especially during storms. Storm-related wave stress results in the local loss of canopy forming seaweeds (Underwood, 1999), and mussel beds (Wootton, 2001) and the destruction of sessile animals such as barnacles through impacts of wave-borne debris (Shanks and Wright, 1986). Loss of seaweed canopies has important consequences for the whole communities, with very slow recovery of long-lived species such as the egg wrack Ascophyllum nodosum (Jenksins et al., 2004) and gaps in canopies filled initially by early successional species such as the sea lettuce Ulva intestinalis. How this increase in storminess will change intertidal rock communities is presently unknown, but it is likely to result in a decrease and loss of wave sheltered species in areas of intermediate wave exposure (Hawkins et al., 2008).

4.4 Measuring community responses to climate change

A promising, recently developed approach to understanding responses to climate across many species is the use of the Community Temperature Index (CTI). CTI measures the status of a community in terms of its composition of cold- and warm-water species (Devictor et al., 2008). Geographical distributions correlate strongly with thermal tolerances in marine species (Sunday et al., 2011; 2012; 2014). In the absence of detailed physiological and ecological studies of the performance of species across wide ranges of temperature, the average temperatures at the range limits of species give a strong indication of the upper and lower limits at which populations can persist. On this premise, CTI represents the average thermal affinity across community members, expressed as midpoints of the distribution of temperatures experienced across their geographical range: the Species Temperature Index (STI).
The Community Temperature Index has been applied to populations of birds and butterflies in Europe (Devictor et al., 2008; 2012), plants in Costa Rica (where local variation in climate along elevation gradients influences CTI) (Feeley et al., 2013) and birds in Sweden (Lindström et al., 2013), among others. At a global scale, the approach has shown that the thermal affinities of commercial fish landings are shifting towards warm-water species almost everywhere where catches are reported (Cheung et al., 2013) as the ocean temperature warms. Patterns of thermal affinities in shallow reef communities around the world show that for some regions, species fall into distinct geographical groups of temperate and tropical species, and that the shifts between communities dominated by either group can be rapid across relatively small ranges of temperature (Stuart-Smith et al., 2015).

For UK rocky intertidal communities, known distributions for conspicuous and regularly sampled species have been combined with global coastal temperature data to give thermal midpoints for 58 species in the MarClim dataset (Burrows et al., 2016; Burrows et al., 2017). Patterns of CTI around the UK generally follow isotherms, but animal and plant species show quite different patterns (Figure 7).

The difference between species thermal affinities and prevailing local temperatures, termed thermal bias (Stuart-Smith et al., 2015), may also indicate the vulnerability of that community to warming. Where thermal bias is negative, that is where the species are mainly cold-water species (defined as those species whose thermal midpoint is at a lower temperature than the local temperature), warming will mainly produce declines in abundance and potential losses of species when thermal bias is large. The opposite is true where thermal bias is positive, where the community is dominated by warm-water species, and where across the whole community species will tend to increase in response to warming. For most communities so far assessed, CTI is close to local temperature and the community is comprised of a mix of warm-water species likely to increase in relation to warming and cold-water ones likely to decrease. In the UK, rocky shore animals have a positive thermal bias while macroalgae are generally negative, and increasingly so towards SW Britain.

Changes in CTI over time are a useful indicator of the response of a community to warming, and preliminary unpublished analyses show that trends in CTI on rocky coasts in the MarClim dataset closely follow trends in sea surface temperature since 2000. The Community Temperature Index is currently being developed as an indicator of Good Environmental Status for the Marine Strategy Framework Directive (Burrows et al., 2017) for rocky shores, and is likely to be a valuable approach for other marine communities, including commercial fish having already been applied to landings and survey data (Cheung et al., 2013).

Figure 7: Regional patterns in Community Temperature Index around the UK (a) for animals, and (b) for plants. CTI values are averaged across all MarClim surveys in 0.5-degree grid cells (Burrows et al., 2017, unpublished).
CITATION

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