

Changes in the range of some common rocky shore species in Britain – a response to climate change?

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Abstract

Since the 1990s there has been a period of rapid climate warming in Europe. Long-term broad scale datasets coupled with time series at specific locations for rocky intertidal species dating back to the 1950s have been collected in Britain and Ireland. Resurveys of the original locations in 2001–2003 have been undertaken to identify changes in the biogeographical range and abundance of these species. The results show that some ‘southern’ species including *Osilinus lineatus* da Costa and *Gibbula umbilicalis* da Costa have undergone north and north-eastern range extensions. Populations have increased in abundance and adult size has decreased since the previous surveys were conducted. These changes have been synchronous throughout Britain, strongly suggesting that climate is responsible. The use of intertidal species as indicators of climate change is proposed.

Introduction

The global average surface temperature has been increasing since records began in 1861. Proxy data for the Northern Hemisphere indicate that the increase in temperature observed during the 20th century is the largest in the last 1000 years (Hulme et al., 2002), with the 1990s the warmest decade and 1998 the warmest year on record (Houghton et al., 2001). The ocean heat content has also increased since modern measurements began in the 1950s. In the western English Channel off Plymouth a 1 °C increase in sea surface temperature has occurred since 1990. This increase exceeds any other change recorded over the past 100 years (Hawkins et al., 2003) and is most apparent in winter months (Fig. 1). Global climate change models predict an acceleration of the current warming trend during the first half of this century as a response to

anthropogenic emissions of greenhouse gases. These models also predict that the earth will become warmer than at any period during the past 40 million years (Houghton et al., 2001). The rate of warming cannot be predicted with certainty but models based on medium-high emissions scenarios indicate that sea surface temperatures around Britain will increase between 0.5 and 5 °C by 2080 (Hulme et al., 2002).

Responses of a wide range of marine biota to oceanic warming have already been documented. These include changes in phenology, as observed in the migration patterns of squid in the English Channel (Sims et al., 2001), shifts in abundance and distribution which have been shown in changes to plankton and fish assemblages in the North Sea and English Channel (Southward et al., 1995; Beaugrand et al., 2002; Stebbing et al., 2002) and changes in the community dynamics of intertidal

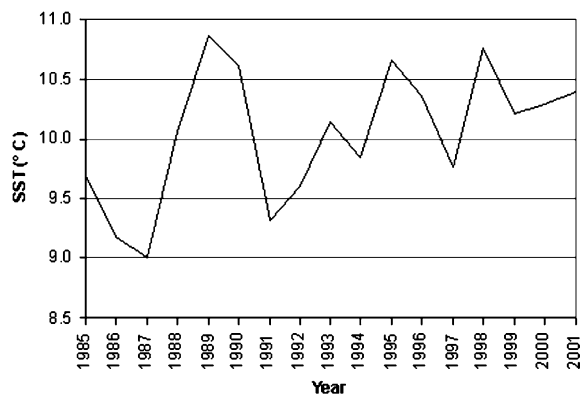


Figure 1. Mean winter (Jan–Mar) SST for the Western English Channel from NOAA Pathfinder AVHRR data for 1° grid square centred on 50° N 4° W. The data were provided by the Earth Observing System Data and Information System (EOS-DIS), Distributed Active Archive Center at Goddard Space Flight Center which archives, manages, and distributes this data set.

invertebrates in the North West Atlantic (Barry et al., 1995; Bertness et al., 1999; Sagarin et al., 1999; Murray et al., 2001). As the climate continues to warm it is hypothesised that a poleward shift in the ranges of species will occur (Graham & Grimm, 1990; Fields et al., 1993; Southward et al., 1995; Parmesan, 1996; Sagarin et al., 1999). Climate-induced changes in the range of terrestrial species have already been documented in a wide variety of systems (Jeffree & Jeffree, 1996; Parmesan et al., 1999; Parmesan & Yohe, 2003; Root, 2003) and similar patterns of change are likely in the marine environment.

Britain and Ireland straddle a biogeographic boundary between cold boreal 'northern' waters and warmer lusitanian 'southern' waters (Forbes, 1853; Lewis, 1964) and many intertidal species reach their northern or southern limits of distribution in or close to the British Isles. Thus it is an ideal location for studying the effects of climate change on these species. The Marine Biodiversity and Climate Change Project, MarClim (established in 2001) was set up to assess and forecast the influence of climate change on marine rocky shore biodiversity in Britain and Ireland, and make use of existing long-term and current data.

It is fortunate that extensive historical broad-scale baseline of data on intertidal rocky shore fauna and flora has been collected in Europe (Southward & Crisp, 1954a; Fischer-Piette &

Prenant, 1956; Crisp & Southward, 1958; Crisp & Fisher-Piette, 1959). Observations at some sites date back to the 1930s, with continuous data since the 1950s for certain species including the barnacles *Chthamalus stellatus* Poli, *Chthamalus montagui* Southward [which were synonymous until 1976 (Southward, 1976)] and *Semibalanus balanoides* Linnaeus (Southward & Crisp, 1954b; Crisp & Southward, 1958; Southward, 1967; Southward, 1991). In addition, the population structures of the 'southern' trochid gastropods *Gibbula umbilicalis* da Costa and *Osilinus (Monodonta) lineatus* da Costa were studied close to the northern limits of distribution in Britain as part of the NERC Rocky Shore Surveillance Group study on processes regulating coastal ecosystems (Kendall & Lewis, 1986; Kendall, 1987).

Methods

The MarClim project collects both broadscale and quantitative data following the methods employed during historical surveys.

Broadscale

Semi-quantitative broadscale surveys of rocky intertidal flora and fauna were undertaken during the 1950s at approximately 400 sites around the coastline of Britain and Ireland (Southward & Crisp, 1954a; Crisp & Southward, 1958). The abundance of each species was assessed using the semi-logarithmic ACFOR abundance scale developed by Crisp & Southward (1958: 160, Table 2) to determine the biogeographic ranges of littoral species. MarClim repeated broad-scale surveys at approximately 300 of the historical sites in 2001–2003 (Fig. 2) using the original ACFOR classification method, including semi-exposed and exposed shores where anthropogenic impacts are often limited in Britain.

Thirty-three of the 39 species that were recorded in the original broadscale surveys of the 1950s were selected for inclusion in the resurveys. An additional 23 species were included in the resurvey list. All species selected reach their northern or southern limits of distribution close to Britain and Ireland and populations are therefore more likely to be sensitive to changes



Figure 2. Locations of broadscale resurveys completed in 2002 and 2003.

in climate than those species that are at the centre of their range (Lewis, 1976). Pairs of northern and southern species whose distributions overlap and are competitors on the rocky shores of Britain were included to determine how climate mediates species interactions. Each shore was searched by 2 operators for a duration of 30 min, and the abundance of each species recorded. Target species were also searched for at sites beyond the last documented range edges to determine whether range expansions had occurred.

Quantitative

Southward and Crisp also undertook quantitative counts of adults of the southern barnacle species *Chthamalus stellatus* and *Chthamalus montagui* and the northern barnacle species *Semibalanus balanoides* in 3–4 quadrats at the MHW, MTL and MLWN shore levels at each sample location (Southward & Crisp, 1954b; Southward, 1991). During the MarClim resurvey, 10 replicated barnacle

counts in 25 or 10 cm² quadrats, were carried out at the same tidal heights at each site. Digital photographic recording of barnacle quadrats was also trialled as a potential replacement for counts *in situ*.

Quantitative counts of the ‘northern’ limpet *Patella vulgata* Linnaeus and the ‘southern’ limpet *Patella depressa* Pennant have been collected on shores in the south and south-west of England, Wales and France since 1980 by S.J. Hawkins. These counts have been continued as part of the MarClim project. Ten replicated counts of individuals in a randomly placed 0.25 m² quadrat were made within the area of the shore where *P. depressa* was most abundant. These surveys complement the research on barnacles (outlined above) and increase the understanding of the role of climate in ‘northern’ and ‘southern’ species competitive interactions.

The population structures of the ‘southern’ trochid *Gibbula umbilicalis* were recorded at 16 sites close to the northern range limits between 1977 and 1985 (Fig. 3) (Kendall & Lewis, 1986). Approximately 200 animals (where available) were collected during each survey and their basal



Figure 3. Survey locations of *Osilinus lineatus* (closed circles) and *Gibbula umbilicalis* (open circles).

diameters measured to the nearest millimetre. Population structures of another 'southern' trochid *Osilinus lineatus* were also studied at 16 sites close to northern range limits in Britain and France in 1986 (Fig. 3), (Kendall, 1987). Replicated timed collections of individuals involving intensive searching of boulders, underlying gravel and bedrock were carried out in areas of the shores where juvenile abundance was estimated to be greatest. The basal diameter of all individuals was recorded and the animals returned to the shore. At each site resurveyed between 2001 and 2003, five replicated timed counts of 3 min duration were carried out in the area of greatest juvenile abundance for *O. lineatus*. The basal diameter to the nearest millimetre was recorded for each individual and the animals replaced on the shore. The same method was adopted for *G. umbilicalis* at historical sites to make them more amenable to statistical analyses than the original dataset. Quantitative counts were also made at an additional 25 sites for *O. lineatus* and 42 sites for *G. umbilicalis* throughout Britain and northern France to allow analyses of the resurvey data in a wider geographical context.

All of the original datasets including metadata have been extracted from field notebooks and electronically archived in a central database. Resurvey data from 2002 to 2003 have also been archived in database and hard copy format. All data entries have been subject to quality assurance checks involving the original collectors.

Results

Changes in biogeographic range

The MarClim project has completed the second year of its 4-year operational schedule and the results of the biogeographic range studies undertaken to date are reported here. The original broadscale surveys were made in the 1950s during a warm climatic period (Fig. 4). A cool period followed, whose onset was dramatically marked by the severe winter of 1962/1963, the coldest since 1740 (Crisp, 1964). Species close to their northern and north-eastern range edges in Britain were severely affected by the extremely cold weather,

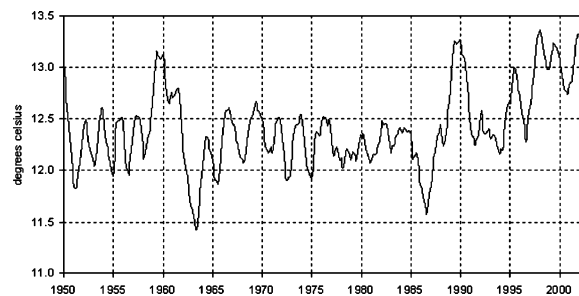


Figure 4. Annual mean sea surface temperature (SST) in the Western English Channel (50–51° N, 4–5° W). Met Office – GISST/MOHMATN4/MOHSST6 – Global Ice coverage and SST (1856–Feb 2003) data provided with kind permission to the MarClim project by the British Atmospheric Data Centre (BADC).

with sea and air temperatures falling to as low as 0.6 °C (Aberthaw, Wales) and –3.4 °C (Swansea, Wales), respectively (Crisp, 1964). Populations of the trochid gastropod *Osilinus lineatus* were wiped out on the island of Anglesey and along much of the Welsh and South West England coastline (Crisp, 1964). The tubeworm *Sabellaria alveolata* Linnaeus and the barnacle *Balanus perforatus* Brugière also suffered severe mortalities along the Welsh and southern English coastlines, where they had previously reached their northern and north-eastern range limits (Crisp, 1964). A second abnormally cold winter occurred in 1978/1979. Populations of these southern species again suffered mortalities during this winter, but these were on a smaller scale, as the weather was not as severe as in 1962/1963 (Kendall et al., 1987). The climate remained in this cool phase until the late 1980's, when the current warming trend began.

Data collected by MarClim has shown that the southern species *Osilinus lineatus*, *Gibbula umbilicalis*, *Sabellaria alveolata* and *Balanus perforatus* have all re-colonised locations close to their northern range limits from where they were lost after the cold winter of 1962/1963. There is also evidence that southern species declined in abundance and northern species increased commensurately in the 1960s, 1970s and early 1980s (e.g., barnacles (Southward, 1967, 1980; Southward et al., 1995; Herbert et al., 2003); limpets (Southward et al., 1995)). This indicates that these re-extensions of range have occurred during the current period of warming since the late 1980s.

Another southern species, the brown algae *Bifurcaria bifurcata* Ross has undergone oscillations in its distribution on the south coast of England. A population was recorded in Dorset during the 1960s (E. Burrows, unpublished), but in recent decades it has been restricted to South Devon, with a sharp range edge between the Salcombe and Dart estuaries in the vicinity of Start Point ((WGS84) 50.22° N, -3.64° W) (JNCC, 1998). Several plants were recorded on Portland Bill (50.51° N, -2.45° W) in 2002 which represent a north-eastern extension in range of approximately 140 km.

The southern trochids *Osilinus lineatus* and *Gibbula umbilicalis* have also extended their northern range edges since the last surveys were conducted in 1985 (Kendall & Lewis, 1986; Kendall, 1987). The previous range edge of *O. lineatus* (defined as the last breeding population) was recorded at Lyme Regis (50.71° N, -2.950° W) on the south coast of England (Kendall, 1987). In 2002 and 2003 a mixed age population including recruits from 2001 and 2002 was found at Osmington Mills (50.63° N, -2.37° W), over 50 km east of the previous range edge population. Individuals had occasionally been recorded at this location in the 1960s (Hawthorne, 1965) and the 1980s (Kendall, pers. obs.), and further east (e.g., Kimmeridge (50.61° N, -2.13° W), Herbert, pers comm.; Preece, 1993) but a multi-cohort population has not been previously documented. The last documented position of the northern range edge of breeding populations of *G. umbilicalis* was Skerry (58.44° N, -4.30° W), on the north coast of Scotland in 1985, although isolated individuals were occasionally found 45 km further north east (Kendall & Lewis, 1986). A breeding population was recorded 55 km north-east of Skerry in 2002, with isolated individuals found up to 20 km past this location (Mieszowska, unpublished data).

Discussion

Mechanisms setting northern range edges

The resurveys have revealed that in recent years, a number of species of invertebrates and macroalgae with southern distributions have ex-

tended their range in the British Isles (Southward & Crisp, 1954a; Hawthorne, 1965; Kendall & Lewis, 1986; Kendall, 1987; JNCC, 1998). The survey sites selected are all semi-exposed or exposed shores, minimising the effects of local environmental and anthropogenic impacts on the system. However, it is very difficult to separate the effects of temperature from other concomitant factors including the effects of coastal and industrial development, and therefore field experiments and laboratory manipulations of temperature are required in order to increase our understanding of the mechanisms driving the observed changes.

The two main biological processes that have been implicated in setting the geographical distribution limits of animals are survival and reproduction (Hutchins, 1947; Lewis et al., 1982). If the limits are determined by survival alone, extreme environmental conditions will cut back the range and less extreme conditions will allow its expansion (Lewis et al., 1982). Adult mortality has been shown to set the range edges of species during two extreme cold periods in Britain (Crisp, 1964; Kendall et al., 1987). However, population and recruitment data from previous studies indicate that in all but the most severe winters low temperatures do not result in a loss of significant adult individuals from populations.

Populations that are limited by poor recruitment success would be expected to have irregular age structures, missing year classes or a bias towards old animals (Lewis et al., 1982). The most northerly populations of *Gibbula umbilicalis* studied between 1976 and 1984 exhibited these characteristics. Partial or full recruitment failure occurred across all of these populations during the 1976–1984 time-series (Kendall & Lewis, 1986). A synchronous, but less well marked pattern of recruitment success/failure was observed at populations further south in Britain, suggesting that a large scale factor such as climate or hydrography may have been responsible (Lewis et al., 1982; Bowman, 1985; Kendall & Lewis, 1986). The size frequencies of all the populations that were revisited in 2002 and 2003 show that recruitment has been more successful in recent years (Mieszowska & Kendall, unpublished data). As a consequence, population densities and the potential reproductive

output of these northern populations has increased as increasing numbers of surviving juveniles become reproductively mature. On the north coast of Scotland, mixed age cohort populations now exist in locations where only occasional individuals were found in the 1980s (Kendall & Lewis, 1986; Bowman, pers comm.). These range extensions are thought to be linked to the increased reproductive/recruitment success of populations close to the range edge.

In both *Gibbula umbilicalis* and *Osilinus lineatus* the length of the breeding period is shorter in populations closer to northern geographic limits than in populations at the centre of the range, suggesting that changes in reproductive activity may be temperature driven (Bode et al., 1986; Kendall & Lewis, 1986; Lewis, 1986; Kendall, 1987). Such temperature sensitivity indicates that the reproductive success of these species may be altered by rapid climate warming. In the cold winter of 1978/1979 Williamson, Kendall and Lewis (Williamson et al., unpublished data) transplanted 1000 adult *O. lineatus* from a breeding population at Aberaeron (52.24° N, -4.26° W), mid Wales to Brighthouse Bay (54.78° N, -4.12° W) in South West Scotland and a further 1000 animals to Burniston (54.33° N, -0.42° W) in the North Sea¹.

At Brighthouse Bay and Burniston, which are both located north of existing range limits, transplanted animals were still able to successfully develop gonads. Interestingly, the mean peak gonad weight for transplanted animals was greater at both sites than in the source population at Aberaeron. The Aberaeron population spawned in June 1979, but spawning was delayed until July in the Burniston population and August in the Brighthouse Bay population (Fig. 5). The mean monthly sea surface temperatures were

¹ The transplant experiments were undertaken in 1978. Since then the scientific community has become fully aware of the implications of moving animals to areas that they had not previously colonised. The data is referred to in this paper as it is of value in determining the mechanisms underpinning species distributions, but the practice of transplants is not supported by the MarClim Project. The animals that were transplanted on the original survey did not colonise on shore and no populations of *Osilinus lineatus* have been recorded at these sites in subsequent years. Such transplants should not be attempted or condoned.

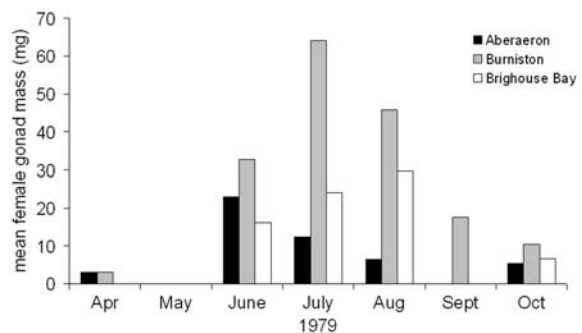


Figure 5. Female gonad cycles of *Osilinus lineatus* in the source population (Aberaeron) and transplant populations (Burniston and Brighthouse Bay).

lower at both Brighthouse Bay and Burniston than at Aberaeron throughout the period of gonad maturation. These results show that changes in reproductive activity occurred in animals transplanted to a colder temperature regime.

Sea and air temperatures are directly linked to latitude, with a temperature gradient extending from the tropics to the poles, although local modifications can occur due to factors such as upwelling and continental influences. Any general latitudinal cline in the length of the reproductive cycle and spawning periodicity would therefore suggest a correlation with temperature (Hutchins, 1947). To investigate the variation in the onset of the reproductive cycle in *Osilinus lineatus* and *Gibbula umbilicalis* along a latitudinal gradient a sample network extending from sites close the northern range edges in Britain and Ireland to mid range sites in Portugal has been established. Gonad samples from adults of both species are taken at monthly intervals from each site and are analysed to determine the timing and periodicity of gametogenesis and spawning at each location. Laboratory experiments are also underway to determine whether changes in temperature can alter the gametogenic period and extend the duration and frequency of spawning events in *O. lineatus* and *G. umbilicalis*. These experiments will increase our understanding of changes to the potential reproductive output as northern range limits are approached, and of the role that temperature plays in setting northern geographical limits of distribution in these southern species.

Table 1. Proposed climate change indicator species

Species	Biogeographic range	Data	References
<i>Ostrea lineatus</i>	Morocco to Eastern English Channel, North Wales & North East Ireland	Baseline data 1952, 1954, 1958, 1964, 1986. Resurvey 2002, 2003. Population studies 1987, 2002, 2003. Reproductive studies.	Southward & Crisp (1954a), Southward & Crisp (1954b), Crisp & Southward (1958), Kendall (1987), Kendall et al. in prep.
<i>Gibbula umbilicalis</i>	Morocco to North Scotland	Baseline data 1952, 1954, 1958, 1964, 1974–1986. Resurvey 2002, 2003. Population studies 1974–1986, 2002, 2003. Reproductive studies 2002, 2003.	Lewis (1952), Southward & Crisp (1954a and b), Crisp & Southward (1958), Garwood & Kendall (1986), Kendall & Lewis (1986), Mieszowska et al. in prep.
<i>Chthamalus montagui</i>	North Africa & Mediterranean to Isle of Wight & Shetland Islands	Baseline data 1954, 1958. Resurvey 2002, 2003. Population studies.	Fischer-Piette (1936 as <i>C. stellatus</i>), Southward & Crisp (1954a), Southward & Crisp (1954b), Crisp & Southward (1958)
<i>Semibalanus balanoides</i>	Northern Spain to Spitzbergen	Baseline data 1954. Resurvey 2002, 2003. Recruitment studies 1997.	Fischer-Piette (1936), Southward & Crisp (1954a), Crisp & Southward (1958), Jenkins et al. (2000)
<i>Balanus perforatus</i>	West Africa to Eastern English Channel & South West Wales.	Baseline data 1936, 1958, 1964. Resurvey 1993/1994, 2002, 2003.	Fischer-Piette (1936), Crisp & Southward (1958), Lewis (1964), Stubbings & Houghton (1964), Herbert et al. (2003)
<i>Patella depressa</i>	Senegal to Eastern English Channel & North Wales	Baseline data 1958. Resurvey 2002, 2003. Population studies 1980–2003.	Fischer-Piette (1936), Crisp & Southward (1958), Crisp & Fischer-Piette (1959), Crisp unpublished.
<i>Patella vulgata</i>	South Portugal to Norway 70° N	Baseline data 1954, 1958. Resurvey 2002, 2003. Population studies 1980–2003.	Fischer-Piette (1936), Crisp & Southward (1958), Bowman (1985)
<i>Sabellaria alveolata</i>	Morocco to Solway Firth, Scotland	Baseline data 1954, 1958, 1984. Resurvey 2002, 2003.	Gruet (1971), Wilson (1974), Cunningham et al. (1984)
<i>Bifurcaria bifurcata</i>	North Africa to Western English Channel and Wales	Baseline data 1936, 1954, 1958, 1959, 1952. Resurvey 2002, 2003.	Fischer-Piette (1936), Valera (1962)
<i>Alaria esculenta</i>	Loire-Atlantique region to Norway, limited to South & West Coasts of England and Wales, present in Scotland. Absent from most of English Channel since 1950s.	Baseline data 1936, 1954, 1955, 1958, 1970. Resurvey 2002, 2003.	Fischer-Piette (1936), Crisp & Southward (1958), Widdowson (1970)

Predicting future changes

From the historical and resurvey data outlined above, the species which have shown clear alterations in their range and population characteristics during the current period of climate warming are suggested as suitable indicator species to monitor and predict the future climate and the potential changes to marine biodiversity in Britain and Ireland (Table 1). They are also of interest as many are keystone or space dominating species whose presence or absence can determine the community composition and dynamics of a shore.

The relative abundance and distribution of the southern warm water species *Chthamalus stellatus* and the northern cold water species *Semibalanus balanoides* in Britain have been shown to be broadly controlled by temperature, with *S. balanoides* being competitively dominant during colder years and *C. stellatus* during warmer years (Southward & Crisp, 1954b; Southward, 1967; Crisp et al., 1981). The proportion of *Chthamalus* adults on shores in south-west England has also been shown to correlate with mean annual inshore sea surface temperature with a 2 year time lag, with temperature accounting for over 40% of the population variance (Southward, 1991; Southward et al., 1995). This time-series is being continued by MarClim and statistical analyses of spatial and temporal trends are ongoing.

As grazers, the trochid species *Osilinus lineatus* and *Gibbula umbilicalis* originally surveyed by Lewis and Kendall are involved in the structuring of rocky shore communities. The analyses of past and current distributions and population dynamics, coupled with experimental work on the mechanisms behind these observed changes will allow future predictions of the responses of these species to climate to be made with a high degree of confidence. Data from historical surveys and MarClim resurveys indicate that changes in climate correlate with changes in the population dynamics of southern trochid species over 3° of latitude, suggesting that a large-scale factor such as climate or hydrography is the underlying driver.

As the climate warms further it is predicted that northern cold-water species will experience a

contraction at their southern range edges as environmental conditions become too warm to facilitate successful recruitment in Britain. This retreat will be compounded by increased competition from southern warm-water species, which are likely to extend their distribution northwards as their reproductive success increases. Contractions and expansions of geographic ranges will lead to species being lost from and introduced to established communities. Fluctuations in climate will also alter the relative dominance of northern and southern competitors within a community.

Research into the responses to climate by marine species using intertidal indicators has both advantages and disadvantages. Rocky shore species are amenable to research due to their accessibility, feasibility of replication in surveying and experimental design, and the ease of identification. The effects of climate change on these species also has strong consequences for community dynamics, biodiversity and the ecology of the rocky intertidal zone which can be experimentally explored (Sagarin et al., 1999; Tomanek & Helmuth, 2002). These changes concord with changes in other marine communities (see above) and may be used to predict changes offshore. There are, however, problems. These include separating the effects of air and sea temperature on the various stages of the life cycle for each species and the relative importance of air and sea temperatures to adult and larval survival. Field resurveys coupled with experimental research will provide a greater understanding of the effects of climate and assist in the correlation of climatic factors with biological responses.

The body of evidence that has been documented on the fluctuation of range and population dynamics of warm and cold water species during changes in the oceanic and air temperatures over the last century is a strong indication that these species are of use in tracking climate change (Southward et al., in press). The ability to predict future changes in the demography of these species has immense scientific, conservation and socio-economic potential. Concern is also growing among coastal zone stakeholders and environmental planners regarding the structure and functioning of marine communities in re-

sponse to global environmental change. Whilst change is inevitable, it is important to incorporate current patterns and future forecasts into marine conservation and management plans.

Conclusions

This paper outlines the preliminary findings of the MarClim project to date, focussing on the responses of species at their northern limits to changes in climate ahead of completion of the resurvey in 2005. The research carried out by the MarClim Project will demonstrate the extent of changes that have occurred in the last 50 years and the results will be used to develop and test hypotheses on changes now occurring. This will allow forecasts of future change to be made with maximum confidence, based on definitive climate models and covering a wide range of temperature-sensitive species. It will also evaluate whether the climate indicator species used in this work have a wider contribution to make as part of the sustainability indicators that are needed to underpin the UK sustainable development strategy.

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