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Effect of changing temperature on benthic marine life in Britain and Ireland

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ABSTRACT

1. The coastal waters surrounding Britain and Ireland became warmer during the 20th Century and, according to the UK Climate Impact Programme predictions, average annual temperatures may rise a further 2°C by 2050. This warming is part of a global rise in sea and air surface temperatures that will cause changes in the abundance and distribution of species.

2. Initially, there will not be a wholesale movement northwards of southern species or retreat northwards of northern species because many additional factors will influence the responses of the different organisms. Such factors include the hydrodynamic characteristics of water masses, the reproductive mode of species, the presence of geographical barriers to spread and the longevity of already established species. Survey data from the past century show how organisms react to changes of the order of 0.5°C, and in the last two decades, when sea temperatures have risen by as much as 1°C, there have been significant local changes in the distribution of intertidal organisms. These past changes provide a clue to more extensive changes expected in the future if global warming develops as predicted.

3. Where species affected by climate change are dominant or key structural or functional species in biotopes, there may be a change in the extent and distribution of those biotopes. Some, dominated by predominantly northern species such as the horse mussel *Modiolus modiolus*, may decline and reduce their value as rich habitats for marine life. Others, characterised by southern species, for example the sea fan *Eunicella verrucosa* and the alcyonacean *Alcyonium glomeratum*, may increase in extent.

4. Using information on the reproductive biology of species, their present distribution and other factors, a decision tree has been constructed to identify 'types' of organisms according to their likely response to temperature rise. Conspicuous and easily identified rocky substratum species are good candidates to track change. Using the key, many species are likely to increase their range northwards significantly. In contrast, fewer will decline in abundance and extent in the north. If, as anticipated, global warming

continues, species with distributions already accurately mapped, or being mapped at present, will provide baseline data to test forecasts.

INTRODUCTION

Origins of the study

In 2000, the authors were commissioned by Scottish Natural Heritage to report on the likely impact of climate change on subtidal and intertidal benthic species in Scotland. The results of that work (Hiscock *et al.*, 2001) have now been revised and expanded to encompass all of Britain and Ireland and are presented here to a wider audience. Since the work undertaken in 2000, the Marine Biodiversity and Climate Change (MarClim: www.mba.ac.uk/marclim) initiative has started a co-operative study looking in much greater detail at rocky shore species distributions from past records and through comprehensive re-survey. Changes in distribution have already been recorded by that initiative.

[Insert Figure 1 about here.]

The work described here builds on past studies of the authors as well as other marine biologists (including Lewis, 1964, 1986, 1996, 1999; Lewis *et al.*, 1982, Todd and Lewis 1984 for animals and, for algae, Dixon 1965, Price *et al.* 1979, Lüning 1990, Tittley & Price 1978, Yarish *et al.* 1986) who have mapped distributions of species and speculated on the reasons for biogeographical limits and on why changes in distribution sometimes occur. The British Isles are well-placed to study changes that might result from rising sea temperature, since many north-east Atlantic continental shelf species reach their southern or northern limits around the coast. Indeed, the study of geographical distribution of species around our coasts has a long history. The first description of the distributional limits of certain species, including a delineation of the “General limit of Southern types”, was prepared by Edward Forbes nearly 150 years ago. His map of distribution of marine life was published posthumously in Johnstone’s Atlas (Forbes, 1858) and many of the details remain correct today (Figure 1). For algae, one of the earliest biogeographic studies was that of Børgesen & Jónsson (1905): a study of marine floristic relationship of the Faroes and other countries in the north Atlantic Ocean. Finding evidence of the marine life occurring around the coasts of Britain and Ireland further ago than 150 years is very difficult although Tittley *et al.* (1999) refer to an account of the algal flora at Margate in 1632. The report recorded species now known as *Fucus serratus*, *Fucus vesiculosus*, *Halidrys siliquosa*, *Laminaria digitata*, *Laminaria saccharina*, *Corallina officinalis*, *Palmaria palmata*, and *Ulva lactuca*: species which form the principal vegetational features of the shores today.

Our aim now is to identify those factors that can be explored to predict likely changes in the abundance and distribution of both ‘northern’ and ‘southern’ species around the British Isles. The methodology developed should be widely applicable in any region where species with sufficient information on their reproductive biology and where residual water movements (currents) around the relevant coastline are known. Our predictions of changes in species distributions are linked to present predictions of climate change, as prepared by the UK Climate Impacts Programme (UKCIP). Most recently, Viles (2001) has also forecast likely impacts of climate change on the marine

environment of Britain and Ireland within the context of the MONARCH (Modelling Natural Resource Responses to Climate Change) project.

Historical context

Considered on a global scale, the past 100 years have seen marked changes in both terrestrial and aquatic ecosystems in response to rising surface temperature (Walther *et al.*, 2002; Parmesan and Yohe, 2003).

The marine fauna and flora around Britain and Ireland has developed within a context of variation in sea and air temperatures. At the end of the last glaciation (approximately 10,000 years BP), there was what has been considered to be a rapid rise in mean sea temperature in the north-east Atlantic although it took almost four centuries for a rise of 10°C to occur (Bard *et al.*, 1987). However, during interglacial periods, there may have been rather abrupt changes in climate, within less than a century (McManus *et al.*, 1994; Broecker, 1997; Adkins *et al.*, 1997). Significant changes in air and seawater temperatures have occurred in the past thousand years or so. Lamb (1977) used various sources of information including direct temperature readings to conclude that, in the previous 150 years, sea temperature in the north Atlantic might have risen by 0.5 to 1.0 °C. Rises in temperatures can occur over short periods of time. Off southern Iceland, the rise in temperature between 1910-1919 and 1940-1949 was 2.1°C (Lamb, 1977). Sometimes those changes took place over only a few years or decades but then stabilised for centuries. Further back in time (between about 800 and 1300 AD), it seems that there was a period when sea temperatures in the north Atlantic were probably warmer than today. Some evidence, such as the occurrence of cod off Greenland (cod require water temperatures above 2°C), does suggest higher temperatures than in more recent times but other evidence is circumstantial (Lamb, 1988).

Temperature records for the 20th Century (Figure 2) show a period of overall warming up to the middle of the century, the exact date of the peak being later for the sea, which normally lags behind trends in air temperature. Then, from the early 1960s there was a period of marked cooling. From the mid-1980s warming resumed again, and in the last decade of the 20th Century the warming trend strengthened – for example there was a rise in annual average sea temperature in the western English Channel of about 1° C (Hawkins *et al.*, 2003).

[Insert Figure 2 about here.]

Information on long-term responses of benthic species to increases (or decreases) in sea temperatures is sparse. In British waters there were changes in the relative abundance of species of intertidal barnacles between the 1930s and 1950s, with cold water species declining in response to a rise in mean sea temperature of the order of 0.5°C (Southward and Crisp, 1954a). Subsequently, further changes were observed, including an increase in the northern species during a period of falling temperatures from 1962 to 1980 and then its decline as warming was resumed (Southward, 1967, 1991). There were corresponding changes in abundance and distribution of intertidal molluscs (Southward *et al.*, 1995), and a hitherto unrecorded warm water barnacle was discovered off Plymouth (Southward, 1995). Records of the occurrence and distribution of algal species may also reflect warming seas. For instance, the occurrence and spread of the kelp *Laminaria ochroleuca* in southern England (Parke 1948) and of the brown

alga *Zanardinia prototypus* in south-west Britain and southern Ireland (Jephson *et al.* 1975, Hiscock & Maggs 1982, 1984). Apart from the species mentioned above there is little evidence of the recent spread of autochthonous algae along the English Channel. Overseas, Barry *et al.* (1995) reported significant increases in number of southern intertidal species and decreases in abundance of northern species at Monterey, California. These changes occurred during the period from 1932 to 1993, when mean summer maximum air temperatures increased by about 2.2 °C and shoreline sea temperatures by about 0.75 °C (Sagarin *et al.*, 1999). Apart from barnacles and gastropod molluscs, changes in benthic animals in south west England have been less obvious, except in occasional very cold spells when warm-water species were killed off (Crisp, 1964). However, recent observations along the English Channel show that the warm water barnacle, *Balanus perforatus*, has extended its range eastward by upwards of 100 km in the past 25 years (Herbert *et al.*, 2003). This species now lives in places in the eastern English Channel that were formerly considered to be too cold for it in winter. Corresponding range extensions have occurred in the topshell *Osilinus lineatus* (pers. comm. N. Mieszkowska) along the south coast. Another warm water barnacle *Chthamalus montagui* has extended its range in eastern Scotland (pers. comm. M.T. Burrows). These recent changes do not fall into the category of a simple northward extension of warm water species, they were either eastward along the Channel or southward down the east coast of Scotland, and are related to corresponding increases in sea temperature in the same direction.

Pelagic species, especially fishes, are more sensitive to climate change than benthos and demersal fish. In the western English Channel, the relative abundance of herring and pilchard has fluctuated in response to climate over the past 400 years, the pilchard being dominant during warmer periods (Southward *et al.*, 1988). These changes are part of the so-called “Russell Cycle”, which is broadly linked to climate (Southward, 1963; Cushing and Dickson, 1976; Southward, 1980). Corresponding changes are reported for other parts of European seas (Alheit and Hagen, 1997). In the Pacific, the well-known switches in relative abundance of Californian sardine and anchovy have been linked to temperature, either directly or indirectly through changes in the oceanographic regime, including upwelling (Soutar and Isaacs, 1969; Cushing, 1975). Cushing and Dickson (1976) summarized climate-related biological trends in north-east Atlantic waters up to 1975. Details of the changes in the plankton off Plymouth were described by Russell *et al.* (1971), Southward (1980) and Southward *et al.* (1995). Long term data from the Continuous Plankton Recorder surveys (Beaugrand *et al.*, 2002) showed that in the 40 years prior to 2000 there was a 10° latitudinal shift northwards in the distribution of southern species of copepods in the eastern North Atlantic. Other species sampled by the CPR survey have also shown long term changes (Lindley and Batten, 2002).

Predicted climatic change

All the evidence currently available suggests that inshore sea temperature will continue to show significant short-term variations. Maximum and minimum sea surface temperatures in any year may range 2 °C above or below the average, but there will be a trend towards higher temperatures.

By the 2050's, average air temperatures relevant to rocky coastal platforms may be up to 2.1°C higher in than at present (Austin *et al.*, 2001), sea-level may have risen by up to 80 cm, and surface sea temperatures may be as much as 2.5°C higher in summer

and 2.3°C higher in winter than in 2000 (Viles, 2001). Coastal water temperatures in Scotland have already risen by about 1°C between 1970 and 1998 (Turrell, 1999). In enclosed waters, the rise in temperature may be higher than the open coast average.

Any true long-term change is likely to be obscured initially by short-term fluctuations driven by the approximately decadal cycle of the North Atlantic Oscillation (Hurrell, 1995) which may also interact with the 11-year cycle of sunspot activity, which represents a guide to solar energy flux (Southward *et al.*, 1975). The Russell Cycle (Cushing and Dickson, 1975) may also be important, reflecting longer amplitude changes in response to climate. There are other uncertainties, including the possibility that melting polar ice may ultimately cause 'switching-off' or slowing of the 'Atlantic conveyor belt' which draws warm water northwards along the western seaboard of Europe (Broecker, 1997). When changes in sea temperature lag behind those on land or are modified by changes in water currents, intertidal organisms will anyway be affected first by increased air temperature and solar radiation during low tides.

KEY ENVIRONMENTAL FACTORS THAT DEFINE DISTRIBUTIONAL RANGE OF SEABED SPECIES

Presence of suitable habitats

Species have required habitats (physical, and sometimes biological) as well as physiological tolerance limits and will only be found within those habitats and limits. Where a habitat is very restricted in occurrence, the distribution of a species will reflect occurrence of the habitat and may not be primarily influenced by physical conditions such as temperature (except where the occurrence of the habitat changes as a result of temperature change). An examples is the sea anemone *Amphianthus dohrnii* which is found only on the sea fans *Eunicella verrucosa* in south-western Britain and south-western Ireland, and on the related species *Swiftia pallida* in Scotland. If *Swiftia pallida* disappears from Scotland, so, most likely, will *Amphianthus dohrnii*.

[Insert Figure 3 about here.]

Temperature

The distributions of many species broadly follow summer or winter isotherms (Figure 3). Environmental temperature may influence:

1. development of eggs or other propagules;
2. release of propagules;
3. survival of larval stages of animals (at extremes of temperature outside normal, larvae may not survive to metamorphosis);
4. survival of post-settlement juveniles;
5. survival of adults (heat or cold stress).

Studies of algae have especially considered effects of temperature on survival and distribution. Van den Hoek (1982a, b) proposed that biogeographic boundaries of marine benthic algae can be defined by the relationship between the distribution boundary of a species and the extremes of temperature within which a species can complete its life history.

For some southern species of algae and animals, local warming is likely to be important. High summer temperatures in surface waters of enclosed areas such as lagoons (including 'obs' in Scotland), sea lochs or even rockpools may enhance the

production of propagules and perhaps increase local populations of southern species in those restricted locations. On the other hand, waters that remain cool because of increased thermal isolation of the deeper layers below a thermocline may encourage reproduction in relict populations of species that were much more widespread in former colder times. In the intertidal, air temperatures can be lethal with both extremes of cold (e.g. Crisp, 1964; Todd and Lewis, 1984) and heat (e.g. Hawkins and Hartnoll, 1985) causing occasional kills. Higher air temperatures would also be expected to speed growth and increased fecundity in southern species but stress cold water species.

[Figure 4 about here]

Hydrographical conditions - direction of currents

The residual direction of currents (the horizontal movement of water masses after the tidal element has been removed) around Britain and Ireland is illustrated in Figure 4. These currents are important in the distribution of water masses, to spreading the characteristics of those water masses (including temperature), and in distributing the pelagic young of benthic species. Currents may also bring larvae from distant sources to establish populations of a species that are not themselves able to reproduce, either because individuals are too distant from each other for male and female gametes to meet or because water temperatures are too high or too low for propagules to develop. In this case, occurrence of the species may be sporadic and they may develop only on outward coasts that 'catch' the currents. Currents may also sweep the larvae of intertidal species offshore, while headlands or similar abrupt changes in orientation of the coastline may entrain larvae. The direction of currents may prevent larval dispersion against the direction of flow. Larval retention in marine inlets and isolated waters such as lagoons could lead to localised pockets of species (Barnes and Barnes, 1977). In some situations, such larval retention, perhaps with the additional warming that occurs in summer in isolated waters, may help to account for the very high diversity of species and the presence of many southern species in large populations in locations such as Lough Hyne in southern Ireland (see Bell and Shaw, 2002 for a general account of Lough Hyne biodiversity).

Currents are only likely to be important to larval distribution where larvae have a phase that spends time in the water column. That phase may last for three to four weeks in barnacles (Burrows *et al.* 1999) and mussels *Mytilus edulis* (Seed, 1976), eight to ten days in *Patella* (Dodd 1957), four days in *Osilinus lineatus* (Crothers 2001) or hours in many algae (Norton 1992).

There are a number of fixed current meters established around the coast which indicate daily, seasonal and annual changes. Tracking the movement of radioactive contaminants from the Sellafield nuclear reprocessing plant in Cumbria has also provided valuable insights into the long-term movement of water masses. For instance, the movement of radiocaesium discharged from Sellafield suggest a residual flow northwards along the west coast of Scotland of about 1.7 km a day (Economides, 1989). Occasional 'jetstream' currents, which might especially occur along shelf sea fronts, may be important. These 'jetstreams' are partly apocryphal but Simpson *et al.* (1979) found residual current velocities of 20 cm/s parallel to the Islay front which would be approximately equivalent to movement of water with passive larvae of about 10 km in one direction in one day. Similar jetstreams may occur across the mouth of the English Channel (Cooper, 1960) and were described as long ago as the end of the 18th century

(Rennell, 1793). Pingree and LeCann (1990) measured residual currents of up to 60 cm/s in the south-western approaches to Britain. Such currents may have the ability to transport larvae of warm water species from southern Brittany to Cornwall during a warm period (Southward and Southward, 1977).

Geographic barriers

The absence of suitable habitats for the settlement of a species over a large area may mean that larvae do not survive long enough to bridge the gap. The English Channel is a significant barrier to larval distribution (Crisp and Southward, 1958). Another significant barrier to extension of distribution from Britain to Ireland is St Georges Channel in the south, which appears to have prevented the southern barnacle *Balanus perforatus* and the limpet *Patella depressa* from colonising Ireland (Crisp and Southward, 1953; Southward and Crisp, 1954b). It might also be the case that the distance between mainland Scotland or Orkney and Shetland, including Fair Isle, is too great for the survival of the larvae of some benthic animals. Seaweeds seem to be much less constrained by ocean barriers in their distribution and exhibit a continuum of change with no obvious boundaries or breaks provided that suitable habitats are present due to their potential propagule dispersal ability and possibly also for detached fragments to remain reproductively viable (Tittley *et al.*, 1990; Tittley and Neto, 1995).

Water ‘quality’

Some species may require a particular water ‘quality’ for propagules to survive or thrive and therefore to colonise an area. This was suggested for the western English Channel, where the numbers of larval fish and the young stages of invertebrates, notably of decapods, are higher when water masses off Plymouth are of the ‘*Sagitta elegans* type’ (Russell, 1973). The influence of such water quality was demonstrated in experimental studies when echinoderm larvae were reared in sea water from different places (Wilson, 1951; Wilson and Armstrong, 1958, 1961). It was concluded that the difference in bottom faunas from one region to another might be related to the ability, or otherwise, of larval stages to develop in the overlying water mass, but the actual factor in the water was never discovered. We know now that there is a climatic element in this puzzle. The ‘*elegans*’ community is of cold water nature and reaches its southern limit in the Celtic Sea. The western Channel population is derived from the Celtic Sea, and if the community there becomes driven northwards by rising temperatures, recruitment to the Channel will be reduced (Southward, 1963). Furthermore, the relative abundance of fish larvae in the plankton is probably related to the presence or absence of southern predators such as the pilchard (Southward, 1963). It might be that occurrence of southern animal species on the west coast of Scotland may have more to do with water quality than with temperature and therefore increase in temperature may not result in wider occurrence of certain species where it is water quality that is important to larval survival.

MECHANISMS OF CLIMATE CHANGE EFFECTS

Increased sea temperatures, especially at the time of breeding and larval dispersal are likely to be effective in increasing the distribution and abundance of southern species through the following mechanisms:

1. Survival of adults of species at the northern limits of their range will be improved.
2. More frequent successful gonad development or more broods will lead to greater reproductive output.
3. Larval development will be accelerated and species that do not presently reach final stages for settlement because water temperature is too low, will then settle.
4. Larval survival will be higher.
5. As a result of 2-4 above, there will be more consistent recruitment among year classes leading to more balanced age distribution.

For northern species, the effects of rising sea temperatures are likely to be the opposite of the above points.

In general, once a species has settled, it will survive unless temperature variation outside of normal range is extreme (for instance, during the 1962-63 winter in Britain: Crisp, 1964). However, algae are particularly affected by temperature and tolerances for survival are described by Lüning (1984, 1990). The following is taken from Breemen (1990) and other workers who have tested experimentally the temperature thresholds for algal occurrences. Breemen (1990) states: "... seaweeds are generally kept within their boundaries by the limiting effects of temperature. Northern boundaries are set by low lethal winter temperatures, or by summer temperatures too low for growth and/or reproduction. Southern boundaries are set by high lethal summer temperatures, or by winter temperatures too high for induction of a crucial step in the life cycle". Breeman (1990) further recognised two types of boundaries set by: (i) lethal limits of the hardest stage in a life history which may be a cryptic microthallus or perennating structure (where a species is exposed over several years to a lethal temperature), and (ii) growth and reproductive limits, where a species is not exposed every year to a sufficiently high or low temperature for growth and reproduction in the favourable season. In a few species photo-periodic responses interact with temperature requirements to determine the location of geographic boundaries. The relationship between temperature and distribution of seaweeds may be confused as temperature response ecotypes have evolved in some seaweed species (Breemen, 1988). For example, populations of *Devaleraea ramentacea* in NE America have different tolerances from those in Europe. According to Breemen (1990) seaweeds are unable to form temperature ecotypes rapidly, and if temperature conditions deteriorate in a season when temperatures are limiting the species will become locally extinct. If temperature conditions improve, the species will extend its geographical range but some time may elapse before a species meets its thermal potential.

Breemen (1990) pointed out that climatic changes probably do not cause whole floras to move unaltered to a different latitude since local floras comprise species with different thermal response types, some being near their thermal limits. Change in climatic conditions, even minor, may alter species composition of community structure. Breemen (1990) considered the effects of a 2°C rise in sea temperature by comparing the position of the isotherm demarcating the boundaries of benthic algae. For many tropical to temperate species reaching their northern boundaries in north western Europe, increasing sea-temperatures will allow them to extend their geographical ranges (range extensions have been identified this century by Lüning, 1985, 1990). Other tropical to temperate species are relatively eurythermal and can tolerate temperature below zero. Their northern boundaries in NW Europe are set by minimum summer temperatures for growth and reproduction. An increase in summer (maximum) sea

temperature would allow a northward extension, changing winter temperatures would not affect distribution as these are not limiting.

Many tropical to warm temperate species are more stenothermal, not tolerating temperatures below 5°C. They require high summer temperatures for growth and reproduction; their northern boundaries on open Atlantic coasts are set by summer growth an/or reproduction limits (occurrence in the North Sea is limited by low lethal winter temperatures). An increase of 2°C would allow only minor range extension in the English Channel. An increase in summer sea temperature would allow northward extension the west coast of the British Isles – but not far because low winter temperatures would become limiting (instead of a summer growth limit such species would meet a winter lethal limit on the Atlantic Coast of Britain and Ireland). This may also constitute an example of where a change in sea temperature would shift selection pressure to a different thermal capacity and season.

The southern boundaries of arctic to temperate species in W. Europe are set by summer lethal limits or winter reproductive limits. Some species (e.g. *Chorda filum*) could tolerate high summer temperatures and the point where they would meet a summer lethal limit lies far to the south of the point where high winter temperatures have become limiting (thus only changing winter temperatures alter distributional range). In other species (e.g. *Laminaria hyperborea*) potential summer lethal and winter reproduction limits are located at approximately same latitudes. A change in temperature in either season would affect the location of the boundary – when changes occur only in one half of the year – the nature of the boundary would alter. For some cold water species selection pressure at southern boundaries has probably varied through time during both glacial and interglacial periods. Upper lethal limits may be genetically more firmly fixed the thermal requirements and extend its range until summer lethal temperatures become limiting (e.g. *Scytosiphon lomentaria*).

Amongst the animals, the importance of temperature and likely favourable effects of increased temperature have been particularly demonstrated in prosobranch molluscs, decapod crustaceans and barnacles (Southward, 1991; Lindley, 1998; Herbert *et al.* 2003). Many species require temperature to rise to certain level before spawning can occur and larvae are produced. Other factors may be important in determining whether larvae survive and settle. For instance, the intermoult times of decapods larvae are much shorter in warmer waters (Lindley, 1998). Such a shortening of the developmental time of larvae provides scope for the progression through different larval stages within the time limits of the primary production season and therefore improved likelihood of survival to settlement. The importance of seawater temperature to larval survival may therefore be one of the factors leading to the latitudinal gradient in the number of brachyuran species with 54 known from the English Channel and only two from Svalbard.

Increased sea temperatures are likely to have an adverse effect on breeding of species that require a low temperature ‘trigger’ to reproduce. Hutchins (1947) noted that the southern limit of distribution of the barnacle *Semibalanus balanoides* was linked to the isotherm of the minimum monthly mean surface temperature of 7.2°C and suggested that if the winter temperature failed to fall below this level, the species might be unable to breed.

Increased sea temperature is not thought likely to have an immediately adverse effect on sessile or sedentary species that are already established. Long-lived species with a predominantly northern distribution are likely to persist as adults well after they have

ceased to reproduce or recruit successfully in the locality. However, it is possible that more sunshine and/or higher air temperatures may kill some northern intertidal species.

Another mechanism to consider is the importance of synchronisation of reproduction with the spring phytoplankton bloom. A good example is the barnacle *Semibalanus balanoides*. It does well in years with clear and early diatom blooms (Barnes, 1956, 1957, 1962; Crisp and Spencer, 1958; Connell, 1961; Hawkins and Hartnoll, 1982), but may suffer if climate change reduces or delays a bloom or if the phytoplankton succession is modified. One of the predictions of the UK Climate Impact Programme is that there will be a more frequent North Atlantic Oscillation positive index (REF**) and therefore a predominance of westerly weather. Such westerly weather could lead to greater turbulence delaying the spring plankton bloom and leading to poor recruitment of *Semibalanus balanoides*. On the other hand, there have been several recent occurrences of extreme negative winter NAO index (in 1990, 1996, 1998 and 2001) resulting in poleward flow of water along the eastern boundary of the North Atlantic Current and anomalous winter warming along the western European Continental Slope (Pingree, 2002). Such a reduction in the frequency of cold winters would be important in allowing survival of established populations of cold-intolerant species. For instance, species harmed by the extreme cold winter of 1962-63 (Crisp, 1964) are likely to be those that will survive further north than at present if milder winters prevail. Recovery rates for species after losses due to cold climatic events may also suggest the rate at which colonisation of previously colder locations might occur. Where such observations are documented, they can be incorporated into detailed assessments of likely rate of change in species distributions.

LIKELY EFFECTS OF CLIMATE CHANGE ON SPECIES

Effects of increase in air temperatures on open shore species

Algae

Many of the intertidal algae characteristic of shores in Britain and Ireland such as species of *Fucus* occur extensively further south (and north) on the coasts of the north-east Atlantic suggesting that they are unlikely to be adversely affected by increased temperatures of the scale currently envisaged. However, higher temperatures and increased insolation could cause mortality in some northern species with subsequent effects on the zonation of shore species. For instance, exposed rocky shores on Fair Isle have an algal zonation with bands of macroalgae growing at up to 8 m above sea level, although the tidal range is only about 2 m (Burrows *et al.*, 1954). This extensive distribution of algae up the shore was attributed to a combination of continual swell and damp climatic conditions. If conditions become less damp, zonal extent might decrease. Similarly, high shore ephemeral algae (for instance, *Porphyra* spp., *Prasiola stipitata*, *Enteromorpha* spp., *Blidingia* spp.) are likely to occur for shorter periods and be absent for most of the summer (see Hawkins and Hartnoll, 1983) as is seen in more southerly latitudes than the British Isles. However, increased air temperatures are unlikely to have either an adverse or a positive effect on the occurrence and abundance of most intertidal algae. If increased storminess occurs, fucoid algae will become less abundant at exposed sites and extension of zones landwards might occur or at least the adverse effects of increased desiccation might be offset.

Some of the species that may be expected to decline in abundance as a result of temperature rise may be restricted in their distribution for reasons other than temperature and may persist. For instance, with the exception of the St Kilda population, the brown seaweed *Fucus distichus distichus* does not occur south of the summer 13°C isotherm in Britain. A simplistic extrapolation from the present distributional range would suggest that following a 1°C and 2°C rise in summer sea temperature the 13°C isotherm would have moved north of the British Isles and *Fucus distichus distichus* would therefore become extinct in Britain. However, laboratory and autecological field studies indicate that mature *Fucus distichus distichus* plants can tolerate higher temperatures (Bird and McLachlan, 1976). Embryos also develop at 15°C (and higher). A critical factor is probably daylength; short daylengths stimulate the onset of receptacle formation and this will not change with global warming. Bird and McLachlan (1976) showed that the formation of receptacles was independent of temperature but maturation progressed with increasing temperature to at least 15°C. It is a possibility that a 2°C rise in sea temperature may make no difference to the populations of *Fucus distichus distichus* in northern Scotland. Stormier sea conditions, predicted by some models of global warming, and competition from other marine organisms may, however, affect these algae.

Animals

Increased air temperatures may result in mortality of some species in some years and therefore reductions in abundance or distributions. For instance, Bowman (1978) observed that ‘overheating’ in upper shore pools and on open rock in 1976 (a particularly hot summer) had resulted in mortality of the cold water limpet, *Patella vulgata*, on the north coast and elsewhere in Scotland.

Conversely, some species might be more likely to survive if the cold winters become less severe. For instance, the snakelocks anemone *Anemonia viridis* is susceptible to low temperatures (Crisp, 1964) and may survive better and spread to new locations as adult individuals if winters are milder. For other species, development of gonads might be favoured by increased air temperatures so that fecundity increases.

Effects of increased air temperatures on species in enclosed waters

There are several locations, especially in Scotland and Ireland, where poor water exchange within sheltered water bodies may result in localised warming in shallow or surface waters. Two significant effects are likely:

1. Shallow waters may become more amenable to ‘blooms’ of species that thrive in warm water during the summer. Such species include the non-native alga *Sargassum muticum* and possibly some fish such as *Ctenolabrus rupestris*.

2. Where the isolated waters have a shallow sill or are sluiced, deeper waters may become isolated through thermal stratification during summer and consequently become deoxygenated. It is likely that only a few habitats may be affected in this way, predominantly in the fjordic habitats that occur in Scotland. There are situations where occasional de-oxygenation events are known to occur (for instance at the head of Sullom Voe (Pearson and Eleftheriou, 1981), Loch Obisary (Mitchell *et al.*, 1980) and such events might become more frequent or occur for the first time in some new locations. Such locations would be those having a sill that isolates the deeper water.

Effects of increased air temperatures on rockpools

It is most likely that milder winter conditions may help survival of species in rockpools. Shore fishes such as blennies and gobies may remain in pools for a longer period of the year instead of moving to deeper water for winter. Other species, including the sea anemone *Anemonia viridis*, may survive better and be able to exist higher up the intertidal zone. Several species extend towards their northern limits primarily in pools rather than the open shores, including the algae *Cystoseira tamariscifolia* and *Bifurcaria bifurcata* and the limpet *Patella ulyssiponensis*. Their extension northwards as a result of climate warming will therefore be initially in pools.

The cold-water northern species *Fucus evanescens* has spread south in recent time according to Lüning (1990) who attributed this spread to cooling of North Atlantic waters in the past half century. An increase in sea-temperature may now reverse this trend. *Fucus evanescens* is known from only 3 locations in Britain (Moray Firth, Scotland Foula and Lerwick – Shetland) thus its foothold in Britain is precarious.

Effects of increase in sea temperatures on coastal and offshore benthos

Wide scale effects including increased abundance and extension of distribution of southern species alongside reduced abundance and retreat in the distribution of northern species are the most likely effects of increased seawater temperatures across the continental shelf. However, the rate at which change occurs and whether any change occurs will vary greatly from species to species.

Amongst species living on or near the seabed, fish are likely to react in concert with temperature change as they are mobile. Crustaceans will also respond fairly rapidly if it is temperature that controls adult distribution. Northern species are likely to retreat from the pre-existing southern limits of their range at least in coastal waters. For instance, the northern stone crab *Lithodes maia* and the viviparous blenny *Zoarces viviparus*. In the case of sedentary or sessile species with long-lived planktotrophic larvae, more larvae are likely to be produced more frequently by southern species leading to an increased abundance of the species locally and the possibility of extension of range. Examples would be the purple sea urchin *Paracentrotus lividus*, and the barnacle *Chthamalus stellatus*. The hermit crab *Clibanarius erythropus*, which briefly extended its range across the western English Channel in the late 1950s (Southward and Southward, 1977, 1988) is another example. The converse would apply to northern species.

Southern species with a short-lived larva or which reproduce asexually and do not have a mobile phase will increase in abundance where they occur at present but may be slow to extend northwards. Such species are unlikely to make the jump across geographical barriers. Extension of range will occur through individuals detaching from the substratum or larvae being carried (usually short distances) in the water column. Few species are likely to detach and float away, an exception being the snakelocks anemone *Anemonia viridis*. Occasional 'jetstream' currents at the time of detachment or reproduction may take individuals or short-lived larvae a considerable distance so that, providing suitable habitats are present, there will be a gradual extension of range. Likely examples are the larvae of the snakelocks anemone *Anemonia viridis*, and the sea fan *Eunicella verrucosa*. In some instances, species that are currently reproducing asexually will reproduce sexually and therefore increase their potential to spread rapidly, for instance, the peacock tail alga *Padina pavonica*. *Padina pavonica*, a southern warm-water species, occurring only on the south coast of England and Ireland, but with strong

circumstantial evidence that past, ephemeral populations occurred considerably further north. Contraction in distributional range may be a periodic response to environmental change at its range periphery. Gametangial plants seem currently to be very rare outside of the Mediterranean Sea, and, in Britain, such plants have only once been recorded. British populations are of sporophytic plants that survive vegetatively (see Price *et al.*, 1979). Dixon's (1965) hypothesis of 'physiological expression of reproductive capacity' suggested that successively from the centre of the distribution of a species is the loss of gametangial, then sporangial production to a terminal peripheral zone of vegetative plants. An increase in sea-temperature may extend the distributional range of this species and perhaps facilitate the development of gametophytic plants.

Rate of retreat of northern species will be very dependent on the longevity of existing individuals with likely long-lived probably persisting for many tens of years even if reproduction ceased. Reduction in abundance and eventual loss will occur through less frequent successful recruitment. Species that reproduce asexually as well as sexually, such as many sea anemones, may continue to produce new individuals even though larvae are not being produced; this category may include the cold water anemone *Bolocera tuediae*. Others, such as the limpet *Tectura testudinalis* and the sea urchin *Strongylocentrotus droebachiensis*, which most likely live for only a few years, will disappear more quickly. *Tectura testudinalis* may already be in decline at its southern limits on the Isle of Man and in Northern Ireland (S.J. Hawkins, personal observations; J. Nunn, pers. comm.).

Exceptions may be found in some of the sea lochs of the western Scottish mainland, where there are relict populations of 'arctic' molluscs, as noted by Forbes (1858). For instance, upper Loch Etive carries a relict population of the arctic bivalve *Thyasira gouldii* (Blacknell and Ansell, 1974) but this may already have experienced adverse effects of climate change (Southward and Southward, 1991).

Effects of increased sea temperature on pelagic species

Free-swimming species are likely to respond immediately and their distribution is likely to 'track' changes in temperature isotherms for critical temperature ranges (i.e. whether they require warm waters in summer or cannot tolerate cold waters in winter). For example, red mullet *Mullus surmuletus*, black sea bream *Spondylus cantharus*, John Dory *Zeus faber* and cuttlefish *Sepia officinalis* have and would all extend their distributions northwards in response to higher sea temperatures. Migratory movements of squid, *Loligo forbesii*, show correlation with the NAO index (Sims *et al.*, 2002) and the time of peak abundance in the western English Channel, and probably elsewhere, would change.

Biotic interactions

Several 'key functional' species are likely to be affected by seawater warming. 'Key functional' species (sometimes called 'keystone species') are ones which, through their feeding activities (for instance, grazing by sea urchins or limpets), or by mediating interaction between species (for instance, by eating sea urchins), maintain community composition and structure in a manner disproportionate to their abundance. 'Key structural' species (sometimes called 'ecological engineers') provide a distinctive habitat (for instance a bed of the horse mussel *Modiolus modiolus*, beds of fucoid algae, a maerl bed) and their loss would lead to the disappearance of the associated community. Other species dominate habitats and define particular biotopes without

being 'key functional' and include, for instance, barnacles. In some cases, loss of a particular species may not be significant in terms of provision or maintenance of habitat and the continued presence of a particular biotope. For instance, loss of the northern sea urchin *Strongylocentrotus droebachiensis*, would most likely be compensated for by increased abundance of the common sea urchin *Echinus esculentus* so that grazing would continue. Expansion of range of the purple sea urchin *Paracentrotus lividus* would produce a new and more efficient grazer into a habitat without such a species, reducing algal abundance in rockpools and shallow subtidal areas where they occur. . Reduction in abundance of the cold water barnacle *Semibalanus balanoides* would be compensated for by increased abundance of *Chthamalus* spp. (Southward, 1967, 1991; Southward and Crisp, 1954a, 1956) However, if the abundance of species such as the horse mussel declined, there may be significant effects on the associated fauna and flora. In the case of loss of horse mussel beds, the biotope would most likely change to a wholly sedimentary one dominated by burrowing infauna.

A most important effect of climate change might be to alter the abundance and quality of meroplanktonic organisms that are important as food to other marine life. For example, the cold water barnacle, *Semibalanus balanoides*, releases its larvae in synchrony over a short period in the spring, usually March to May, the exact timing depending on latitude (Southward and Crisp 1963; Stubbings 1975; Runnström 1926). The nauplii can be numerically dominant in the plankton, prior to the late spring outburst of copepods and may constitute an important food for larvae and juvenile stages of spring spawning herring, gadoids and other fish, especially in enclosed bays and lochs. If *Semibalanus balanoides* is replaced by *Chthamalus* as the dominant barnacle, this resource is lost. *Chthamalus* breeds over a longer period in summer, with successive broods of lesser intensity than the single brood of *Semibalanus balanoides*, at a time when other zooplankton species are available to the young fish and other animals that feed on plankton. Similar considerations may apply to meroplanktonic larvae of other animals, such as the zoea larvae of crabs and prawns that can be very abundant in the spring. Such effects of climate change are much more difficult to observe and to take into account than conspicuous events in shore or sublittoral seabed organisms, but are important when predicting change.

LIKELY EFFECTS OF CLIMATE CHANGE ON BIOTOPES

Whilst climate change is unlikely to affect the physical habitat part of a biotope, it may affect the biotic element, the community. Effects on biotopes will therefore be 'driven' by effects on component species. If those species are key structural, key functional or are characteristic species that help to identify a particular biotope, then the biotope may cease to exist and will change to a different biotope at affected locations. For instance, Breemen (1990) suggests that far-reaching effects are to be expected by northward shifts of southern boundaries of some arctic to cold-temperate seaweeds. For instance, following a rise in summer and/or winter temperatures, marked northward shifts of the southern boundaries of the kelps *Laminaria digitata*, *Laminaria hyperborea* and *Laminaria saccharina* are to be expected. In the extreme case of summer temperatures rising by 4°C, these *Laminaria* species would disappear from the Iberian Peninsula, the Atlantic coast of France, the southern parts of the British Isles, the North Sea, and Southern Norway. As major canopy forming algae, they determine the community structure in subtidal kelp forests. Except where replaced by the southern kelp *Laminaria*

ochroleuca, their extinction would undoubtedly cause major changes in these ecosystems.

Seabed biotopes for Britain and Ireland are classified and described in Connor *et al.* (1997a&b) and revised in Connor *et al.* (2003). Those catalogues of biotopes have been inspected to identify ones that may change (because key or characteristic component species may be affected by seawater warming). Additionally, biotopes that occur in UK Biodiversity Action Plans (see www.ukbap.org.uk) have been considered as there is concern about impacts on them. Table 2 is a summary and explanation of possible effects on biotopes resulting from seawater warming and includes biotopes that are of geographically restricted distribution.

CONCLUSIONS

Our review suggests that the following scenarios of change or stability in marine species and biotopes in response to current climate change expectations are likely to occur:

1. Populations of boreal-arctic species at the southern limits of their range in Britain and Ireland, where higher temperatures will make reproduction or survival difficult, will decline in abundance or disappear at their southern limits. Those already occurring only in northernmost parts of the islands of Britain and Ireland are likely to disappear altogether from the British Isles.
2. If the species that decline in abundance are characterising or key structural or functional species in biotopes, the biotope that they represent may be changed or be lost.
3. Species at the northern limits of their range in Britain and Ireland, where higher temperatures will make reproduction more likely or frequent or will improve prospects for larval survival, will increase in abundance where they already occur and extend in their distribution providing that they are not prevented by geographical or hydrographical barriers. Species that have life cycles that include a planktonic phase are likely to extend their distributional limits in concert with isothermal changes.
4. If the species that increase in abundance are characterising or key structural or functional species in biotopes, the biotope that they represent is likely to increase in geographical extent.
5. Changes will be most apparent first in mobile species such as plankton and fish. Amongst benthic species, response will be fastest in those with a planktonic stage in their life history.
6. Changes (both increases and decreases) are likely to be particularly marked in enclosed waters where local warming occurs.
7. Increased surface warming may isolate more frequently the deeper parts of some enclosed water bodies where a thermocline forms behind a sill, leading to deoxygenation.
8. There may be locations where sea level rise will introduce seawater into currently fresh water habitats creating new brackish water habitats.
9. There may be locations where sea level rise will cause a marine transgression although, in other situations, it may reduce the extent of communities of intertidal wave-cut platforms.
10. Increased storminess may modify communities, particularly intertidal communities, to those characteristic of more wave exposed conditions.

DEVELOPING A DECISION TREE FOR ASSESSING LIKELY EFFECTS FOR A PARTICULAR SPECIES

Components

The rate of geographical extension or reduction of distributional extent or change in the abundance of species at existing locations in response to increases or decreases in temperature are likely to be determined by:

1. Mobility of existing populations – can they swim, drift or walk or are they fixed and dependent on larval dispersal?
2. Presence of viable populations for the production of larvae – ‘relict’ populations or populations that have recruited from distant sources and do not produce gametes, or populations where individuals are too widely separated for gametes to meet may not be reproductively viable and so not be a source for range extension.
3. Type of reproductive and dispersal mechanisms – sessile or sedentary benthic species which reproduce asexually or that have a benthic or short-lived larval/juvenile stage will extend their distributions less rapidly than those with long-lived planktonic propagules, but may persist longer in the face of adverse conditions.
4. Survival of larvae in relation to water temperature – some larvae require threshold temperatures to develop to a final settlement stage and will perish if those temperatures are not reached.
5. The presence of suitable habitats for settlement within the potential extension of range according to mobility of dispersive stages.
6. Lethal and sublethal temperature effects on adults – in the case of lower temperatures, some adults may perish in the winter or not reproduce if they require warm water for maturation of gonads. In the case of higher temperatures, some species that require a low temperature trigger to reproduce may fail or some might be killed by high spring or summer temperatures.
7. Presence or absence of geographical barriers to potential spread (for instance, offshore currents may sweep larvae away from suitable inshore habitats).
8. Presence of favourable currents to enable spread (residual currents in the direction of temperature increase, occasional fast currents bringing larvae from distant sources).
9. Longevity of individuals in existing populations – if warming ‘shuts-down’ reproduction and therefore local recruitment, existing populations will persist until the end of their natural life span is reached.

A variety of scenarios are likely and the key given below and decision tree (Figure 4) can be applied to a wide range of species – if sufficient is known about their mode of reproduction and effect of temperature especially on the success of reproduction.

Exceptions – human influences

The following are impacts that should be taken into account when separating climate change effects from those resulting from localised human activities.

1. The abundance of fish is likely to be affected by intensity of fishing that reduces the spawning stock. Thus, for instance, whilst cod numbers might decline in temperate waters as a result of temperature rise, over-fishing may be a more important factor. Similarly, whilst numbers of southern species such as the John Dory *Zeus faber* might be expected to rise, effects of fishing may prevent increases in stock. The beds of the horse mussel *Modiolus modiolus*, a northern species, have declined greatly in extent and abundance in Strangford Lough since 1990 (Maggorian, 1995). This decline could well be a result of warming but the species may have suffered through a combination of

several factors including scallop dredging, industrial contaminants and agricultural runoff as well as temperature change. In such a case, warming may prevent natural recovery, as may well have happened also with over-fishing of the Plymouth herring (Southward, 1963).

2. Geographical barriers may be ‘bridged’ by human activities including ‘hitchhiking’ of organisms on vessels, ‘island hopping’ via artificial reefs such as breakwaters, sea defences, and offshore wind farms and also deliberate introductions for fisheries (for instance, of ormers *Haliotis tuberculata* from the Channel Isles into south-west England) and discards from marine aquaria.

THE ‘KEY’ - DETERMINING THE LIKELY EFFECTS OF TEMPERATURE INCREASE ON A PARTICULAR SPECIES

The following key and description of types assumes an increase in air and seawater temperatures and is based on the components described above.

- | | | |
|----|---|---------|
| 1. | The species is pelagic (swims or drifts in the water column) | 2 |
| | The species is sedentary or sessile (attached to or crawling on the seabed) | 3 |
| 2. | The species is northern in distribution | Type A |
| | The species is southern in distribution | Type D* |
| 3. | The species has a planktonic distributional phase | 4 |
| | The species has a benthic larva, very short lived (a few hours) pelagic phase or reproduces asexually | 5 |
| 4. | The species are long-lived (>5years) and likely to reproduce infrequently or not at all, at least at its geographical limits. (“infrequently” means only every few years) | Type F* |
| | The species is short-lived (<5 years) and currently reproduces frequently (usually once a year and over a prolonged period) | 6 |
| 5. | The species currently reproduces infrequently or not at all, at least at its geographical limits. (“infrequently” means only every few years) | 7 |
| | The species currently reproduces frequently (usually once a year and over a prolonged period) | 8 |
| 6. | Species is northern in distribution | Type C |
| | Species is southern in distribution | 9 |
| 7. | Species is northern in distribution | Type B |
| | Species is southern in distribution | Type E |
| 8. | Species is northern in distribution | Type C |
| | Species is southern in distribution | Type E |
| 9. | The species occurs in populations sufficiently dense or close so that gametes will meet . | Type G* |

The species occurs as isolated individuals and gametes are unlikely to meet OR the species occurs at isolated locations or habitats where other suitable locations or habitats are likely to be too distant for propagules to reach. Type E

* Use the decision tree that follows (Figure 5) to determine importance of barriers to spread.

Type A (northern volatiles)

Species that currently have a northern distribution that are pelagic or demersal (such as plankton and fish) where the adults respond rapidly to temperature change. Significant changes will occur in relation to annual variations in temperature with an overall reduction in abundance and 'retreat' northwards over the next 50 years.

Type B (northern stables)

Benthic species that currently have a northern distribution that will 'retreat' northwards but very slowly as individuals are long-lived and recruit irregularly. Reproductive success at current southern limits will be reduced as a result of higher temperatures. Decline in abundance at southern limits but no significant change expected in distribution in the next 50 years.

Type C (northern 'retreaters')

Benthic species that currently have a northern distribution which will decline in abundance and 'retreat' northwards rapidly (in 'concert' with isothermal changes), are short-lived (<5years) and rely on regular recruitment from the plankton or from benthic larvae. The speed of change in abundance and distribution might fluctuate depending on the occurrence of particularly warm years. Significant reductions in abundance and distributional extent are to be expected in the next 50 years.

Type D (southern volatiles)

Species that currently have a southern distribution, are pelagic or demersal (such as plankton and fish) where the adults respond rapidly to temperature change. Significant changes will occur in relation to annual variations in temperature with an overall expansion in distribution northwards and increase in abundance within their present limits over the next 50 years.

Expansion of distribution northwards may be prevented or slowed by geographical barriers such as locations where currents sweep offshore or extensive areas where favoured (demersal) habitats are absent.

Apply Figure 5, the water currents and quality decision tree.

Type E (southern stables)

Benthic species that currently have a predominantly southern distribution which will expand northwards or become more abundant within their present range but slowly. Individuals are long-lived and reproduce infrequently by benthic or short-lived larvae or by asexual division. Reproductive success at current northern limits of distribution will improve as a result of higher temperatures. Abundance of individuals will increase at locations where they are already found. Northward extent will increase very little in the next 50 years and not at all where significant hydrographical or geographical barriers exist.

Type F (southern gradual extenders)

Benthic species that currently have a predominantly southern distribution that will expand northwards and increase in abundance at their current locations and in a sporadic way dependent on particularly favourable years for reproduction. The species currently reproduce infrequently at least at their geographical limits but have a planktonic larva. There will be a 'lag' period between temperature increase and expansion in abundance or northern extent.

Expansion of distribution northwards may be prevented or slowed by geographical barriers such as locations where currents sweep offshore or extensive areas where favoured habitats are absent.

Apply Figure 5, the water currents and quality decision tree.

Type G (southern rapid extenders)

Benthic species that currently have a predominantly southern distribution which will expand northwards at about the same rate as isothermal changes in sea or air temperatures providing that currents are favourable and there are no barriers to spread. Species will become more abundant within their present range.

Expansion of distribution northwards may be prevented or slowed by geographical barriers such as locations where currents sweep offshore or extensive areas where favoured habitats are absent. Water quality may also be important in determining whether or not larvae settle and survive. The decision tree below is for species that have the ability to spread (Types D, F, G).

Apply Figure 5, the water currents and quality decision tree.

SPECIES AND BIOTOPES TO STUDY

This paper does not attempt an exhaustive listing of species and biotopes likely to change in distribution in the event of significant increases of air and sea temperatures. Rather, rocky shore and subtidal species that are conspicuous, easily recognised and, in general, well studied have been selected and included in Table 1. The species selected also include UK Biodiversity Action Plan species. Table 2 includes a selection of biotopes that are of conservation concern because they occur in Biodiversity Action Plan Habitats. Recording the current distribution and abundance of species listed, including by enlisting volunteer recorders, could provide a baseline against which to assess changes that may take decades or hundreds of years to take place.

WILL CHANGE 'MATTER'?

Change is likely to matter most visibly if commercial species are adversely affected, harmful species (such as toxic algae) increase, or if species that are of marine natural heritage importance (nationally rare or scarce species, species already in decline, key structural or functional species in biotopes) decline in abundance. Changes in the abundance (whether increases or decreases) may change the status of a species from a marine natural heritage point-of-view. For instance, a nationally rare southern species may become common or a common northern species may become scarce; a biotope that was the reason for establishing a marine protected area may disappear (or become very common elsewhere) with implications for de-notification of a conservation site. If

changes are identified as a result of monitoring programmes, including investigations undertaken for statutory reporting of water or natural heritage ‘quality’, any interpretation of results will need to take account of likely climate change effects.

There may be less obvious effects on ecosystem functioning. For instance, the balance between fucoids and barnacles along the gradient of wave exposure on rocky shores which changes with latitude (Ballantine, 1961). Fucoids become more restricted to shelter in southern Europe (Hawkins and Hartnoll, 1985; Hawkins *et al.* 1992). In a warmer world, fucoid cover would be expected to lessen on shores in Britain and Ireland with implications for primary production and associated epiphytic species. Thus, whilst the faunistic and floristic composition may not change much, there may be implications for functioning of coastal ecosystems.

In Britain and Ireland, localised warming, perhaps in combination with increased levels of nutrients resulting from human activities, may cause some severe adverse effects such as mortalities of seabed species observed in the north-eastern Mediterranean in 1999 (Perez *et al.*, 2000). However, since Britain and Ireland straddle biogeographical regions, the main effect of warming will be a shift in boundaries. Overall, more species are likely to be ‘gained’ than ‘lost’.

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Table 1. Northern and southern species with good distributional records that are considered to have climatically restricted distributions in or near Britain and Ireland.
 * = Species recommended for establishment of current distribution and abundance and to be considered in schemes for monitoring change. (Names follow Howson and Picton, 1997 except for *Pentapora fascialis* (Pallas))

Southern species not currently recorded in northern Britain but which may spread there	Southern species currently recorded in northern Britain and in Ireland whose extent of distribution or abundance might increase	Northern species which may either decrease in abundance and extent or disappear from northern Britain
<i>Ciocalyptra penicillus</i> *	<i>Axinella dissimilis</i> *	<i>Crassostrea virginica</i>
<i>Haliclona angulata</i>	<i>Hemimycale columella</i>	<i>Cerastoderma glaucum</i>
<i>Gymnangium montagui</i> *	<i>Phorbas fictitius</i>	<i>Gari depressa</i>
<i>Eunicella verrucosa</i> *	<i>Haliclona cinerea</i>	<i>Pentapora fascialis</i> *
<i>Aiptasia mutabilis</i>	<i>Haliclona fistulosa</i>	<i>Asterina gibbosa</i>
<i>Balanus perforatus</i> *	<i>Haliclona simulans</i>	<i>Paracentrotus lividus</i> *
<i>Maja squinado</i> *	<i>Alcyonium glomeratum</i> *	<i>Holothuria forskali</i> *
<i>Diogenes pugilator</i>	<i>Anemonia viridis</i> *	<i>Centrolabrus exoletus</i>
<i>Osilinus lineatus</i> *	<i>Aulactinia verrucosa</i> *	<i>Crenilabrus melops</i>
<i>Patella depressa</i> *	<i>Corynactis viridis</i>	<i>Ctenolabrus rupestris</i> *
<i>Crepidula fornicata</i>	<i>Sabellaria alveolata</i>	<i>Labrus mixtus</i> *
<i>Tritonia nilsodheri</i>	<i>Chthamalus montagui</i> *	<i>Thorogobius ephippiatus</i>
<i>Solen marginatus</i>	<i>Chthamalus stellatus</i> *	<i>Scinaia trigona</i>
<i>Phallusia mammillata</i>	<i>Hippolyte huntii</i>	<i>Asparagopsis armata</i> *
<i>Scinaia furcellata</i>	<i>Palinurus elephas</i> *	<i>Bonnemaisonia hamifera</i>
<i>Chondracanthus acicularis</i>	<i>Polybius henslowi</i>	<i>Naccaria wiggii</i>
<i>Stenogramme interrupta</i> *	<i>Ebalia tumefacta</i>	<i>Jania rubens</i> *
<i>Laminaria ochroleuca</i>	<i>Corystes cassivelaunus</i>	<i>Mesophyllum lichenoides</i>
<i>Lithothamnion corallioides</i>	<i>Liocarcinus arcuatus</i>	<i>Calliblepharis ciliata</i>
<i>Bifurcaria bifurcata</i> *	<i>Liocarcinus corrugatus</i>	<i>Kallymenia reniformis</i>
<i>Cystoseira baccata</i> *	<i>Goneplax rhomboides</i>	<i>Rhodymenia delicatula</i>
<i>Cystoseira</i>	<i>Pilumnus hirtellus</i>	<i>Rhodymenia holmesii</i>
		<i>Thuiaria thuja</i> *
		<i>Swiftia pallida</i> *
		<i>Bolocera tuediae</i> *
		<i>Phellia gausapata</i> *
		<i>Lithodes maia</i> *
		<i>Tonicella marmorea</i>
		<i>Margarites helycinus</i> *
		<i>Tectura testudinalis</i> *
		<i>Onoba aculeus</i>
		<i>Colus islandicus</i>
		<i>Akera bullata</i>
		<i>Limaria hians</i>
		<i>Anomia ephippium</i>
		<i>Thyasira gouldii</i>
		<i>Leptometra celtica</i>
		<i>Leptasterias muelleri</i>
		<i>Semibalanus balanoides</i> *
		<i>Lithodes maia</i> *
		<i>Strongylocentotus droebachiensis</i> *
		<i>Cucumaria frondosa</i> *
		<i>Styela gelatinosa</i>
		<i>Lumpenus</i>

<i>foeniculaceus</i>			<i>lumpretaeformis</i>
	<i>Xantho incisus</i>	<i>Rhodymenia pseudopalmata</i>	<i>Zoarces viviparus</i>
	<i>Xantho pilipes</i>	<i>Halurus equisetifolius</i>	<i>Lithothamnion glaciale</i>
	<i>Tricolia pullus</i>	<i>Sphondylothamnion multifidum</i>	<i>Phymatolithon calcareum</i>
	<i>Gibbula umbilicalis</i> *	<i>Drachiella heterocarpa</i>	<i>Callophyllis cristata</i>
	<i>Patella ulyssiponensis</i> *	<i>Drachiella spectabilis</i>	<i>Odonthalia dentata</i> *
	<i>Bittium reticulatum</i>	<i>Stilophora tenella</i>	<i>Sphacelaria arctica</i>
	<i>Cerithiopsis tubercularis</i>	<i>Halopteris filicina</i>	<i>Sphacelaria mirabilis</i>
	<i>Melaraphe neritoides</i>	<i>Dictyopteris membranacea</i> *	<i>Sphacelaria plumosa</i>
	<i>Calyptreaea chinensis</i>	<i>Taonia atomaria</i> *	<i>Chorda tomentosa</i>
	<i>Clathrus clathrus</i>	<i>Carpomitra costata</i> *	<i>Fucus distichus distichus</i> *
	<i>Ocenebra erinacea</i>	<i>Cystoseira tamariscifolia</i>	<i>Fucus evanescens</i>
	<i>Acteon tornatilis</i>	<i>Codium adhaerens</i> *	
	<i>Pleurobranchus membranaceus</i>	<i>Codium tomentosum</i>	
	<i>Atrina fragilis</i>		

Table 2. Biotopes with good distributional records that appear to have climatically restricted distributions in Britain and Ireland. Likely change is identified on the basis of the biology of component species, especially those that are key structural or functional species. The biotopes classification is from Connor *et al.* (1997a&b) and published revisions (Connor *et al.*, 2003). The table identifies where a biotope is a component of A UK Biodiversity Action Plan habitat so that account can be taken of possible climate change effects in those plans.

NOTE TO EDITOR/REFEREES – THE REVISED BIOTOPES CLASSIFICATION IS BEING PUBLISHED ON THE INTERNET AT PRESENT. FURTHER 2003 VERSION NAMES AND CODES WILL BE ADDED AS THEY BECOME AVAILABLE TO THE TABLE BELOW BEFORE PUBLICATION.

Biotopes found only or predominantly found in northern Britain and Ireland		Biotopes found predominantly in the south of Britain and Ireland	
Name and code (03 refers to Connor <i>et al.</i> , 2003; 97 refers to Connor <i>et al.</i> , 1997a&b).	Likely change in biotope extent and distribution in response to warming	Name and code (03 refers to Connor <i>et al.</i> , 2003; 97 refers to Connor <i>et al.</i> , 1997a&b).	Likely change in biotope extent and distribution in response to warming
<i>Fucus distichus</i> and <i>Fucus spiralis</i> f. <i>nana</i> on extremely exposed upper shore rock. 03=LR.HLR.FR.Fdis 97=ELR.FR.Fdis*	<i>Fucus distichus distichus</i> appears to have a distribution mainly controlled by day length so that occurrence is not related to temperature and no change in distribution is therefore expected.	<i>Chthamalus</i> spp. on exposed upper eulittoral rock. 03=LR.HLR.MusB.Cht 97=ELR.MB.Bpat.Cht*	The biotope is likely to extend further north, replacing biotopes dominated by <i>Semibalanus balanoides</i> .
<i>Ascophyllum nodosum</i> ecad. <i>mackii</i> beds on extremely sheltered mid eulittoral mixed substrata. 03=LR.LLR.FVR.Ascmac 97=SLR.FX.AscX.mac* (The biotope that constitutes the UK Biodiversity Action Plan habitat ‘ <i>Ascophyllum nodosum</i> ecad <i>mackii</i> beds’.)	The detached form of <i>Ascophyllum nodosum</i> is determined by salinity and, although restricted to the west coast of Scotland, the biotope appears not to be climatically determined and no change in distribution is expected.	<i>Sabellaria alveolata</i> reefs on sand-abraded eulittoral rock. 03=LR.MLR.Sab.Salv 97=MLR.Sab.Salv* The biotope that constitutes the UK Biodiversity Action Plan habitat ‘ <i>Sabellaria alveolata</i> reefs’.)	Where suitable conditions of sand in suspension occur and rocks are present, likely to grow in extent where it currently occurs and extend distribution northwards.
Coralline crusts, <i>Parasmittina trispinosa</i> , <i>Caryophyllia smithii</i> ,	Whilst this biotope is especially found in western Scotland and	Coralline crusts and <i>Paracentrotus lividus</i> in shallow	Occurrences of <i>Paracentrotus lividus</i> in the southwest of Britain and western

<p><i>Haliclona viscosa</i>, polyclinids and sparse <i>Corynactis viridis</i> on very exposed circalittoral rock. 97=ECR.Efa.CCParCar*</p>	<p>Northern Ireland, the reason is most likely extreme wave action rather than temperature. However, several southern species that occur in the biotope are likely to increase in abundance as a result of warming seas: <i>Corynactis viridis</i>, <i>Holothuria forskali</i>, <i>Pentapora fascialis</i>, <i>Alcyonium glomeratum</i> and <i>Parazonathus axinellae</i>.</p>	<p>eulittoral rockpools. 03=LR.FLR.Rkp.Cor.Par 97=LR.Rkp.Par</p>	<p>Scotland are likely to increase in frequency and some examples of this biotope may develop in place of biotopes such as LR.FLR.Rkp.Cor.Bif (dominated by <i>Bifurcaria bifurcata</i>) and LR.FLR.Rkp.Cor.Cys (dominated by species of <i>Cystoseira</i> and other algae).</p>
<p>Erect sponges and <i>Swiftia pallida</i> on slightly tide-swept moderately exposed circalittoral rock. 03=CR.HCR.XFA.SwiLgAs 97=MCR.Xfa.ErSSwi*</p> <p><i>Caryophyllia smithii</i> and <i>Swiftia pallida</i> on circalittoral rock 03=CR.MCR.ECCR.CarSwi</p>	<p><i>Swiftia pallida</i> is the only northern species in these biotopes which include several west coast species. Loss of <i>Swiftia pallida</i> and likely increased abundance of southern species would change the biotope, possibly to CR.HCR.XFA.ByErSp.Eun (see opposite) although <i>Eunicella verrucosa</i> would be unlikely to spread so far north.</p>	<p><i>Sargassum muticum</i> in eulittoral rockpools. 03= LR.FLR.Rkp.FK.Sar 97= LR.Rkp.FK.Sar</p>	<p><i>Sargassum muticum</i> occurs in shallow habitats in Norway suggesting that the current restricted distribution in Britain and Ireland is in part due to lack of spread. Although <i>Sargassum muticum</i> will extend its distribution and the biotope become established further north, the role of seawater warming in encouraging spread will be unclear.</p>
<p><i>Alcyonium digitatum</i> dominated biotopes. For instance: <i>Alcyonium digitatum</i>, <i>Pomatoceros triqueter</i>, algal and bryozoan crusts on wave-exposed circalittoral rock 03=CR.MCR.ECCR.FaAlCr.Adig (97=ECR.Alc ECR.AlcC);</p>	<p><i>Alcyonium digitatum</i> is a predominantly northern species and often dominates rocks. The presence of large amounts of <i>Alcyonium digitatum</i> may also be related to urchin grazing which, again, is more prevalent in the north. Reduction of urchin grazing and less than ideal conditions for <i>Alcyonium digitatum</i> may result in a shift to</p>	<p><i>Corallina officinalis</i> and coralline crusts in shallow eulittoral rockpools. ¹ 03=LR.FLR.Rkp.Cor 97=LR.Rkp.Cor*</p>	<p>The biotope includes several sub-biotopes including ones characterised by <i>Paracentrotus lividus</i> (see above), <i>Cystoseira</i> species and <i>Bifurcaria bifurcata</i> which are likely to extend their distribution northwards.</p>

	<p>the more erect bryozoan communities of further south. Also, the brown (rather than the white) form of <i>Alcyonium digitatum</i> is predominant in the north and the balance of colour types may change.</p>		
<p><i>Modiolus</i> dominated biotopes. For instance: 97=MCR.M.ModT* SCR.Mod* CMX.ModMx* CMX.ModHo (Biotopes constituting the UK Biodiversity Action Plan habitat ‘<i>Modiolus modiolus</i> beds’.)</p>	<p><i>Modiolus modiolus</i> is a northern species that forms beds of large individuals only in the north of Britain and Ireland. These beds of long-lived individuals are being adversely affected by trawling and possibly other human influences such as nutrient run-off. Warmer seas may prevent recovery of damaged beds and recruitment to undamaged beds so that decline in occurrence of beds can be expected at least in the south of their range.</p>	<p>03= <i>Eunicella verrucosa</i> and <i>Pentapora foliacea</i> [now <i>fascialis</i>] on wave-exposed circalittoral rock CR.HCR.XFA.ByErSp.Eun</p> <p>97=Erect sponges, <i>Eunicella verrucosa</i> and <i>Pentapora foliacea</i> [now <i>fascialis</i>]. MCR.Xfa.ErSEun</p>	<p>The characteristic species in the biotope name will increase in abundance where they already occur and <i>Pentapora fascialis</i> is likely to increase its distribution northwards. However, <i>Eunicella verrucosa</i> is unlikely to spread rapidly. Nevertheless, the biotope, with or without <i>Eunicella verrucosa</i>, is likely to replace more northern biotopes such as MCR.Xfa.ErSSwi characterised by the northern sea fan <i>Swiftia pallida</i>.</p>
<p><i>Phymatolithon calcareum</i> maerl beds in infralittoral clean gravel or coarse sand. 97= IGS.Mrl.Phy* (One of the biotopes constituting the UK Biodiversity Action Plan habitats ‘Maerl beds’ and ‘Sublittoral sands and gravels’.)</p>	<p>Maerl beds composed of <i>Phymatolithon calcareum</i> are found in southern Britain and well-developed beds are also found in Brittany where the more southern species <i>Lithothamnion corallioides</i> is a significant component. The best developed examples of this biotope are in Scotland. Whilst the relative abundance of <i>Lithothamnion corallioides</i> may increase, maerl</p>	<p><i>Sabellaria spinulosa</i> and <i>Polydora</i> spp. on stable circalittoral mixed sediment 03= SS.SBR.POL.SspiMx 97=CMX.SspiMx* (The biotope that constitutes the UK Biodiversity Action Plan habitat ‘<i>Sabellaria spinulosa</i> reefs’)</p>	<p>The distribution of this biotope is predominantly southern but is poorly recorded and appears to be associated with areas where mobile coarse substrata occur in areas of high turbidity. It is likely that substratum type and the presence of sand in suspension are most likely key environmental factors and the species (and therefore the biotope) is unlikely to extend northwards in distribution.</p>

	beds will persist together with their associated species.		
<p><i>Lithothamnion glaciale</i> maerl beds in tide-swept variable salinity infralittoral gravel. 97= IGS.Mrl.Lgla* (One of the biotopes constituting the UK Biodiversity Action Plan habitats 'Maerl beds' and 'Sublittoral sands and gravels'.)</p>	<p><i>Lithothamnion glaciale</i> is a northern species and this biotope is found only in Scotland especially in locations with variable or reduced salinity. A decline in response to warming is therefore likely.</p>	<p><i>Ostrea edulis</i> beds on shallow sublittoral muddy sediment 97=IMX.Ost (A biotope that is included in the UK Biodiversity Action Plan habitat 'Sheltered muddy gravels'.)</p>	<p><i>Ostrea edulis</i> suffered severe decline in abundance in the latter part of the 19th century and continues to have a restricted distribution mainly confined to inlets in eastern and southern Britain but with a significant population in Loch Ryan south-west Scotland. Suitable habitats occur further north especially in western Scotland and it might be that warming seas will encourage extension northwards.</p>
<p><i>Lithothamnion corallioides</i> maerl beds on infralittoral muddy gravel. 97= IMX.MrlMx.Lcor* (One of the biotopes constituting the UK Biodiversity Action Plan habitats 'Maerl beds' and 'Sublittoral sands and gravels'.)</p>	<p>Although this biotope is identified for western Scotland and for southern England, recent studies have suggested that <i>Lithothamnion corallioides</i> does not occur in Scotland (Hall-Spencer 1995). Seawater warming might enable <i>Lithothamnion corallioides</i> to expand its distribution and abundance so that this biotope becomes established.</p>		
<p><i>Halcampa chrysanthellum</i> and <i>Edwardsia timida</i> on sublittoral clean stone gravel. 97= IGS.FaG.HalEdw* (One of the biotopes constituting the UK Biodiversity Action Plan habitat 'Sublittoral sands and gravels'.)</p>	<p>This biotope is recorded from a few locations in western Scotland. However, the component species are rare and it is most likely physical habitat specificity that determines their presence so that no change is expected.</p>		

<p><i>Ruppia maritima</i> in reduced salinity infralittoral muddy sand. 97=MS.Sgr.Rup*</p>	<p>Although examples of this biotope are particularly well-developed in Scotland, the biotope is not unique to northern areas and its presence is due to suitable low salinity isolated shallow habitats rather than temperature.</p>	
<p><i>Zostera marina/angustifolia</i> beds in lower shore or infralittoral clean or muddy sand. 97=IMS.Zmar (One of the biotopes constituting the UK Biodiversity Action Plan habitat 'Seagrass beds'.)</p>	<p>Seagrass beds are especially well developed in Scotland compared to other parts of Britain and Ireland. However, development is most likely due to the presence of extensive suitable habitats and possibly uncontaminated waters. Dense seagrass beds occur further south than the British Isles in the north-east Atlantic and warming is not expected to affect beds.</p>	
<p><i>Serpula vermicularis</i> reefs on very sheltered circalittoral muddy sand. 97= CMS.Ser* (The biotope that constitutes the UK Biodiversity Action Plan habitat 'Serpula vermicularis reefs')</p>	<p><i>Serpula vermicularis</i> reefs appear to occur particularly in Scotland and Northern Ireland although, in Scotland, only now exist in Loch Creran. It might be that warming will have an adverse effect.</p>	
<p>Seapens, including <i>Funiculina quadrangularis</i>, and burrowing megafauna in undisturbed circalittoral soft mud. 97=CMU.SpMeg.Fun*.</p>	<p>Suitable habitats exist for <i>Funiculina quadrangularis</i> and some other species in the biotope south of their known distribution in Scotland and it might be that</p>	

(One of the biotopes constituting the UK Biodiversity Action Plan habitat 'Mud habitats in deep water'.)	increased temperature may adversely affect characteristic species and therefore the biotope.	
Foraminiferans and <i>Thyasira</i> sp. in deep circalittoral soft mud 97=COS.ForThy (One of the biotopes constituting the UK Biodiversity Action Plan habitat 'Mud habitats in deep water'.)	These communities have been considered 'relict'; remaining following more extensive distribution in colder times. They may therefore decline further.	

¹ Sub-biotopes especially

Additionally, some biotopes present throughout Britain and Ireland or with no apparently climatically determined distribution may change as a result of climate change. (For instance 'CMU.Beg*: *Beggiatoa* spp. on anoxic sublittoral mud' is likely to increase in occurrence and extent due to thermal isolation of deeper waters and consequent de-oxygenation.)

FIGURES

Figure 1. Biogeographical characteristics of the coast of the British Isles including the range limits of some species. Re-drawn from Forbes (1858) and including absence of the island of Anglesey as in the original publication. Current nomenclature is: *Acmaea testudinalis* = *Tectura testudinalis* (a limpet); *Cytherea chione* = *Callista chione* (a bivalve); *Echinus lividus* = *Paracentrotus lividus* (purple sea urchin); *Fusus norvegicus* = *Volutopsis norvegicus* (a snail); *Haliotis* = *Haliotis tuberculata* (the ormer); *Rhynconella psittacea* = *Hemithiris psittacea* (a snail); *Trichotropis borealis* (a snail); *Echinus neglectus* = *Strongylocentrotus droebachiensis* (a sea urchin).

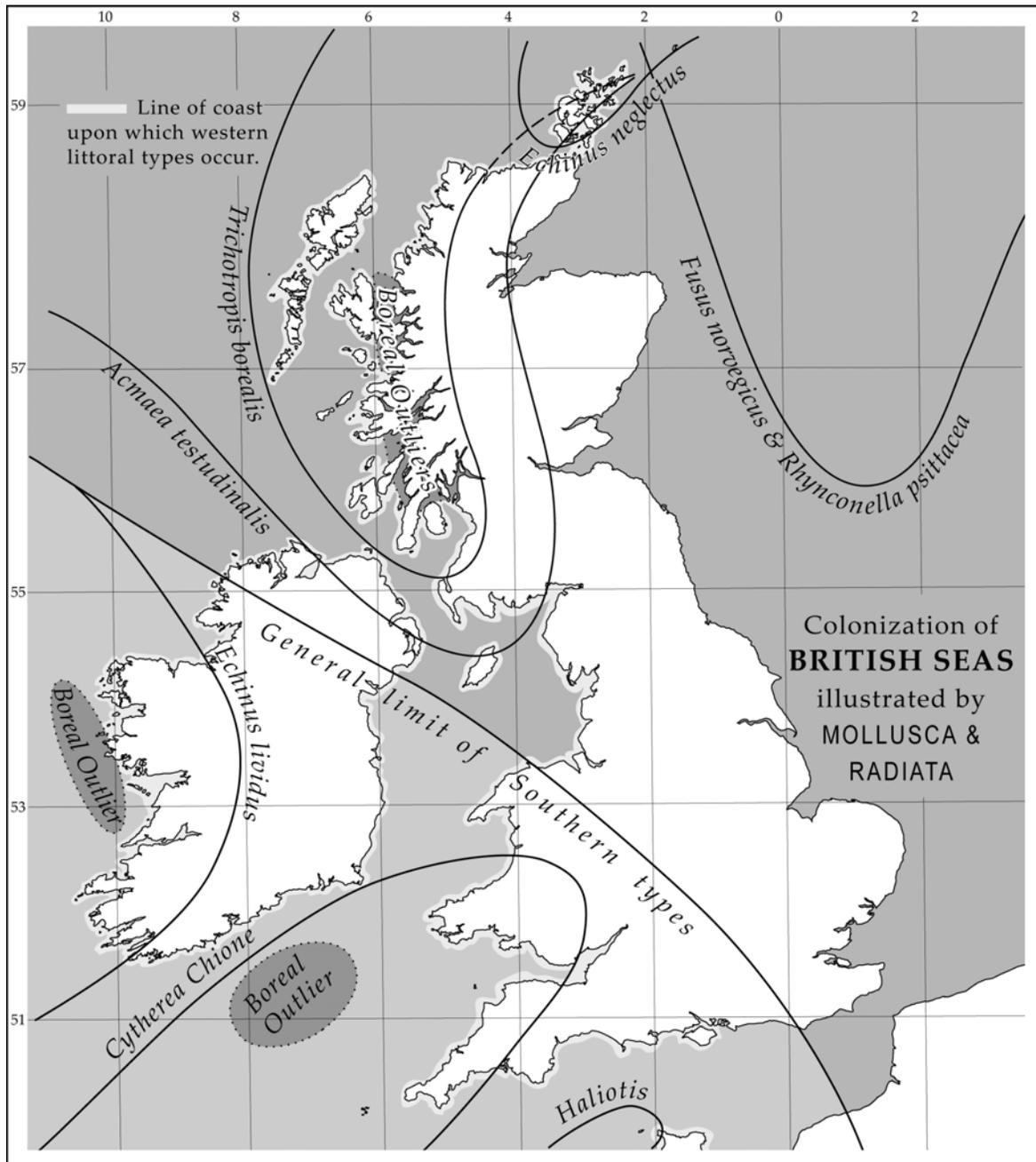
Figure 2. Annual mean sea surface temperatures from 1900 to 2000 and polynomial fitted trends. North Biscay data are for the five degree square at 45° to 50° N, 5° to 10° W. Off Plymouth data are for the one degree square at 50° to 51° N, 4° to 5° W. Both data sets are courtesy of the Hadley Centre for Climate Research. The Port Erin data are for the Breakwater, courtesy of the University of Liverpool Marine Laboratory.

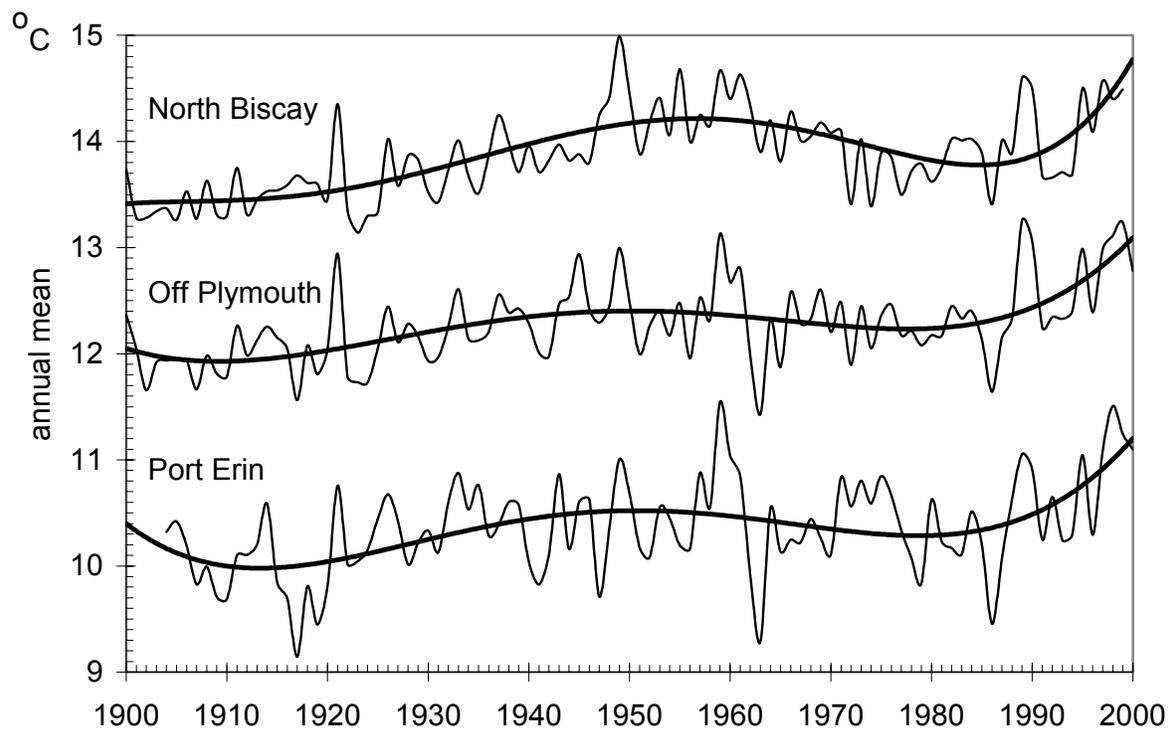
Figure 3. Summer and winter isotherms for surface waters around the British Isles. (From Hiscock, 1998, re-drawn from Lee and Ramster, 1981.)

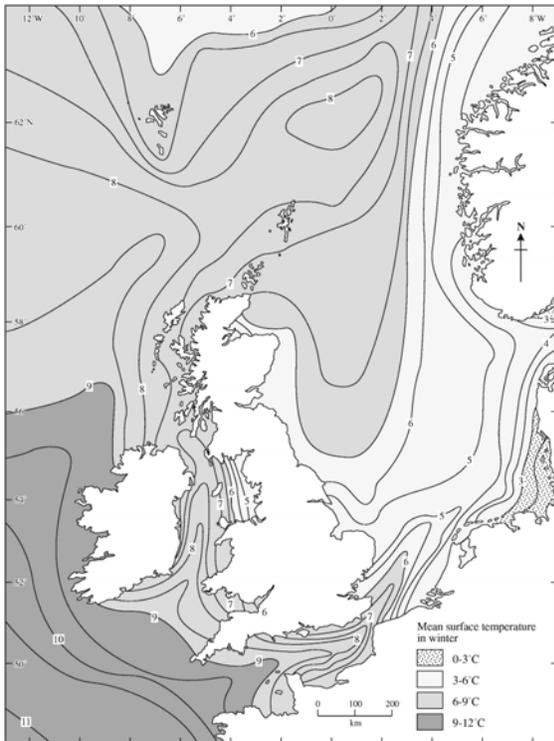
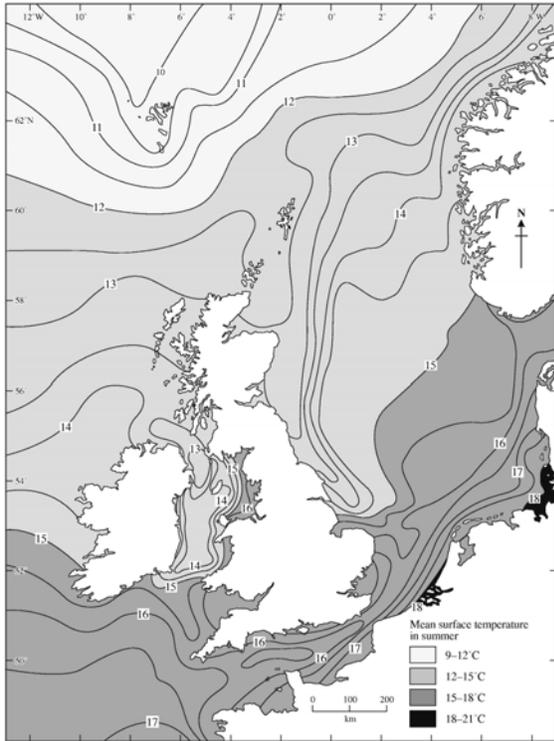
Figure 4. The direction of near-surface residual currents around the British Isles. (From Hiscock, 1998, re-drawn from Lee and Ramster, 1981.)

Figure 5. Water currents and quality decision tree for southern species.

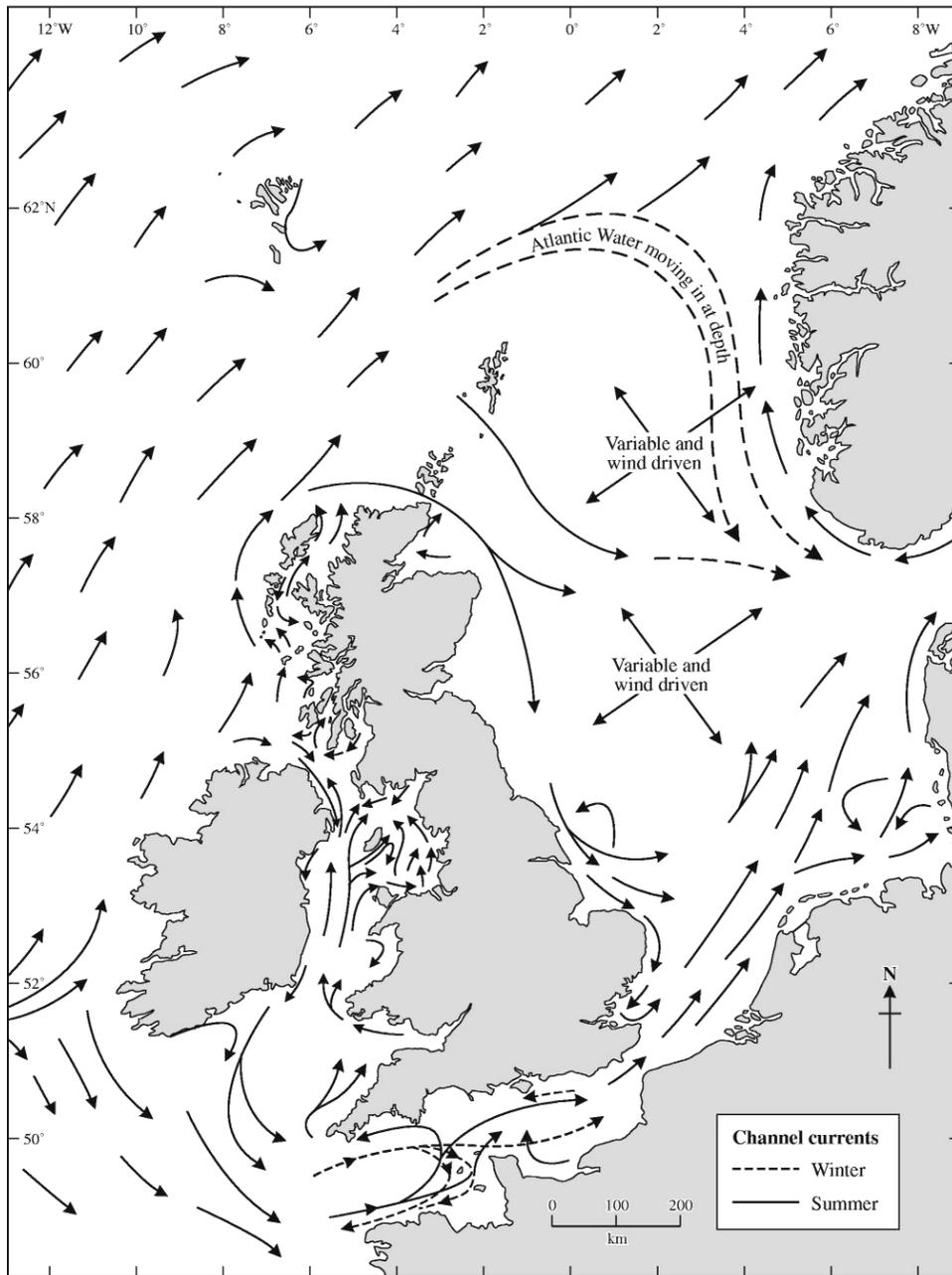
Hiscock *et al.* Figure 1



Hiscock *et al.* Figure 2

Hiscock *et al.* Figure 3

Hiscock *et al.* Figure 4



Hiscock *et al.* Figure 5