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The effects of climate change on rocky shore communities in the Bay of Biscay, 1895–2050

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UNIVERSITY OF SOUTHAMPTON: **ABSTRACT**

SCHOOL OF BIOLOGICAL SCIENCES, BIODIVERSITY AND ECOLOGY DIVISION

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During the 20th century, anthropogenic emissions of greenhouse gases have caused global mean temperatures to rise by 0.4–0.8°C. Further warming of 0.4–1.1°C is projected by 2050. Climate change during the 20th century has had effects on many terrestrial and marine ecosystems. This thesis investigates the effects of changes in climate on rocky shore communities in the Bay of Biscay, northeast Atlantic. This is a zone of biogeographical transition with sharp temperature gradients resulting in unusual spatial patterns of cold- and warm-temperate species, likely to be particularly sensitive to climate change.

Chapters 2 and 3 collect existing data on climate and species distribution in the region and analyse the data in novel ways. Chapters 3, 4 and 5 present and analyse new data on the distribution of rocky shore species in the region, and on the mechanisms of their responses to environmental gradients in temperature and other physical factors. Chapter 6 develops an original model based on existing and new data on the distribution and responses to climate of key rocky shore species.

In Chapter 2, analysis of several data sets showed that both summer and winter, sea and air temperatures in the Bay of Biscay region have on the whole risen since 1950, at a rate consistent with the global average rate of warming. There have, however, been warmer and colder periods, and local variations. Indices of upwelling calculated from alongshore wind stress show increasing trends throughout the 20th century in northwest Spain and northern Portugal; no clear trends were found along the north central coast of Spain.

In Chapter 3, analyses of past studies and my surveys during 2000–01 show that the distribution of rocky shore species in the Bay of Biscay has varied considerably since 1895. The abundance and distribution of several common cold-temperate species of brown algae on the north coast of Spain show significant negative correlations with variations in temperature during the 20th century, suggesting that climate change has indeed affected these species. The species studied are ecologically important canopy-forming algae: the changes in distribution observed are thus likely to have had important consequences for rocky shore communities in the region as a whole.

In Chapter 4, the responses of two common and ecologically important species of limpet, Patella vulgata L. (cold-temperate) and P. depressa Pennant (warm-temperate), to the gradient in sea temperature along the coast of northern Spain, and the mechanisms governing these responses, were investigated. The abundance of the two species and (especially) two indices of their relative abundance, $\log_{10}$ (Pv/Pd) and Pv/(Pv+Pd), were strongly correlated with summer temperature. A similar relationship of relative abundance of the same two species with spatial variations in summer sea temperature was found in data collected in the 1950s in the English Channel. The modal shell size of both species of limpets was smaller in areas of the coast with higher summer sea temperatures. Individuals of P. vulgata seem to change sex from male to female at a smaller size in northern Spain than has been found in previous studies in Britain. The timing of reproduction in northern Spain in both species fits with previously observed patterns in other parts of Europe. It is likely that the mechanisms governing the response of these species to temperature gradients act principally during the summer, suggesting that heat-related mortality and interspecific competition for microalgal food resources were likely to play an important role.

In Chapter 5, the responses of the same two species of Patella to gradients in wave exposure, salinity and temperature were studied in two estuaries on the Basque coast, inner Bay of Biscay. The relative abundance of the two species was strongly correlated with distance up the estuaries. Wave action or some physical factor correlated with it is likely to play an important role in determining these patterns of distribution. A translocation experiment found no significant difference between species in mortality or growth at two different sites in the Mundaka estuary.

In Chapter 6, I present a new graphical forecasting model and use it to project future changes in the distribution of 18 common rocky shore species in the northeast Atlantic under three climate change scenarios for 2025–2050. The method transforms distribution data from axes of latitude and longitude to axes of summer and winter temperature. I forecast that many cold-temperate rocky shore species now common in northern and northwest Spain are likely to disappear from the area in the next 50 years. In some cases this will depend on whether wind-driven upwelling increases during the same period. Many warm-temperate species are likely to expand their ranges in northern Europe and colonise parts of the British Isles where they have hitherto not been found.

In Chapter 7 the effects of climate change on ecosystems in general and rocky shore communities in particular are discussed and set in a broader ecological context, and future work suggested.

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Chapter 1: General Introduction

1.1. Overview

In recent years, evidence has been mounting that human activities are altering the climate of the planet (Warwick *et al.,* 1996; Mann *et al.*, 1998; Barnett *et al.,* 1999; Crowley, 2000; Zwiers and Weaver, 2000; Houghton *et al.*, 2001; Pearce, 2003). The effects of climate change on terrestrial and marine ecosystems worldwide are already visible in the form of changes in species distribution and phenology (Walther *et al.*, 2002; Parmesan and Yohe, 2003). Future consequences for ecosystems are predicted to be devastating, including widespread extinctions (Thomas *et al.,* 2004) and changes in ecosystem functioning (Gitay *et al.*, 2002). It is important to understand the effects of climate change on ecosystems in order to forecast and, where possible, mitigate these effects.

The responses of marine ecosystems to climate change have been studied extensively over the past 50 years (Southward and Crisp, 1952, 1954a; Southward, 1958, 1967, 1980, 1983; Southward and Boalch, 1988; Southward *et al.*, 1995; Barry *et al.,* 1995; Sagarin *et al.,* 1999; Sims *et al.,* 2001; Beaugrand *et al.*, 2002a,b). There are, however, few long-term data sets stretching back more than a few decades. Fortunately, some data are available for easily sampled rocky shore habitats over the course of the twentieth century.

My thesis investigates the responses of rocky shore organisms to the changes in climate seen during the twentieth century on the north coast of Spain and in the Bay of Biscay: an area of biogeographical transition, with steep spatial gradients in temperature. The processes driving change are explored, and forecasts are made, based on the future climate scenarios of the Intergovernmental Panel on Climate Change (IPCC) and extrapolations of recent climatic trends.

Chapter 1 gives a general introduction to the subject. The nature and effects of global climate change, observed and projected, are reviewed in §1.2, with an emphasis on marine ecosystems in general and rocky shores in particular. This is followed by a general review, in §1.3, of existing knowledge about the key processes structuring rocky shore ecosystems, with special reference to the effects of climate. The advantages of using rocky shores in the Bay of Biscay as the specific area for this research on responses to climate change are outlined in §1.4. Gaps in existing knowledge are then identified in §1.5, and the overall rationale and specific objectives of subsequent chapters are presented.

1.2. Global climate change: its nature and effects

1.2.1. Natural changes in climate up to 1850

The climate of the Earth has been varying continually throughout the history of the planet (Tajika, 1998; Crowley and Berner, 2001). Atmospheric samples from polar ice cores, together with sediments, tree rings and other "natural archives" (Guilizzoni and Lami, 1999; Sheppard *et al.*, 2002), make it possible to reconstruct changes in the climate and atmosphere over the past 420,000 years in great detail (Lorius *et al.*, 1990; Kerr, 1996; Smith *et al.*, 1997; Stauffer, 1999; Petit *et al.*, 1999). During this time the climate has fluctuated markedly, alternating between cold ice ages and warmer interglacial periods. There have been long-term (1450-year to 40,000-year period) cyclical changes, associated with variations in the orbit and rotation of the Earth, and perhaps in solar activity (Kerr, 1996). There have also been rapid shifts in global mean temperatures of up to 6°C in as little as a century (Mayewski *et al.*, 1993; Taylor *et al.*, 1997; Smith *et al.*, 1997; Stauffer, 1999), with regional temperatures in the Arctic changing by as much as 15°C (White and Steig, 1998). Palaeoecological studies (reviewed by Bartlein and Prentice, 1989; Schoonmaker and Foster, 1991; Jablowski and Sepkoski, 1996) have linked changes in terrestrial (e.g. forests: Russel *et al.,* 1993) aquatic (e.g. lakes: Guilizzoni and Lami, 1999) and marine (Schäfer, 1972; Molfina, 1994) ecosystems with past climate change.

These rapid shifts in climate can be explained by cyclical variations in the solar energy received by the Earth that have repeatedly triggered a switch between stable, cold and warm climate states (Lorius *et al.*, 1990; Smith *et al.*, 1997; Stauffer, 1999). These variations have been amplified by positive feedback elements, including the thermohaline ocean circulation system (Broecker, 1997; Tziperman, 1997; Clark *et al.*, 2002), greenhouse gases (Petit *et al.*, 1999) and ice sheets (Stauffer, 1999). These and other factors in the global climate system have interacted to produce these rapid shifts in climate, although exactly how these occurred is open to debate (White and Steig, 1998; Stauffer, 1999).

The last major episode of climate change was the Younger Dryas event, a relatively brief but intense period of re-glaciation between about 13,000 and 11,500 years ago (Mayewski *et al.*, 1993; Taylor *et al.*, 1997; Lea *et al.*, 2003). This was followed by a transitional period of as little as 10–40 years when temperatures rose rapidly (Mayewski *et al.*, 1993; Taylor *et al.*, 1997). Since then no comparable major climatic shifts have taken place, although climate patterns have been variable, with periods of warmer (e.g. between 1040 and 1390 CE) and colder climate (e.g. the "Little Ice Age" between about 1400 and 1900 CE: O'Brien *et al.*, 1995), whose onset has in some cases been extremely rapid (Alley *et al.*, 1997). It has been speculated that this unusually long period of relatively stable climate may have been the key factor that enabled the development of human settlements and agriculture, and the ensuing revolutions in culture and industry (Alley *et al.,* 1999).

1.2.2. Natural and anthropogenic climate change since 1850 and its effects on ecosystems

During the series of ice ages and interglacials from 420,000 years ago until about 1850 CE, global mean temperatures and atmospheric composition of greenhouse gases remained within certain fairly broad limits (Stauffer, 1999; Petit *et al.*, 1999). Concentrations of carbon dioxide varied from about 180 parts per million by volume (ppm) in cold periods to 280–300 ppm in warm periods; methane varied from 0.32–0.35 ppm in cold periods to 0.65–0.77 ppm in warm periods (Stauffer, 1999; Petit *et al.*, 1999).

By contrast, since 1850 atmospheric concentrations of greenhouse gases have been rising rapidly, and continue to do so at an accelerating rate, mainly due to human agriculture and industry (Keeling *et al.*, 1995; Houghton *et al.*, 2001). In 2000, CO_2 was present in the atmosphere at 368 ppm, 30% higher than pre-industrial levels, with CH_4 at 1.75 ppm, 150% higher than pre-industrial levels. Concentrations of other greenhouse gases such as nitrous oxide and chlorofluorocarbons have also been rising (Houghton *et al.*, 2001).

The link between greenhouse gases and global temperatures is now well established (Barnett *et al.*, 1999; Crowley and Berner, 2001; Houghton *et al.*, 2001). During the 20th century, global mean surface temperatures rose by 0.4–0.8°C (Cane *et al.*, 1997; Jones, 1998; Mann *et al.*, 1998, 1999; Houghton *et al.*, 2001). The 1990s were the warmest decade since formal records began in 1860, and probably the warmest of the last two millennia (Mann *et al.*, 1999, 2003; Pearce, 2003). It is not possible to say with absolute certainty to what extent the temperature rise is anthropogenic because of the natural variability of the climate system (O'Brien *et al.*, 1995; Jones, 1998). It is now widely believed, however, that most of the warming observed since 1950 is likely to be due to emissions of greenhouse gases from human activities (Mann *et al.*, 1998; Barnett *et al.*, 1999; Crowley, 2000; Houghton *et al.*, 2001; Kerr, 2001).

Long-term studies have found a consistent pattern of changes in many ecosystems worldwide that are related to climate change (reviewed by Walther *et al.*, 2002, Gitay *et al.*, 2002, and Parmesan and Yohe, 2003). Examples can be found in almost every ecosystem on the planet. In terrestrial habitats, there have been widespread phenological changes (Wuethrich, 2000) in plants (Abu-Asab *et al.*, 2001), amphibians (Beebee, 1995) and birds (Forchhammer *et al.*, 1998; McCleery and Perrins, 1998; Wuethrich, 2000). The growing season of trees in Europe has extended by 11 days on average since the early 1960s (Menzel and Fabian, 1999). There have been poleward shifts in the ranges of butterflies (Parmesan, 1996, 1999), birds (Thomas and Lennon, 1999), and mammals (Hersteinsson and MacDonald, 1992). There have also been upward shifts in the altitudinal ranges of plants (Wardle and Coleman, 1992; Grabherr *et al.*, 1994; Meshinev and Apostolova, 2000; Kullman, 2001), butterflies (Parmesan, 1996) and birds (Pounds *et al.*, 1999). These changes have in turn prompted widespread reorganisations in the communities affected by them, interacting with other anthropogenic changes, especially habitat degradation and fragmentation (Gitay *et al.*, 2002; Walther *et al.*, 2002).

Climate-related changes in marine systems have been no less pronounced. Coral reefs are one of the marine ecosystems most threatened by global change (Pittock, 1999) with widespread coral bleaching linked to sea temperature rise (Pittock, 1999; Hoegh-Guldberg, 1999; Wilkinson, 2000; Buddemeier, 2001).There have been large-scale climate-related shifts in pelagic ecosystems in the north Atlantic, recorded by the

Continuous Plankton Recorder Survey (Beaugrand *et al.*, 2002a,b), and in the north Pacific (Hare, 2003). Off southwest Britain, catches of herring, a cold-water species, and pilchard, a warm-water species, have been shown to be related to climatic fluctuations over the past four centuries, with herring dominating in cold periods and pilchard in warm periods (Southward, 1980; Southward *et al.*, 1988, 1995; Hawkins *et al.*, 2003). Analogous changes have taken place during the 20th century in the abundance and distribution of other warm- and cold-water species of fish in the same area (Southward and Boalch, 1998; Hawkins *et al.*, 2003) as well as off southern California (Brooks *et al.*, 2002). The abundance and distribution of warm- and cold-water plankton species have also varied with temperature over the past seventy years (Southward, 1963, 1980, 1983, 1984; Southward *et al.*, 1975, 1995). The timing of events such as the migration of squid (earlier in warm years: Sims *et al.*, 2001) and flounder (earlier in cold years: Sims *et al.*, 2004) have been shown to respond to sea temperature rises driven by the North Atlantic Oscillation which may be changing with climate (Houghton *et al.*, 2001).

In rocky shore communities, studies since the 1950s of the relative abundance of warm- and cold-water species of barnacles and limpets in southwest Britain have shown strong correlations with temperature (Southward and Crisp, 1952, 1954, 1956; Southward, 1967, 1991; Southward *et al.*, 1995). Increasing abundances of warm-water species were also seen on rocky shores in California, between surveys carried out in the 1930s and in the 1990s (Barry *et al.*, 1995; Sagarin *et al.*, 1999). Warm-water rocky shore species have extended their range and abundance in the Mediterranean (Astraldi *et al.*, 1995) and the English Channel (Herbert *et al.*, 2003). Retreat of cold-water species has occurred in the northwest Mediterranean during the hot summer of 1997 (Garrabou *et al.*, 2002).

In view of the many natural and artificial sources of change, it is not easy to interpret changes in communities with respect to any single factor such as temperature. While climate change is most commonly discussed in terms of temperature, in reality it is only a surrogate for the broad range of factors, acting directly and indirectly, involved in climate change. These include ocean circulation patterns, cloud cover and rainfall, wind, upwelling and wave regimes, sea level changes, and changes in not only average climate but also the frequency of extreme events. This applies particularly strongly to coastal marine ecosystems because of their high inherent variability (Lewis, 1976; Hartnoll and

Hawkins, 1985; Underwood, 1999). Rocky shores in particular are affected by many environmental factors, other than temperature, that show complex natural long-term and large-scale variability. These include tidal oscillations (Denny and Paine, 1998; Helmuth *et al.*, 2002; see §1.3.1.1 and further discussion in Chapter 2), wind-induced upwelling (Bakun, 1990; see §1.3.3), and wave action (Lynagh, 1997; see §1.3.1.2), as well as pollution (Hawkins *et al.*, 2002), harvesting (Castilla, 1999) and other anthropogenic impacts (Thompson *et al.*, 2002). Long-term studies that look at all relevant factors are therefore essential in order to detect broad-scale climate-related change, and distinguish it from natural spatial and temporal variability of coastal ecosystems (Southward, 1980, 1995; Southward *et al.*, 1995; Lewis, 1996; Underwood, 1999; Underwood and Chapman, 2000; Hawkins *et al.*, 2003). Nonetheless, temperature can be seen as an underlying factor that drives change both by directly influencing organisms (Orton, 1920; Allee, 1923; Hutchins, 1947; Southward, 1958; Hoek, 1982; Luning, 1984; Todd and Lewis, 1984; Breeman, 1988; Hoek and Breeman, 1990; Wiencke *et al.,* 1994) and by indirectly altering their ecological interactions (Menge *et al.,* 1997; Sanford, 1999, 2002; Leonard, 2000).

1.2.3. Projected future climate change and its likely effects

Climate models published by the IPCC estimate that global mean temperatures will rise by 1.4–5.8°C during the 21st century, from a 1990 base (Houghton *et al.*, 2001). The rate of warming will depend both on future emissions of greenhouse gases, and on the response of the climate system to past and future emissions, which is subject to considerable uncertainty. Different authors have estimated the 5–95% probability limits of warming at 1.1–4.5°C (Reilly *et al.*, 2001) and 1.7–4.9°C (Wigley and Raper, 2001). These ranges do not take into account the likelihood of non-linear responses to warming in the carbon cycle or abrupt, major changes in the thermohaline ocean circulation (Broecker, 1997; Allen *et al.*, 2001; Clark *et al.*, 2002) which have yet to be incorporated into the models. A reduction in the thermohaline circulation could lead to the diversion of the North Atlantic Drift, which at present gives northern Europe a climate that is exceptionally warm for its latitude; rapid regional cooling would probably then take place (Broecker, 1997; Clark *et al.*, 2002). Such responses could bring about a rapid shift in the global climate regime – comparable to those that have occurred at intervals during the past 400,000 years (Smith *et al.*, 1997; Stauffer, 1999), most recently in the Younger Dryas event (Mayewski *et al.*, 1993; Taylor *et al.*, 1997; Lea *et al.*, 2003). Even without such non-linear change, the projected rate of warming during the 21st century is highly likely to be greater than any comparable period during the past 10,000 years (Houghton *et al.*, 2001). This projected warming will lead to other physical changes, including sea level rise of 0.8–8 mm per year (Warrick *et al.* 1996) and increases in the frequency and intensity of extreme weather events including droughts, heavy precipitation, and heat waves (Houghton *et al.*, 2001; Hulme *et al.*, 2002), as well as increases in storms and hence wave action (Weaver and Green, 1998).

Predicting future effects of climate change on ecosystems faces similar problems to those encountered when detecting and attributing past effects. If anything prediction is more difficult because of the many unknowns. The majority of studies that attempt to do so use the "climate envelope" (Davis *et al.*, 1998a,b) or "ecosystem movement" (Gitay *et al.*, 2002) approach; this is based on the assumption that species and ecosystems will simply shift to areas that are similar to their current climate and environment (e.g. Hiscock *et al.*, 2003). In reality, there are many reasons why this is unlikely to occur. The dispersal and migratory abilities, life cycles and life spans of different species vary (Davis *et al.*, 1998a,b). In some cases, climate-related changes in other environmental factors such as the frequency and intensity of fires (Flannigan *et al.*, 2000) will have a greater effect on ecosystems than warming itself. Differences in the responses of interacting species to climate change may result in reorganization of ecosystems (Beebee, 1995; Brown *et al.*, 1997; Post *et al.*, 1999). Barriers to dispersal and habitat loss and fragmentation will make it difficult for many species to shift their range in response to climate change (Davis *et al.*, 1998a,b; Hiscock *et al.*, 2001, 2003; Gitay *et al.*, 2002). Anthropogenic changes (land use, predation, pollution) are also expected to alter the effects of climate change on ecosystems (Bianchi and Morri, 2000; Thompson *et al.*, 2002).

The alternative to the "climate envelope" approach is to construct a detailed model of the ecosystem as a whole in order to predict changes *in situ*. This approach presents very considerable difficulties due to complexity and lack of knowledge about many important contributing factors (Gitay *et al.*, 2002). These include the extent of phenotypic plasticity and the genetic variability available to species (Fields *et al.*, 1993). Community structure may be affected by the decline or loss of vulnerable species, especially of "keystone" species (Paine, 1966; Sanford, 1999) or "ecosystem engineers" (Jones *et al.*, 1994). Climate change can also influence larval recruitment (Fields *et al.*, 1993) as well as interspecific relationships (Fox and Morin, 2001) such as competition (Southward and Crisp, 1954a; Leonard, 2000). It is not surprising, therefore, that most studies that attempt to predict the effects of climate change on ecosystems do so on the basis of the climate envelope approach, despite its limitations (Gitay *et al.*, 2002). This approach can at least provide an initial estimate of the theoretical potential for future changes in distribution (Hiscock *et al.*, 2001, 2003) as long as it is informed by knowledge of past distributions, life histories, habitat availability and barriers to dispersal.

1.3. The ecology of rocky shores: A review of key processes, with special reference to climate

The biology and ecology of rocky shores have been studied extensively for a long time (Flattely and Walton, 1922; Lewis, 1964; Stephenson and Stephenson, 1971; Newell, 1979; Ricketts *et al.,* 1985; Little and Kitching, 1996; Raffaelli and Hawkins, 1999), and they have often been used as a tractable model system for experimental studies (Connell, 1972; Paine, 1977; Underwood, 2000). Thus the key ecological processes structuring rocky shore communities are fairly well understood, although many uncertainties still exist. This section reviews the current state of knowledge about these processes, with special reference to the effects of climatic factors and the potential impacts of climate change.

1.3.1. Environmental gradients on rocky shores

On scales of metres to kilometres, the rocky shore environment is characterised by two sharp gradients: the vertical gradient from land to sea, and the horizontal gradient of wave exposure, from very sheltered to very exposed conditions. A third, more gentle, latitudinal gradient of temperature, insolation and other climatic factors, acts on scales of hundreds of kilometres.

Together, these gradients largely determine the environmental conditions in which a given organism lives and the extent to which it is exposed to physical stress and disturbance. Stress during emersion due to cold, heat, desiccation, and/or variable salinity, and disturbance due to the action of waves and wave-borne material (Denny, 1994, 1995), both play a key role in structuring rocky shore communities. Other important factors include biological interactions (Connell, 1972; Hartnoll and Hawkins, 1985; Hawkins *et al.*, 1992; Menge, 1995; Johnson *et al.,* 1997; see also §1.3.2.2) and the influence of oceanic conditions on larval recruitment (Gaines and Roughgarden, 1985; Lewin, 1986; Underwood and Fairweather, 1989; Connolly and Roughgarden, 1998; see also §1.3.3).

Rocky shore organisms also experience stress and disturbance from a variety of other sources, particularly anthropogenic, such as pollution (e.g. oil spills: Southward and Southward, 1978; Jones *et al.*, 1998) or trampling (Fletcher and Frid, 1997; Keough and Quinn, 1998; Schiel and Taylor, 1999), which will not be discussed in detail here (see also review by Thompson *et al.*, 2002).

1.3.1.1. The sea-land gradient

Rocky shore organisms live at the boundary between two very different environments. The sea provides physical support, nutrients and raw materials, and relatively stable physical conditions (see §1.3.2). The terrestrial environment, in contrast, is characterised by high variability in temperature and humidity. Conditions during emersion are therefore stressful much of the time for most rocky shore organisms; even organisms in rock pools experience considerable variation in salinity and temperature during low tide (Morris and Taylor, 1983). The vertical position of an organism on the shore largely determines how often, and for how long, it is emersed, and therefore the extent to which it is subject to stress associated with emersion. Widespread mortality during emersion has been recorded in rocky shore organisms, due to extremes of heat (Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985; Garrabou *et al.*, 2002) or cold (Crisp, 1964a; Todd and Lewis, 1984), or to ice scour (McCook and Chapman, 1993). Sub-lethal effects are much more common, although it remains unclear just how these affect the survival, growth and reproduction of organisms (Davidson and Pearson, 1996; Pfetzing *et al.,* 2000). Tolerance of physical stress during emersion is thus a key factor determining patterns of vertical zonation on rocky shores, especially the upper limits of species (Broekhuysen, 1940; Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985). In the physically stressful environment of the upper shore, positive biological interactions (e.g. habitat modification, facilitation) contribute to survival and growth of organisms (Bertness, 1989; Bertness and Leonard, 1999). On the lower shore, in contrast, negative biological interactions such as competition for space (Connell, 1961), grazing (Jenkins *et al.*, 1999a,b; Boaventura *et al.*, 2002a) and predation (Paine, 1974; Connell, 1972), which are likely to be indirectly affected by stress during emersion, are important in determining patterns of vertical zonation (Underwood, 1981; Hawkins and Hartnoll, 1985; Boaventura *et al.*, 2002a).

Some species retreat down the shore as they approach their southern range limits (e.g. the fucoid algae *Fucus serratus, F. vesiculosus* and *F. spiralis*: Fischer-Piette, 1955a; the limpet *Patella vulgata* and the barnacle *Semibalanus balanoides*: Lewis, 1986). Climate change is therefore likely to alter patterns of vertical zonation on rocky shores, particularly if it leads to more extreme weather events, as models predict (Houghton *et al.*, 2001), and as has already been observed in some areas (Easterling *et al.*, 2000). However, the conditions experienced by rocky shore organisms during emersion do not always vary in a simple way with latitude, but can depend on complex interactions between diurnal, seasonal and tidal cycles (Helmuth *et al.*, 2002): episodes of stress are more severe when extreme low tides coincide with daily temperature maxima in summer or minima in winter.

1.3.1.2. The exposure gradient

The action of waves is the other main source of physical stress and disturbance for rocky shore organisms. Waves and wave-borne material can impair the settlement of larvae and propagules, and damage or dislodge plants and animals. Wave action can also be beneficial to rocky shore organisms, however, supplying food, nutrients, oxygen, and larvae, and increasing the vertical breadth of the zone in which can live. The forces exerted by waves, and their effects on organisms, are highly complex (Denny, 1994, 1995) and difficult to quantify or measure directly, although many methods have been proposed (Palumbi, 1984; Bell and Denny, 1994; Castilla *et al.,* 1998; Gaylord, 1999). The extent to which a given shore is exposed to wave action (its wave exposure) is therefore normally estimated rather than measured directly, based on either physical (Thomas, 1986) or biological (Ballantine, 1961a) criteria. Most waves result from the action of wind on open water, but as swell they can propagate far from their area of origin. Nonetheless, estimates of wave exposure calculated from local measurements of wind energy, fetch (the distance of open water over which the wind can blow) and the presence of shallow or deep water offshore, are strongly correlated with the vertical positions of biologically defined zones on the shore (Thomas, 1986).

Wave action is a key influence on rocky shore community structure. In the northeast Atlantic, in cool-temperate conditions, exposed shores are typically occupied by grazers and filter-feeders, and sheltered shores by macroalgae, which are competitively dominant in the absence of disturbance (Ballantine, 1964a; Lewis, 1964; Stephenson and Stephenson, 1971). On moderately exposed shores, disturbance due to wave action periodically removes or damages algae, maintaining a dynamic mosaic of different functional groups (Hawkins and Hartnoll, 1985). Disturbance due to wave action also affects diversity on boulder shores: intermediate levels of disturbance maintain a diverse mosaic of different successional stages, with the highest species diversity found in mid-successional assemblages (Sousa, 1979).

Predictions of climate change include an increase in the incidence of storms in some regions (Houghton *et al.*, 2001). This would lead to more frequent and severe disturbance to rocky shore communities and a shift in the competitive balance away from macroalgae and towards grazers and filter-feeders.

1.3.2. Sea temperature as an ultimate factor

Rocky shore organisms carry out much of their metabolic activity (feeding, photosynthesis, reproduction) while immersed. The sea provides a relatively stable and benign environment in which to do so. Except under special circumstances such as upwelling (see §1.3.3), there is little small-scale variation in sea temperature, pH or salinity (other than in estuaries), or in the concentrations of nutrients, oxygen or carbon dioxide. On seasonal, interannual, and latitudinal scales, however, sea temperature does vary considerably, although to a lesser extent than air temperature. Thus sea temperature is a major underlying influence on rocky shore organisms.

Since sea and air temperature tend to be strongly correlated in space and time, their effects are hard to distinguish, even though they affect rocky shore organisms in very different ways. Thus, although most studies of the responses of rocky shore species to climate concentrate on monthly mean sea temperatures (e.g. Hoek *et al.*, 1990; Southward *et al.*, 1995; Sagarin *et al.*, 1999), air temperature is probably a contributing factor in many cases. It is important when discussing the effects of temperature on rocky shore organisms to distinguish between the effects of sea and air temperature, and between the overall effects of average temperatures, and the punctual effects of extreme temperatures.

Extensive studies have been made of the effects of temperature on rocky shore organisms at the individual level. There have been investigations of thermal effects on photosynthesis (Davison, 1987; Pfetzing *et al.*, 2000), growth (Moss and Sheader, 1975; Stromgren, 1983), reproduction (Orton, 1920; Lewis *et al.*, 1982; Lewis, 1986; Bowman and Lewis, 1986), larval development (Lough and Gonor, 1973) and mortality (Newell *et al.*, 1971; Cornelius, 1972; Todd and Lewis, 1984; Yarish *et al.*, 1987), integrating individual responses likely to affect population processes. The effects of temperature on patterns of distribution have been investigated at local scales (e.g. vertical zonation: Broekhuysen, 1940; Schonbeck and Norton, 1978, 1980; Hawkins and Hartnoll, 1985; Johnson *et al.*, 1998) and at broader geographical scales (Hutchins, 1947; Southward, 1958; Hoek, 1975, 1982; Hoek *et al.*, 1990; Lüning, 1984; Breeman, 1988, 1990; Pakker and Breeman, 1996), including the effects on limits to distribution. The effects of temperature in modulating biological interactions within communities have also been studied (Southward and Crisp, 1954a; Coates, 1998; Bertness *et al.*, 1999; Sanford, 1999, 2002a,b; Leonard, 2000; Moore *et al.*, 2003). Some research has also explicitly addressed responses to past and future climate change (e.g. Lewis, 1984, 1996; Breeman, 1990; Southward, 1991; Southward *et al.*, 1995; Fields *et al.*, 1993; Barry *et al.*, 1995; Sagarin *et al.*, 1999; Hiscock *et al.*, 2001, 2003).

1.3.2.1. Near range limits: Temperature as a limiting factor

The effects of temperature on rocky shore organisms are most important near range limits. The exact position of the range limits of a given species may be determined by any of a number of proximate causes, including dispersal ability, lack of suitable habitat or adverse currents (Crisp and Southward, 1958; Andrew and Viejo, 1998; Gaylord and Gaines, 2000; Herbert *et al.*, 2003). In some cases limits are related to a failure to recruit new members to the population, while in others the limit is established by periodic mortality of adult organisms. In the absence of unsurpassable physical barriers, however, the ultimate or underlying factor determining the geographic range of most rocky shore species is temperature (Orton, 1920; Allee, 1923; Hutchins, 1947; Hoek, 1982; Breeman, 1988; Lüning, 1990). For certain species of algae in high latitudes, the limiting factor can be day length (Breeman, 1988), but this has little effect in mid-latitudes, the area covered in my study. Because populations that already experience suboptimal climatic conditions are likely to be the first to respond to warming or cooling, range limits are the first place to look for the effects of climate change (Crisp, 1964a; Southward *et al.*, 1995; Lewis, 1984, 1996; Herbert *et al.*, 2003).

The thermal limits of rocky shore species can be categorised according to the stage of the life cycle on which they act (Hutchins, 1947). In invertebrates the stage with the greatest thermal tolerance is typically the adult, but in macroalgae it may be a perennating structure such as a cryptic microthallus (Breeman, 1990; Hoek *et al.*, 1990). The range of temperatures tolerated by the most hardy stage is generally much wider than that required by the most sensitive stage of its life cycle, be it reproduction, growth or settlement. The term "repopulation" (Hutchins, 1947) has been applied as a catch-all for these more sensitive stages. Species are thought to adapt their life cycles so that the more thermally sensitive stages take place at the most favourable time of year for them (Hutchins, 1947; Hoek, 1982; Bowman and Lewis, 1986). Therefore the equatorward expansion of a species (southward, in the Northern hemisphere) will tend to be limited when either (a) winter temperatures are too high to permit successful repopulation or (b) summer temperatures are lethal to the hardiest stage. Likewise poleward expansion (northward, in the Northern hemisphere) will be limited when either (a) summer temperatures are too low for repopulation or (b) winter temperatures are lethal to the hardiest stage. Figure 1.1

illustrates this schematically, showing how lethal limits will tend to act in areas with wide annual variations in temperature (such as the east coast of North America), and repopulation limits in areas with narrow annual variations (such as the west coast of Europe).

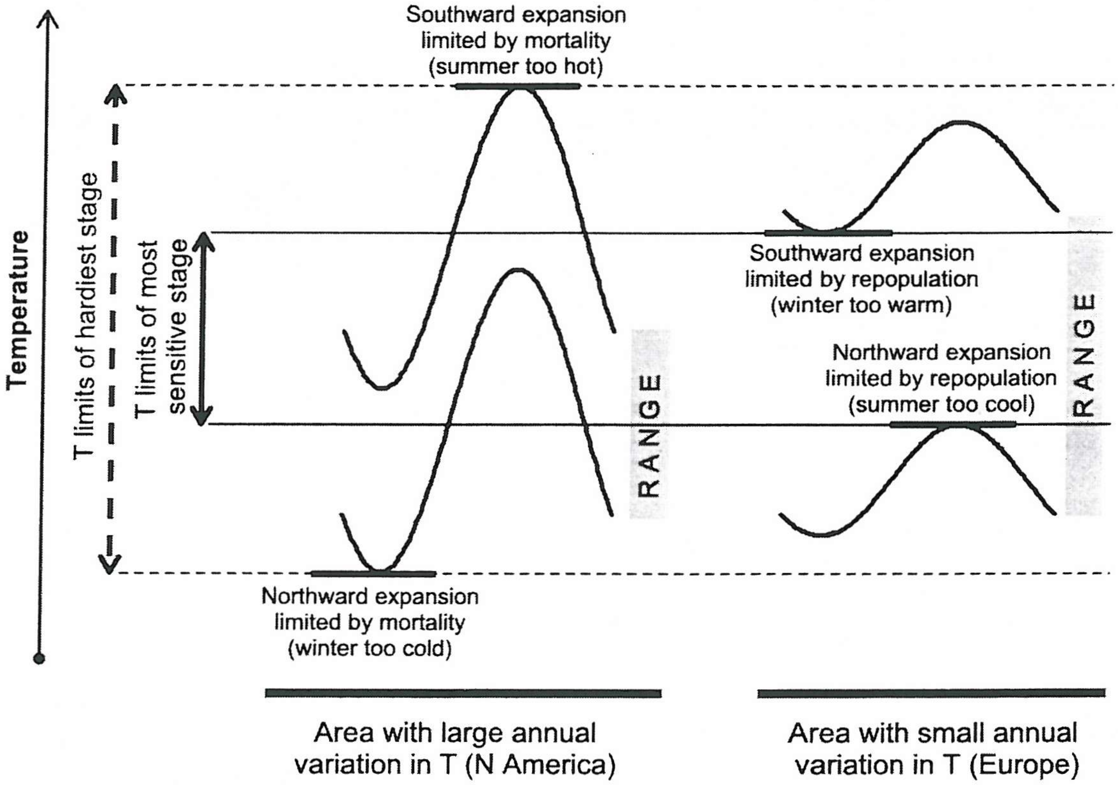


Figure 1.1. Schematic diagram showing how the northern and southern geographical limits of a hypothetical Northern hemisphere species are set by summer or winter temperatures in areas with different annual temperature ranges. See text for explanation. Adapted from Breeman (1988).

The southern or northern limits of many amphi-Atlantic species of algae follow this pattern, including the southern limits of *Chorda filum, Chorda tomentosum, Laminaria digitata, Dumontia contorta, Chondrus crispus,* and *Scytosiphon lomentaria* and the northern limits of *Centroceras clavalatum, Coelothrix irregularis, Gracelaria foliifera* and *Ceramium gracillimum* (Hoek, 1982; Hoek *et al.*, 1990; Yarish *et al.*, 1986; Breeman, 1988, 1990; Wiencke *et al.*, 1994; Breeman and Pakker, 1994; Pakker and Breeman, 1996). All these limits are set by survival in the western Atlantic and by repopulation in the eastern Atlantic. Similar patterns have been found for many other species.

Figure 1.1 gives a simplified view. Temperature range varies with latitude, and the thermal requirements of many species are asymmetrical or vary between regions (Breeman, 1988). Thus many, perhaps most, species diverge in one way or another from the pattern given in Figure 1.1. For example, the northern limits of *Dumontia contorta, Sphacelaria rigidula* and *Calliothamnion hookeri* are set by summer temperatures too low for repopulation, and the southern limits of *C. hookeri* and *L. digitata* are set by lethal summer temperatures, in both the eastern and western Atlantic (Norton, 1970; Hoek, 1982). Within a single region, many species are limited by repopulation at one end of their range and by survival at the other. Examples include *Saccorhiza polyschides,* which is limited at its northern extremes in western Norway and the eastern North Sea by lethal winter temperatures (4°C winter isotherm), and at its southern extremes in north Africa by summer temperatures too low for reproduction of the female gametophyte (15°C February isotherm: Hoek, 1982). In other cases, limits set by survival and repopulation happen to coincide in space. This is true for *Laminaria hyperborea* in northern Portugal: its southern expansion is limited by both lethal summer temperatures (18°C August isotherm) and by winter temperatures too high for successful reproduction (13°C February isotherm: Breeman, 1990). The failure of *L. hyperborea* and many other cold-water species to extend into the Bay of Biscay (Figure 1.2) appears, however, to be due to high summer temperatures.

Repopulation may be limited by temperature during both summer and winter if the organism does not attain full adult size within a single growing season. For example the range of *Gibbula umbilicalis* in northern Scotland is probably limited both by poor reproduction in summer and by juvenile mortality in winter (Mieszkowska, *pers. comm.*) The geographical ranges of rocky shore species are thus established by an interaction between the thermal requirements of their life cycles and spatial and temporal variations in climate. The position of the limits of a particular species, and the stage of the life cycle which is limited, will depend on local climatic conditions. It is therefore not very useful to classify species into different groups based on whether their northern or southern expansion is limited by survival or repopulation in different areas (Hutchins, 1947; Hoek, 1982). In order to predict the response of species to climate change, it is more important to establish their thermal requirements and compare these with existing and projected climatic patterns.

Several changes have been observed as populations approach the edge of their geographic range. They tend to become restricted to the most favourable habitats. For instance fucoid algae, a northern group, retreat to estuaries and other sheltered places towards their southern limits (Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959; Ballantine, 1961). Certain rocky shore species approaching their southern limits tend to retreat further down the shore: examples include the fucoid algae *Fucus serratus, F. vesiculosus* and *F. spiralis* (Fischer-Piette, 1955a). Changes in population structure also occur near range limits, which depend on, and may help to identify, the type of limit. Populations in areas that are marginal for repopulation tend to have a very uneven age or size structure, with gaps in years of repopulation failure (Lewis *et al.*, 1982; Bowman and Lewis, 1986; Lewis, 1986).

1.3.2.2. Modulating effects of temperature

There is evidence that rocky shore organisms and their interactions are mediated by variations in temperature across the whole of their range, not only in situations where climate is a limiting factor.

As noted above (§1.3.1.2), the competitive balance between macroalgae and grazers/filter feeders on rocky shores depends on the intensity of disturbance due to wave action. There is also evidence that this balance is influenced by temperature, and that the interaction between climate, wave exposure and community structure may turn out to be crucial to the response of rocky shore species to climate change. Communities dominated by grazers and filter-feeders (limpets and barnacles), typical of exposed habitats in northern Europe, extend further into shelter towards the south, while communities dominated by fucoid algae are progressively restricted to greater shelter (Ballantine, 1961a; Hawkins and Hartnoll, 1983; Hawkins *et al.*, 1992). Thus the species composition of communities on sheltered shores in northern Spain resembles that of communities on exposed shores in south-west Norway, some 3000 km further north (Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959; Ballantine, 1961a). There is little evidence of an increase in wave exposure across the same gradient, which was one proposed explanation for this phenomenon (Ballantine, 1961a). In fact, the dynamic interaction between grazers, filter-feeders and macroalgae appears to be mediated by climate. In warmer weather limpets are more active (Thompson *et al.*, 2000; Jenkins *et al.*, 2001). Macroalgae are thus less able to "escape" by growing to a size that frees them from microphagous grazing (Southward, 1964a; Hawkins, 1981; Hawkins *et al.*, 1992). It has also been suggested that the greater species diversity of limpets in southern than northern Europe may lead to more consistent, less variable grazing pressure on algae (Jenkins *et al.*, 1999a,c).

Small changes in temperature can also affect the activity of predators, leading to substantial changes in the structure of rocky shore communities. One example is the sea star *Pisaster ochraceus* in western North America, whose predation of mussels is dramatically reduced by small reductions in sea temperature (Sanford, 1999), potentially leading to increased dominance by mussels and a reduction in overall diversity of these communities. Predation plays a similar role in maintaining diversity in many other rocky shore communities (Paine, 1974; Menge *et al.*, 1997, 1999).

Thus the effects of climate change on rocky shores may not be limited to a simple shift in the geographical distribution of species, but may include large-scale reorganization of communities, with impacts on diversity and community structure that may be difficult to predict.

1.3.3. Links with the open sea: Upwelling and larval supply

Most rocky shore organisms spend part of their life cycle attached to the substrate, and the remainder free-living as larvae or propagules. As a result, conditions in the open sea and factors that affect the ability of larvae to settle in a suitable location can have profound effects on the structure of rocky shore communities. The influence of larval supply on the ecology of rocky shores, so-called "supply-side ecology" (Lewin, 1986), has been much studied (Underwood and Fairweather, 1989; Menge, 1991, 2000; Menge *et al.*, 1997; Shkedy and Roughgarden, 1997; Connolly and Roughgarden, 1999). Levels of recruitment can determine the intensity of interactions between organisms on the shore (Gaines and Roughgarden, 1985). Climate-driven variations in recruitment can cause fluctuations in adult populations, as observed in barnacles in the western English Channel over the past fifty years: the relative abundance of adults of *Chthamalus*, warm-water species, and *Semibalanus balanoides,* a cold-water species, were correlated with temperature in the Bay of Biscay, with a two-year time lag (Southward and Crisp, 1954a; Southward, 1967, 1983, 1991; Hawkins *et al.*, 2003).

A key process that links the rocky shore with the open sea, and which is chiefly driven by climate, is the phenomenon of coastal upwelling. Wind-induced upwelling is the result of Ekman transport, a movement of water 90 degrees to the right (in the northern hemisphere) of the wind direction, due to the Coriolis force (Ekman, 1905). When the wind is alongshore in the appropriate direction, this leads to net offshore transport of surface water. On deep-water coasts, this surface water moving offshore is replaced from below by an upwelling of cold, oxygenated, nutrient-rich water (Sverdrup, 1938; Richards, 1981). Upwelling takes place mainly along mid-latitude, west-facing coasts with deep water close inshore (Richards, 1981; Bakun, 1990). The west coast of the Iberian peninsula is a major upwelling zone, with upwelling frequent between April and October (Molina, 1972; Bakun, 1990; Nykjaer and Van Camp, 1994; Castro *et al.*, 1994, 2000; Jewell, 1994; Nogueira *et al.*, 1997; Casas *et al.*, 1997; Prego and Varela, 1998; Rocha *et al.*, 1999; Alvarez-Salgado *et al.*, 2000, 2001, 2002). Summer upwelling has also been observed along the north coast of Spain (Crisp, 1989; Botas *et al.*, 1989, 1990).

Upwelling events are often a very localized phenomenon in time and space, dependent on coastal topography as well as wind direction and strength (Sverdrup, 1938; Nykjaer and Van Camp, 1994; Tenore *et al.*, 1995; Nogueira *et al.*, 1997; Prego and Varela, 1998; Johnson and Nelson, 1999). Upwelling water may be 5–10°C colder than surface water, and the transition between the two water bodies can take place over a distance of hundreds of metres or less (Molina, 1972; Botas *et al.*, 1989). As a result, it is difficult to monitor directly the physical and biological conditions associated with upwelling. It is therefore common practice to estimate upwelling intensity indirectly using alongshore wind stress, defined as the square of wind speed (Bakun, 1973, 1990; Johnson and Nelson, 1999). This index can be calculated from wind or pressure data. Upwelling indices for the west coast of the Iberian Peninsula and three other major upwelling zones (off California, Morocco and Peru) all show a consistent rising trend during the years 1948–1979 (Bakun, 1990).

Upwelling influences rocky shore communities in several ways: through a sharp reduction in sea surface temperature, increased nutrient supply and consequently primary productivity, and by affecting the transport and settlement of the pelagic stages of many organisms (e.g. McQuaid and Branch, 1984; Menge *et al.*, 1997, 1999; Shkedy and Roughgarden, 1997; Sakko, 1998; Bustamante *et al.*, 1998; Rocha *et al.*, 1999; Connolly and Roughgarden, 1999; Menge, 2000). Upwelling also contributes greatly to the productivity of fisheries (Richards, 1981), including those of the northwest Iberian Peninsula (Tenore *et al.*, 1995; Nogueira *et al.*, 1997; Alvarez-Salgado *et al.*, 2001, 2002). Upwelling is thus an important factor in economic as well as ecological terms.

1.4. Rocky shores in the Bay of Biscay: an area of special interest for studying the effects of climate change

The Bay of Biscay is a zone of biogeographical transition in rocky shore species, from northern, cold-temperate assemblages, typically dominated by canopy-forming brown algae (fucoids and kelps), to southern, warm-temperate assemblages, dominated by grazers, filter-feeders and (on the lower shore) red algae, but with few species of brown algae (Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959; Ballantine, 1961a; Hawkins *et al.*, 1992; Southward *et al.*, 1995). The northern or southern limits of many ecologically important species fall within this region (Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959; Lüning, 1990; Southward *et al.*, 1995). As species are likely to be most sensitive to climate change near their geographical limits (Lewis *et al.*, 1982; Lewis, 1996), this makes the Bay of Biscay a promising area in which to study the ecological impacts of climate change.

Furthermore, this biogeographical transition does not conform to a simple north-south latitudinal pattern (see Figure 1.2). Cold-temperate species are abundant both in Brittany and in Galicia, northwest Spain. On the Basque coast (inner Bay of Biscay) and in southern Portugal, cold-temperate species are mostly absent, and rocky shores are typically dominated by warm-temperate species (Sauvageau, 1897; Fischer-Piette, 1955a;

Crisp and Fischer-Piette, 1959; Ardre 1971; Santos, 2000). Thus the transition between cold- and warm-temperate assemblages in this region, in effect, takes place three times, along approximately 1500 km of coastline between 48°N (Brittany) and 38°N (southern Portugal). Unusually for biogeographical studies, this means that there are replicated range edges to be studied.

This unusual pattern of species distribution is associated with sharp gradients in summer sea surface temperature in the region (Fischer-Piette 1955a). These are influenced by three main factors: stratification of surface water in the Bay of Biscay (Crisp, 1989), the continental influence of the surrounding land masses (Ibañez, 1990), and wind-induced upwelling of cold, nutrient-rich deep water off northwest Spain (Molina, 1972; Botas *et al.*, 1990; Tenore *et al.*, 1995).

As discussed in §1.3.3, upwelling affects the structure and interactions of rocky shore communities in ways that are important but not yet fully understood (Shkedy and Roughgarden, 1997; Connolly and Roughgarden, 1998; Sakko, 1998; McGowan *et al.*, 1998; Menge *et al.*, 1999; Menge, 2000). Coastal upwelling may increase in future due to stronger equatorward winds (Bakun, 1990). On the other hand, some global climate models predict greater ocean stratification and reduced upwelling strength under global warming scenarios (Bopp *et al.*, 2001).

For all these reasons, rocky shores in the Bay of Biscay region are an area of special interest for investigation of the effects of climate change on ecosystems, including the effects of possible changes in the intensity and frequency of coastal upwelling.

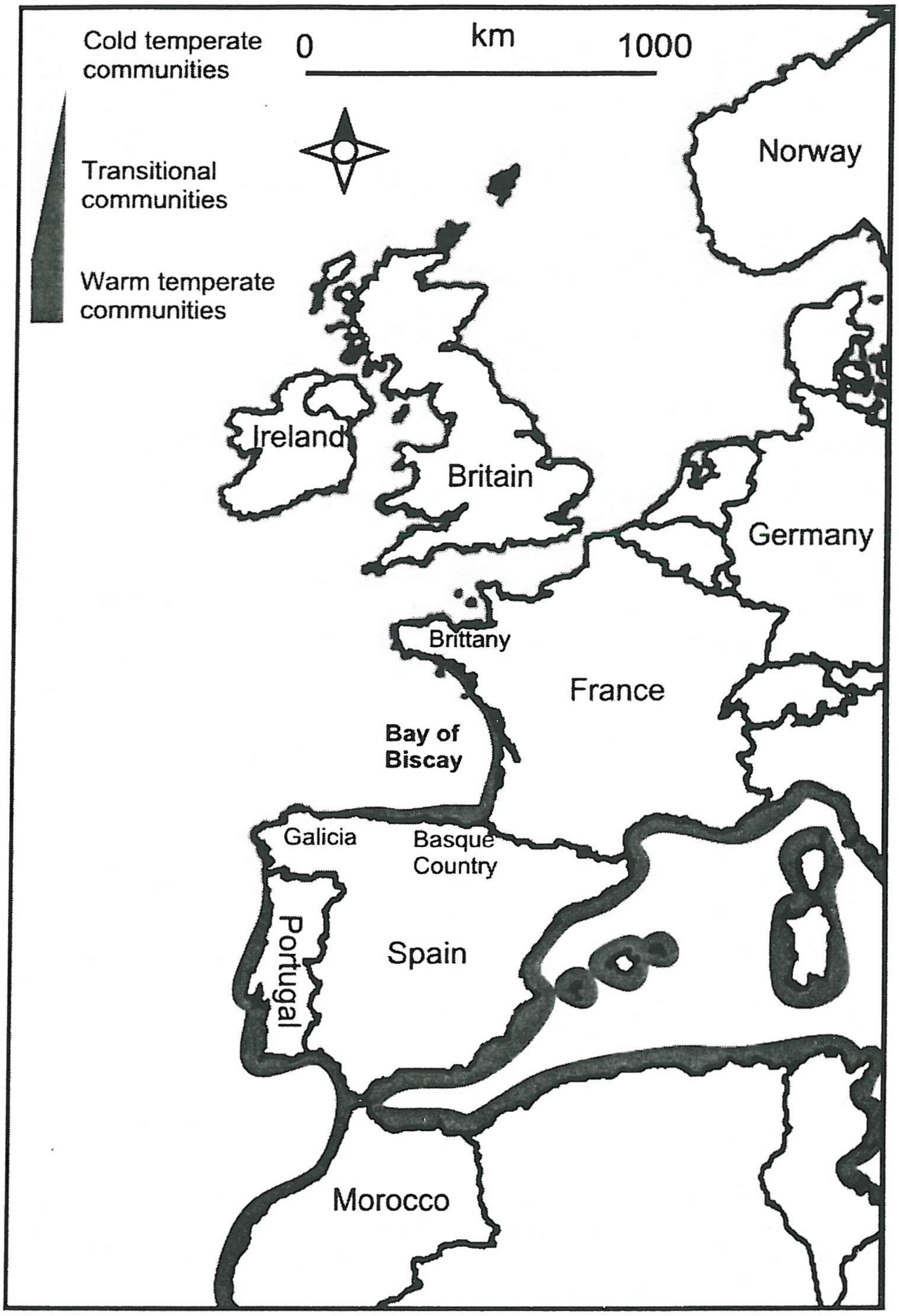


Figure 1.2. The approximate distribution of predominantly cold- and warm-temperate rocky shore communities in the northeast Atlantic in the mid-twentieth century. Summarised from Fischer-Piette (1955a, 1958) and Crisp and Fischer-Piette (1959).

1.5. Rationale and aims of thesis

The rationale behind my thesis is that rocky shores in the Bay of Biscay constitute a suitable system in which to study the ecosystem effects of climate change. This is an area of biogeographical transition in which many species reach their range limits, and where there are steep spatial gradients in temperature. Historical records of climate and species distribution are available dating back to the late 19th century, and rocky shores are a widely studied and well-understood system in which to carry out ecological studies.

The overall aims of my thesis are as follows:

1. To describe spatial and temporal patterns in both climate and the distribution of rocky shore species in the Bay of Biscay since the late 19th century, and the relationship between them.
2. To investigate the mechanisms governing the response of rocky shore organisms to climate.
3. To make forecasts of the effects of climate change on rocky shore organisms in the next 50 years.

The background and specific questions addressed by the different chapters of the thesis are as follows.

Data on climatic conditions in the Bay of Biscay region are available from many sources (e.g. Southward *et al.*, 1995; Borja *et al.*, 2000; NOAA-CIRES Climate Diagnostics Centre, 2003; Jet Propulsion Laboratory/British Atmospheric Data Centre, 2003). To date no integrated overview of climatic conditions has been made with reference to the factors affecting rocky shore ecosystems in the region. Estimates of upwelling indices have only been made for certain areas and years (Bakun, 1990; Borja *et al.*, 2000). To fill these gaps, **Chapter 2** gives an overview of the main climatic factors likely to influence rocky shore communities, including upwelling, in the Bay of Biscay from 1880 to 2001. The Bay is then placed in the context of the surrounding region, from the Straits of Gibraltar to the English Channel.

Studies of the geographical distribution of rocky shore species in the region have been carried out at irregular intervals since the late 19th century, with a wide range of aims and methods (for example Dautzenberg, 1894; Sauvageau, 1897; Fischer, 1899; Beauchamp, 1907; Miranda, 1931; Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959; Fischer-Piette and Gaillard, 1959; Anadon and Neill, 1981; Anadon, 1983). Much of the early work consisted of qualitative surveys or catalogues of flora and/or fauna. Several studies have looked at changes in distribution over time, with respect to selected species within limited geographical areas (Fischer-Piette and Dupérier, 1960; Gorostiaga, 1986; Borja and Gorostiaga, 1990). Other studies have described change on a large scale, but in a non-quantitative way (e.g. Fischer-Piette, 1955b, 1957b,c; Fernandez *et al.*, 1988; Ibañez, 1988, 1989, 1990). **Chapter 3** reviews studies carried out between 1895 and the present day, including some previously unpublished or limited circulation studies in Spanish. The chapter combines and synthesizes data from these studies with those from my own surveys in 2000–01. A better picture of change in the distribution of some of the key rocky shore species during the course of the 20th century is thereby achieved.

Long-term studies on rocky shores in southwest Britain (Southward, 1967, 1991; Southward *et al.*, 1995) have looked at the response to climate change of similar warm- and cold-water species of benthic invertebrates with overlapping ranges. The reproduction of these species show important relationships with latitude, with implications for their response to climate change (Lewis, 1986; Bowman and Lewis, 1986). Two of the species studied by Southward *et al.* (1995), the limpets *Patella vulgata* L. (a northern species) and *P. depressa* Pennant (a southern species), are also found together in the Bay of Biscay, but no studies of their response to climate have been carried out in this area. **Chapter 4** investigates the abundance, size frequency and reproductive biology of these two limpet species, across the north and northwest coasts of Spain, in order to assess their likely responses to climate change and their potential value as indicators of ecosystem responses to climate change.

An interesting question with respect to the distribution of rocky shore species in the Bay of Biscay area, with relevance to the question of climate change, has to do with the distribution of species in estuaries. In Europe, northern rocky shore species tend to retreat to more sheltered habitats towards the southern end of their range (Ballantine, 1961a). On the north coast of Spain populations of northern species are found on rocky shores in estuaries in greater abundance than on the adjacent open coast, where in some cases they are completely absent (Fischer-Piette, 1955a). These estuarine populations may represent relicts of more widespread populations that have taken refuge in estuaries because of changing climatic conditions. Gradients of salinity, turbidity and wave action may be important physical factors permitting the survival of refugee/relict populations, but the detailed distribution of northern and southern species in these estuaries, and the mechanisms that maintain these distributions, are unknown. **Chapter 5** investigates the distribution of the same two species of limpets studied in Chapter 4, *P. vulgata* and *P. depressa,* in two estuaries on the Basque coast of northern Spain. Their distribution is mapped in detail, and manipulative experiments and analysis of physical data are used to investigate the mechanisms causing the observed distribution.

The "climate envelope modelling" approach (Davis *et al.* 1998a,b; Gitay *et al.*, 2002; Walther *et al.*, 2002; Parmesan and Yohe, 2003) is still the basis for most forecasts of the future effects of climate change on ecosystems. This approach has been applied to rocky shores (Hiscock *et al.*, 2001, 2003) but only in a limited geographical area. Based on existing knowledge about the geographical limits of rocky shore species, **Chapter 6** presents a new graphical method based on the transformation of species distribution maps from axes of latitude and longitude to axes representing summer and winter temperature, enabling easier forecasts of the future distribution of species under different climate scenarios. My method is then applied to 18 common species in the northeast Atlantic.

Finally, **Chapter 7** integrates the results of the thesis including consideration of methodological problems, before drawing some conclusions and making suggestions for future investigations.

Chapter 2: The climate of the Bay of Biscay region from 1880 to 2001

2.1. Introduction

In order to understand the effects of climate change on rocky shore organisms it is necessary to have a broad overview of the patterns and variation of key climatic factors in space and time. There are several long-term climate data sets for the Bay of Biscay (Borja *et al.*, 2000), the surrounding region (Southward *et al.*, 1995) and the world (Jet Propulsion Laboratory/British Atmospheric Data Centre, 2003; NOAA-CIRES Climate Diagnostics Centre, 2003). These data sets have not, however, previously been analysed and compared in order to assess their relevance to studies of rocky shore species and their responses to climate change.

This chapter describes spatial and temporal patterns of key climatic factors in the Bay of Biscay since 1880, and places them in the context of the surrounding region: the northeast Atlantic from North Africa to the British Isles. It also compares different data sets in order to assess similarities and differences between them. The starting date of 1880 was chosen because climate data from before that date are less reliable, scarce and patchy. Additionally, no formal studies of rocky shores in the region were undertaken prior to that date.

As discussed in §1.3, temperature is one key physical factor affecting rocky shore organisms. Sea and air temperature affect organisms in very different ways, but their effects are often difficult to distinguish because they are strongly correlated in space and time. Both sea and air temperature are considered in the present chapter, as is cloud cover, which is associated with rainy, humid conditions, and less desiccation stress on rocky shore organisms during emersion.

Wave action is another key physical factor affecting rocky shore organisms (see §1.3.1). The main climatic variables affecting wave action are wind strength and direction. Wind also drives coastal upwelling (see §1.3.3).In §2.2, spatial variations in seasonal mean values (1950–1979) of sea surface temperature, air temperature, wind and cloud cover, for the Bay of Biscay and surrounding region, are plotted and discussed. Spatial variations in wave height along the north coast of Spain (during 1972–1994) are also considered in §2.2.

In some areas variations in the time of low tide can lead to important changes in the conditions experienced by rocky shore organisms during emersion (Lewis, 1964; Helmuth *et al.*, 2002). To see whether this might occur in the Bay of Biscay, spatial variations in the time of low tide within the region are also considered in §2.2.

In §2.3, temporal variations in sea and air temperature from 1880 until 2001 are analysed. Seasonal anomalies in sea and air temperatures for the region are calculated based on several different data sets, which are then compared. Indices of upwelling for 1900–1997 (for spring–summer of each year) are then calculated, based on wind data from the COADS data set (NOAA-CIRES Climate Data Centre, 2003), for six locations on the north and west coasts of Spain and northern Portugal in §2.4. Following this there is a general discussion of the physical data synthesized in this chapter, to set the scene for the rest of the thesis.

2.2. Spatial variation in climate

2.2.1. Data sources and methods

Mean climate data from the Comprehensive Ocean Atmosphere Data Set (COADS) are publicly available (NOAA-CIRES Climate Diagnostics Centre, 2003). These long-term means are calculated for the period 1950–1979. To give an overview of spatial variation in climate, charts for four climatic variables (sea surface temperature, air temperature at sea level, wind speed, and cloud cover) were generated for the area 35–55 degrees N by 0–15 degrees W, using the Climate Diagnostics Centre website. For each variable four charts were generated of seasonal means: for January to March (winter), April to June (spring), July to September (summer), and October to December (autumn). These seasonal periods have been chosen because they best represent annual variation in sea surface temperature, which is the key variable of interest and which generally reaches a minimum in February and a maximum in August in the region of study (see Figures 2.1, sea surface temperature; 2.2, air temperature; 2.3, wind speed; and 2.4, cloud cover).

The time of low tide, and the interaction between tidal, diurnal and seasonal cycles, are important factors in determining the conditions experienced by intertidal organisms in some regions such as the Pacific coast of North America (Helmuth *et al.*, 2002). To determine whether the time of low tide is likely to affect the conditions experienced by rocky shore organisms in the Bay of Biscay, the times of morning ELWS from January to October 2002 were calculated for different locations in the region (see Figure 2.5), using data from Admiralty Tide Tables (2002) and the computer programme TideWizard (2003).

Mean wave height and the percentage of waves over 5m in height were calculated based on data from 1972–1994, collected by the Spanish Ports Authority (Puertos del Estado, 2003) at seven points off the north coast of Spain (see Figure 2.6).

2.2.2. Results

2.2.2.1. Sea surface temperature

In the northeast Atlantic sea temperatures get colder from south to north as expected (Figure 2.1). Two additional features make the Bay of Biscay an interesting area from the marine biogeographical perspective. Both can be seen on the July-September chart in Figure 2.1. Along the coast at the north-west of the Iberian peninsula (marked "A") the water is about a degree Celsius cooler than it is offshore at the same latitude (43°N), due to the effects of wind-driven coastal upwelling (Molina, 1972; Bakun, 1990; see also §1.4.2). Also at the same latitude, in the inner Bay of Biscay (marked "B"), the water is about two degrees Celsius warmer than it is offshore, due to stratification as well as the effect of the continent. The combined effect of these two phenomena is that in following the coast from Brittany to southern Portugal, temperatures get warmer, colder, and warmer again. This reversal in the normal N-S temperature gradient is the main factor responsible for the unusual distributions of rocky shore species in the Bay of Biscay area (Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959; see Chapter 1) that make it the focus of this thesis.

2.2.2.2. Air temperature

Long-term mean air temperatures for 1950–1979 (Figure 2.2) closely reflect spatial patterns of sea surface temperature for the same period (Figure 2.1). One difference between air and sea temperatures is noticeable off northwest Spain and northern Portugal (marked "A"): not surprisingly, the effect of summer coastal upwelling appears to be considerably less on air temperature than on sea surface temperature (compare A in Figure 2.1). Also, while spring and summer (April–September) mean air temperatures throughout the region are very similar to sea surface temperature, in autumn and winter (October–March) mean air temperatures are about 0.5–1 °C less than sea surface temperatures.

2.2.2.3. Wind speed

Mean wind speeds are higher in autumn and winter than in spring and summer. In general they decrease from the north and west of the region towards the south and east, and from the outer to the inner Bay of Biscay (Figure 2.3). In general, wind speed is inversely correlated with summer sea temperature across the region (compare Figure 2.3 with Figure 2.1). This spatial variation in wind speed is likely to have an effect on wave action (see §2.2.2.6).

2.2.2.4. Cloud cover

Cloud cover in oktas is shown in Figure 2.4. (1 okta is equivalent to cloud covering one-eighth of the sky. 8 oktas is 100% overcast). The general pattern is of higher cloud cover in the north and west. Two features are worth mentioning are the low cloud cover in the eastern Bay of Biscay (marked "D") and the high cloud cover along the north coast of northwest Spain ("C"). This area of high cloud cover is also notable when compared with the west coast of northwest Spain, which has considerably lower mean cloud cover (3.5–4 oktas compared with 4.75–5), but with similar sea and air temperatures (Figure 2.1 and Figure 2.2).

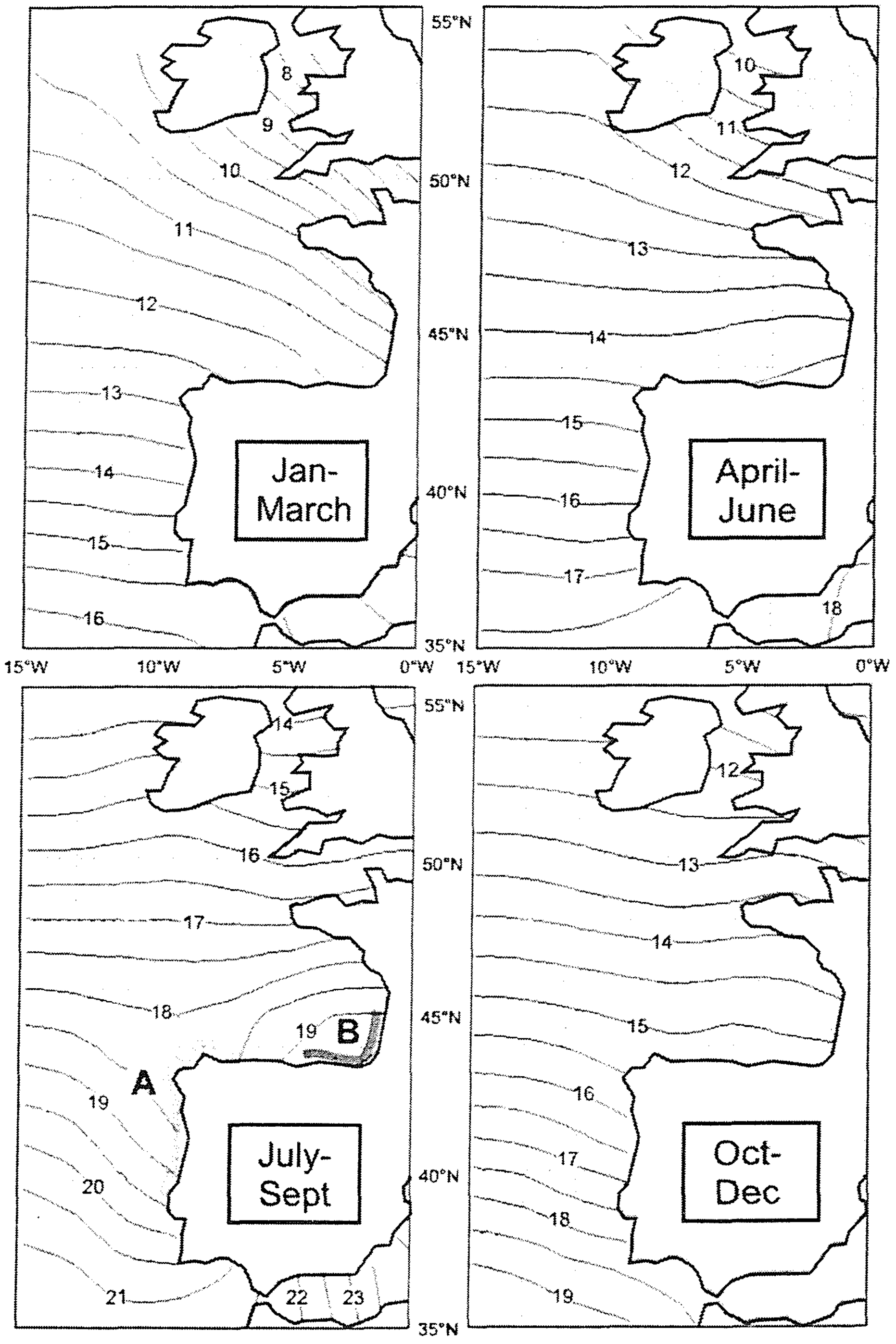


Figure 2.1. Mean sea surface temperatures in the northeast Atlantic for 1950–1979, in degrees Celsius. **A** represents the upwelling zone off NW Spain and Portugal; **B** represents the summer warm water pocket in the Bay of Biscay. Charts generated from COADS LTMs data using the website of the Climate Diagnostics Centre (www.noaa.cdc.gov).

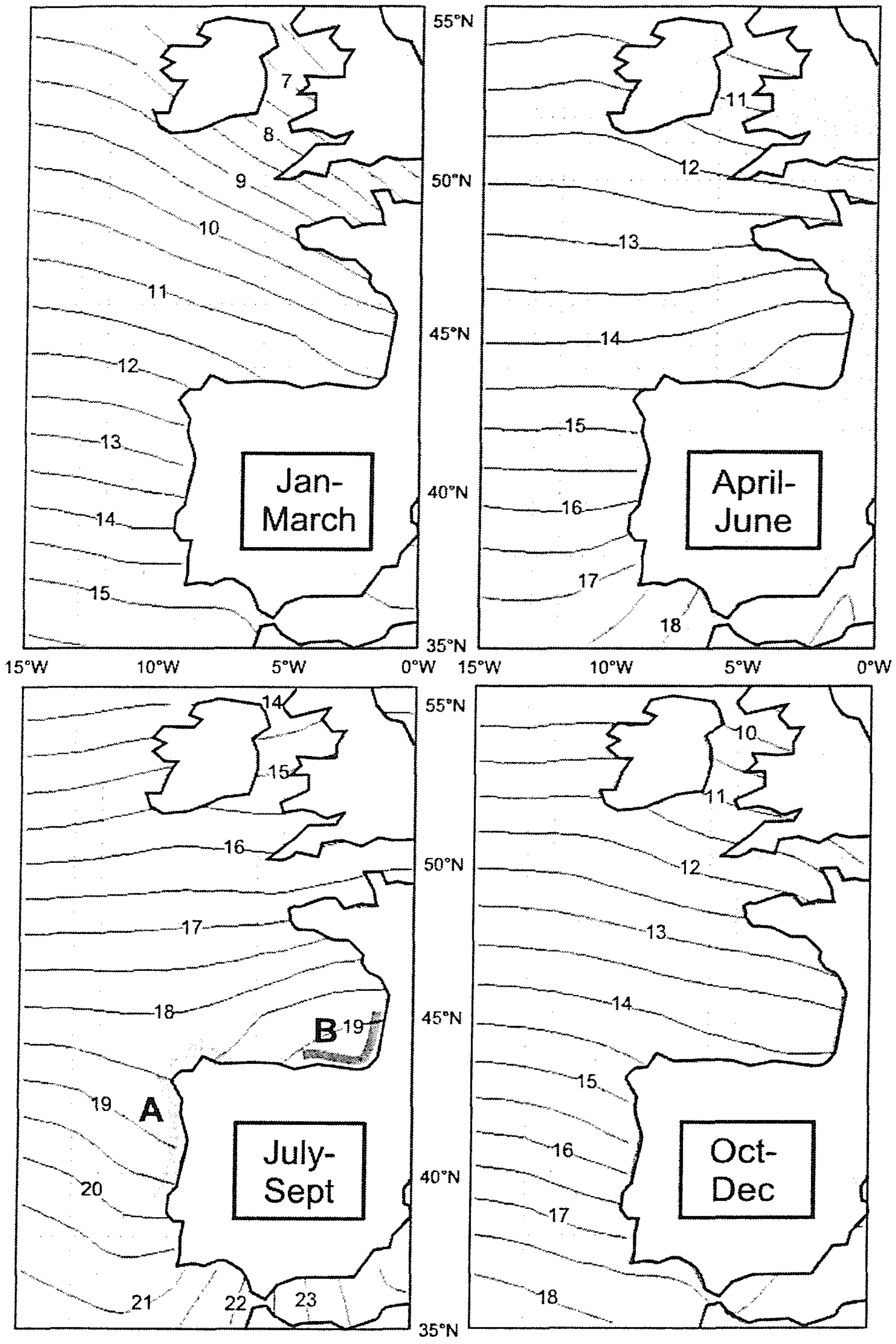


Figure 2.2 Mean air temperatures at sea level in the northeast Atlantic for 1950–1979, in degrees Celsius. **A** represents the upwelling zone off NW Spain and Portugal; **B** coincides with the summer warm water pocket in the Bay of Biscay. Charts generated from COADS LTMs data using the website of the Climate Diagnostics Centre (www.noaa.cdc.gov).

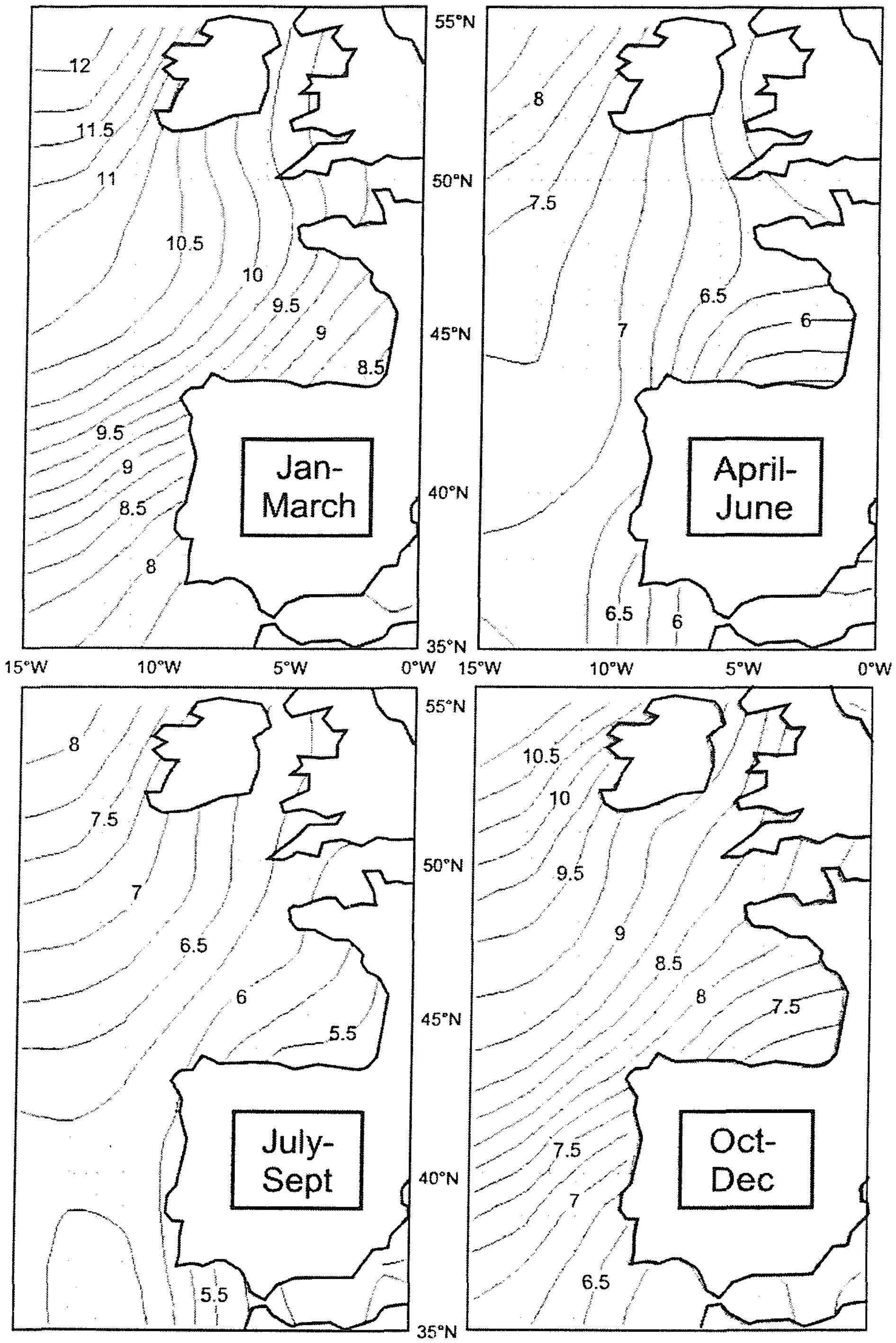


Figure 2.3. Mean wind speed in the northeast Atlantic for 1950–1979, in metres per second. Charts generated from COADS LTMs data using the website of the Climate Diagnostics Centre (www.noaa.cdc.gov).

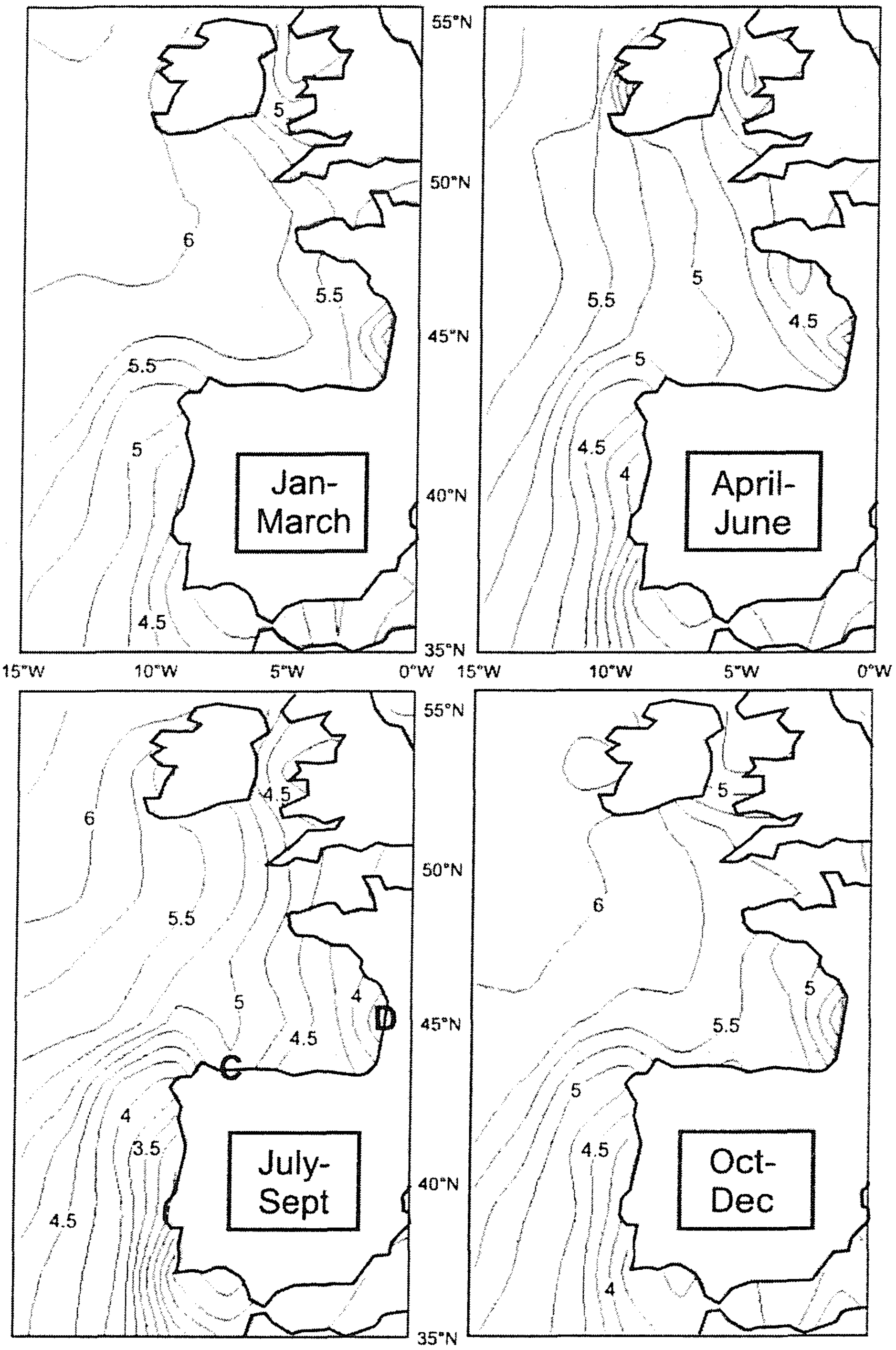


Figure 2.4. Mean cloud cover in the northeast Atlantic for 1950–1979, in oktas. **C** and **D** represent areas of maximum and minimum cloud cover within the Bay of Biscay. Charts generated from COADS LTMs data using the website of the Climate Diagnostics Centre (www.noaa.cdc.gov).

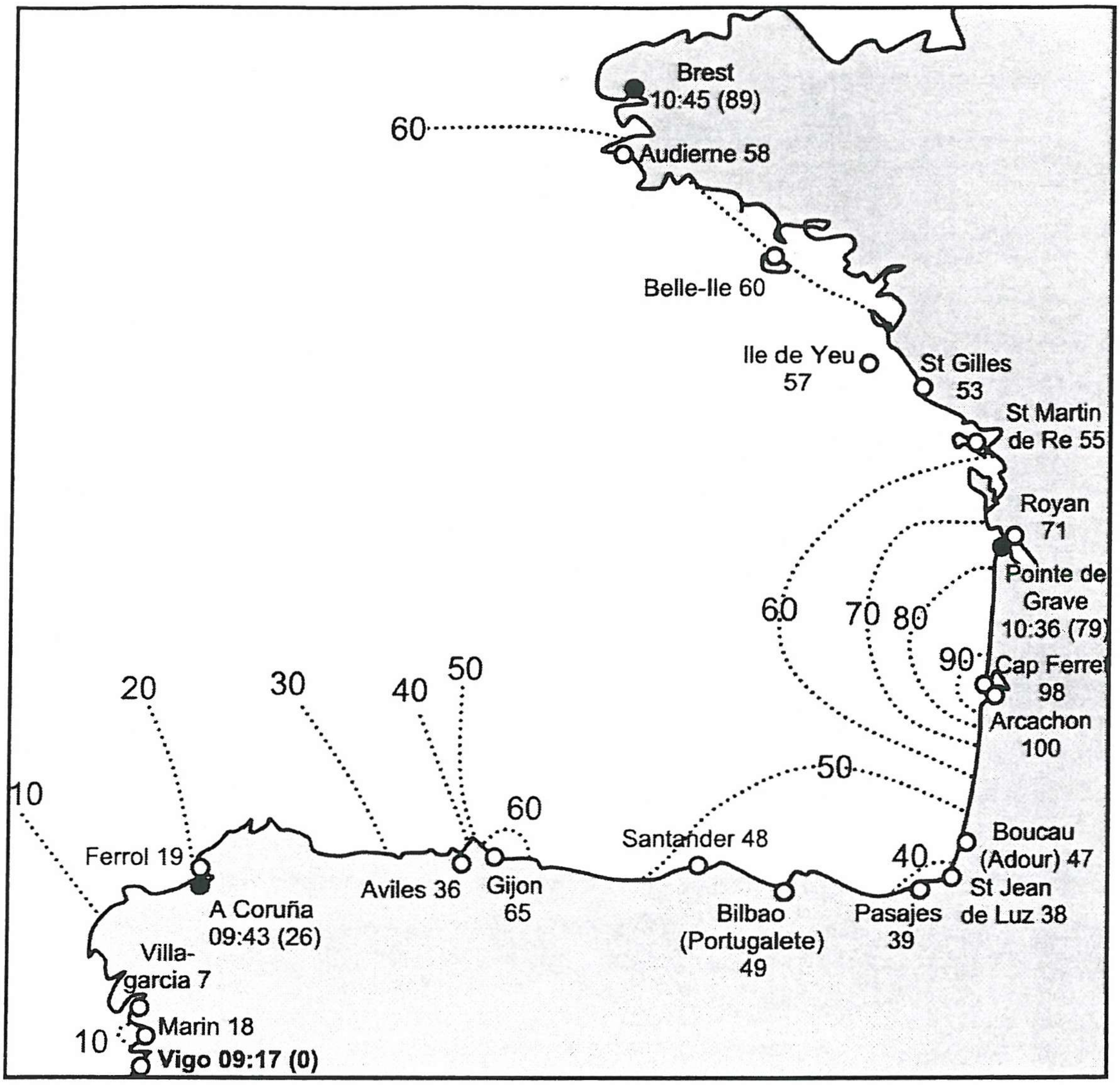


Figure 2.5. Average times of extreme low water spring (ELWS) tides in the Bay of Biscay region.
Sites where tide data were available are represented by circles. Times (e.g. Vigo 09:17) give the time (GMT) of morning ELWS at the specified location; numbers (e.g. Gijon 65) number of minutes of lag in the time of low tide, relative to Vigo, which is the location of earliest low tide. Dotted lines are isochrones, linking locations of equal time (minutes of lag are given next to each isochrone).
Solid circles: Data from Admiralty (2002). Open circles: Data from TideWizard (2003). All data averaged for the period January–October 2002.

2.2.2.5. Time of low tide

The time of morning ELWS in the Bay of Biscay region for the first ten months of 2002 (Figure 2.6) can be seen to follow a complex pattern, with the earliest tides occurring in northwest Spain (Vigo at 09:17 GMT) and the latest in the Arcachon Basin, western

France (10:57 GMT). The difference between these extremes is no more than 100 minutes, and for most of the region, the range in time of ELWS is less than an hour. Therefore it is unlikely that the time of low tide plays a significant role in determining the conditions experienced by rocky shore organisms in the region.

2.2.2.6. Wave height

The mean height of waves and the percentage of waves higher than 5m (Figure 2.6) both decrease from west to east along the north coast of Spain, consistent with the trend in wind speed (Figure 2.3). As an exception to this general trend, wave heights at 6.75°W and 6°W were lower than at the other sites.

Temporal trends in wave height from 1972 to 1994 (Puertos del Estado, 2003) indicate a decline in both mean wave height and the percentage of waves higher than 5m during this period. The likely implications for rocky shore communities are discussed in §2.5.1.

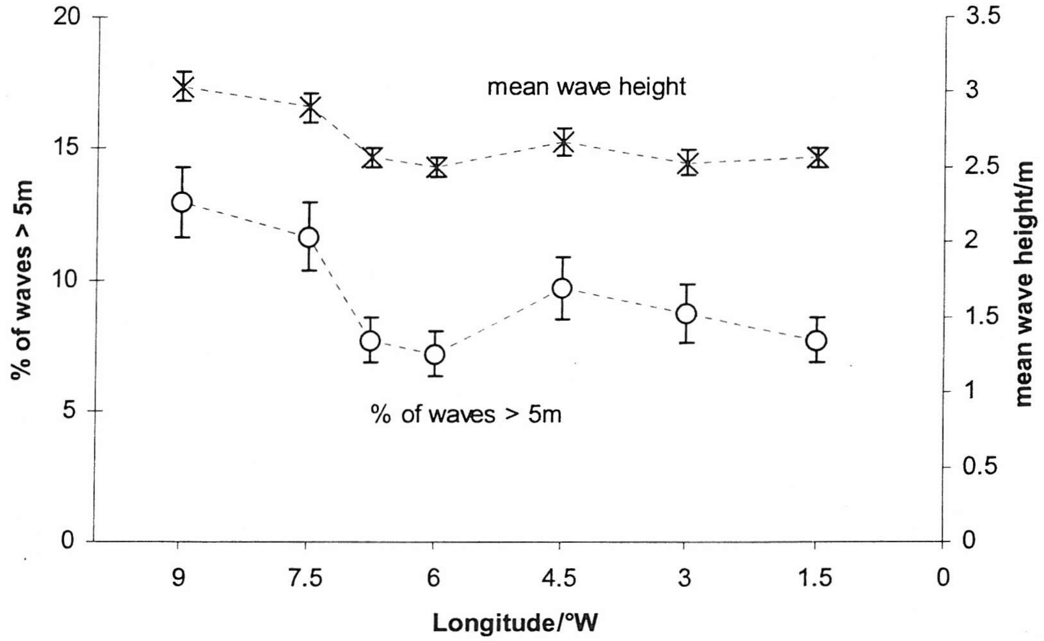


Figure 2.6. Mean wave height (upper line) and percentage of waves with height greater than 5m (lower line) at seven points off the north coast of Spain, all at latitude 44°N. Error bars represent standard error of the mean based on the variation between years. Data are averages for 1972–1994. Data from Puertos del Estado (2003).

2.3. Temporal variations in sea and air temperature in the Bay of Biscay region, 1880–2001

2.3.1. Data sources and methods

This section analyses trends and temporal patterns in both seasonal mean and extreme values of temperature over the period 1880–2001. Unfortunately, obtaining long time sequences of daily temperature values proved difficult. Daily air temperature data since about 1945 are available from the Spanish Meteorological Office but at a cost that exceeds the budget of a project such as this. Daily values of sea surface temperature since 1947 are, however, freely available from the San Sebastian Aquarium. The analysis of these data with respect to extreme temperatures is described later.

Time series of monthly mean temperature were obtained from several different sources, listed in Table 2.1. These sources span the area of interest from the western Iberian Peninsula to the English Channel. Monthly means were also calculated from the San Sebastian Aquarium data. Since summer and winter temperatures have greatest effect on rocky shore communities, particularly from the point of view of setting thermal limits (see §1.3), the analysis of mean temperatures was made on this basis, taking summer to be July–September and winter January–March (the hottest and coldest three-month periods of the year in this region, especially with respect to sea surface temperatures).

The data were treated as follows to show long-term trends:

1. Temperature anomalies were calculated by subtracting long-term means for 1880–2001 (or the subset of this period for which data were available) from monthly temperatures at each sampling location. Anomalies were used to avoid bias due to missing data from localities with higher or lower average temperatures than the region as a whole.
2. Seasonal anomalies were calculated by averaging monthly anomalies for January–March (winter) and July–September (summer).
3. For the COADS and GOSTA data sets, seasonal anomalies were averaged across the different sampling locations in the area of interest.

All statistical analyses throughout the thesis were performed using the Microsoft Excel spreadsheet package.

Each set of seasonal anomalies was plotted against time (Figures 2.7 through 2.11.) Five-year running means of each data set were also plotted to give a visual indication of trends.

Regression analysis was performed to test for trends in temperature anomalies over time. As the Marine Biological Association E1 data set had several gaps, including the period from 1988 to the present, no regression analysis could be performed on these data. For the other data sets, straight lines or second-order polynomial curves were fitted to the data where appropriate to show long-term trends. The five-year running means were shaded in to indicate warm and cold periods relative to the long-term mean or long-term trend (if any), and visually inspected to give a description of patterns.

To test the similarity between the different data sets, correlation analysis was performed between each pair of data sets, comparing summer with summer and winter with winter temperatures. The significance of each correlation was tested (see Table 2.2a–b.) Autocorrelations were also calculated within each data set, between temperatures for each winter and the following summer, and for each summer and the following winter (see Table 2.2c). These were tested using one-tailed tests to see whether there was a dependence of summer on previous winter temperatures or vice versa.

The San Sebastian Aquarium SST data set, which was the only data set consisting of daily values, was analysed to see whether there were trends over time in the frequency of extreme temperatures. Because the number of missing data varied considerably between years, comparing the highest and lowest temperatures in each year or other time frame would not yield an unbiased result. Instead, a cumulative frequency procedure was used to estimate the extreme temperatures that would be expected N times each year, during each of the five decades covered by the data (1950–59, 1960–69, 1970–79, 1980–89, and 1990–99). The procedure used was as follows: after pooling the data in decades and calculating cumulative frequencies (scaled to unity to account for missing data), the temperature likely to be encountered N times per year was calculated for N = 4, 2, 1, 1/2, and 1/4 (see Figure 2.11). Because very hot and very cold temperatures almost invariably occur in summer and winter respectively, the cumulative frequencies for minimum temperatures were based on data from December, January, February and March only, and those for maximum temperatures were based on data from June, July, August and September only. This approach corrected for the fact that there were more missing data in winter than in summer. Since four months (120 days) were sampled per year, the critical frequencies were equal to N/120. A bootstrap method (Sokal and Rohlf, 1995) was then used with N=100 to estimate standard errors for the maximum and minimum temperature statistics.

In addition, to see whether there was a relationship between extreme temperatures in summer and winter, a correlation analysis was performed between the maximum and minimum temperatures recorded in each year at San Sebastian. A negative relationship (hot summers correlated with cold winters and vice versa) would indicate fluctuations between periods of more extreme, "continental" climate and milder "maritime" climate.

2.3.2. Results

Relationships against time ($p<0.01$) were found for both the COADS sea surface temperature and the GOSTA LandSST data sets. For both data sets the estimated rate of warming since 1880 was higher in winter than in summer: +0.82°C per century in winter compared with +0.59°C in summer (GOSTA); +0.68°C per century in winter compared with +0.43°C in summer (COADS SST). No straight-line relationship against time ($p>0.05$) was found for the COADS air temperature data set or for the San Sebastian Aquarium data set. Second-order polynomial curves were fitted to summer and winter COADS air temperatures and summer San Sebastian sea temperatures (COADS winter: $y = 0.00012(x - 1929.58)^2 - 0.151$; $R^2 = 0.0342$; $F_{(1,113)} = 4.0$; $p = 0.048$. COADS summer: $y = 0.00012(x - 1940.16)^2 - 0.143$; $R^2 = 0.0365$; $F_{(1,113)} = 4.3$; $p = 0.04$. San Sebastian summer: $y = 0.00069\ (x - 1977.07)^2 - 0.175$; $R^2 = 0.073$; $F_{(1,53)}=4.2$; $p=0.046$) All three curves show rising temperatures in recent decades, since 1930 (COADS winter), 1940 (COADS summer) or 1977 (San Sebastian). So all the data sets tested, except San Sebastian winter temperatures, showed a rising trend in temperature during the last 25 years.

Visual inspection of five-year running means of both GOSTA and COADS sea temperature data sets shows that the 1990s were the warmest period, followed by the mid-twentieth century, roughly 1945–1960. The half-century up to 1930 was generally cold, apart from a warm spell in the early 1900s; there was another cold period between about 1960 and 1985 (relative to the overall warming trend, not the long-term mean). Similar patterns are visible in both summer and winter. The main patterns in the sea temperature data from San Sebastian are a cold period in the 1950s (especially in winter), and another cold period in both summer and winter between the early 1970s and early 1990s; the late 1940s, 1960s, and 1990s were mostly warm in both summer and winter.

The COADS air temperature data show greater variability, with less clear decade-scale warm and cold periods, and less correspondence between summer and winter patterns. Winter air temperatures were warm in the 1880s, the 1940s, and the 1990s, and cold in the 1980s and especially the 1910s and 1920s. Summer air temperatures were warm in the 1880s, the early 1900s, the period around 1920, the 1930s, 1950s, and 1990s, and cold in the late 1900s and early 1910s, the late 1920s, and the 1960s and 1970s.

The correlation analysis (see Table 2.2) found that all the data sets were correlated with each other except for the two point source data sets: San Sebastian Aquarium SST and MBA E1 SST. These two point source data sets both showed correlations with the regional average data sets but not with each other. This is unsurprising given the large distance (approximately 1000 km) between the two sampling locations.

The only data set that showed positive autocorrelations between winter and summer was the GOSTA data set, and then only between winter and following summer temperatures (see Table 2.2).

The analysis of extreme temperature values at San Sebastian (Figure 2.11) shows that extreme high sea surface temperatures in the 1990s were clearly much higher than in other decades. Temperatures that were only observed once in four years in other decades occurred twice or even four times a year in the 1990s. Differences between the other decades were small, with a gradual downward trend in the frequency of extreme high temperatures from the 1950s to the 1980s. The difference between the 1990s and the other decades is considerably greater than the respective standard errors, indicating that there has been a real increase in the incidence of extreme high temperatures.

Extreme low winter temperatures show a quite different pattern: the 1970s were clearly the decade with the least severe winters, while the most severe winters were in the 1950s. The other decades were intermediate in the severity of their winters.

No relationship was found between the maximum and minimum temperatures recorded in each year (r = -0.03; $F_{(1,53)} = 0.05$; p = 0.83). There does not seem to be any relation, either positive or negative, between extremely hot summers and extremely cold winters, showing no evidence for the existence of more "continental" and "maritime" periods in climate.

Table 2.1. Sources of data used to generate time series of summer and winter temperature anomalies.

Abbreviation	Type	Source	Resolution time/space	Time period	Area used	Figure
GOSTA	Sea & Air	GOSTA LandSST data set, JPL/British Atmospheric Data Centre, www.badc.rl.ac.uk	Monthly/ 5° x 5° lat x lon	1851–1995	40–50N, 0–10W	2.7
COADS Air	Air	Comprehensive Ocean-Atmosphere Data Set, NOAA-CIRES Climate Diagnostics Centre, www.noaa.cdc.gov	Monthly/ 2° x 2° lat x lon	1848–1997	42–50N, 0–10W	2.8
COADS SST	Sea					2.9
MBA E1	Sea	Station E1, UK Marine Biological Association / Marine Environmental Change Network (Southward *et al.*, 1995)	Monthly/ point source	1921–1987	50.03N, 4.37W	2.10
SSA	Sea	San Sebastian Aquarium (Borja *et al.*, 2000)	Daily/ point source	1947–2001	43.33N, 2.00W	2.11, 2,12

Table 2.2. Pearson r-value correlation coefficients between winter (a) and summer (b) temperature anomalies from different pairs of data sets, and autocorrelations (c) between winter and summer temperatures within each data set. See Table 2.1 for data sources. *** means correlation significant at $p<0.00003$; ** means $p<0.0003$; * means $p<0.00175$; *n.s.* means $p \geq 0.00175$. (Critical values were corrected for the number of tests performed = 30.) In (c), A v B: summer compared with the preceding winter (e.g. July–Sept 1900 compared with Jan–Mar 1900). B v A: winter compared with the preceding summer (e.g. Jan–Mar 1901 compared with July–Sept 1900).

(a) Winter temperatures

	MBA E1	**COADS Air**	**COADS SST**	**GOSTA**
COADS SST				0.744*** $F_{(1,114)}$=141, p<0.00001
COADS Air			0.691*** $F_{(1,114)}$=104, p<0.00001	0.711*** $F_{(1,112)}$=114, p<0.00001
MBA E1		0.649*** $F_{(1,63)}$=46, p<0.00001	0.605*** $F_{(1,63)}$=36, p<0.00001	0.554*** $F_{(1,63)}$=28, p<0.00001
SSA	0.245 *n.s.* $F_{(1,39)}$=2.5, p=0.12	0.426 *n.s.* $F_{(1,49)}$=10.9, p=0.002	0.466* $F_{(1,49)}$=13.6, p=0.0006	0.519* $F_{(1,39)}$= 14.4, p=0.0005

(b) Summer temperatures

	MBA E1	**COADS Air**	**COADS SST**	**GOSTA**
COADS SST				0.829*** $F_{(1,114)}$=251, p<0.00001
COADS Air			0.807*** $F_{(1,114)}$=213, p<0.00001	0.752*** $F_{(1,112)}$=145, p<0.00001
MBA E1		0.627*** $F_{(1,63)}$=41, p<0.00001	0.593*** $F_{(1,63)}$=34.2, p<0.00001	0.613*** $F_{(1,63)}$=38.0, p<0.00001
SSA	0.445 *n.s.* $F_{(1,39)}$=9.6, p=0.004	0.560*** $F_{(1,49)}$=22.4, p=0.00002	0.632*** $F_{(1,49)}$=32.6, p<0.00001	0.617*** $F_{(1,39)}$=24.0, p=0.00002

(c) Autocorrelations
(AvB: summer vs. preceding winter; BvA: winter vs. preceding summer)

	Data set				
Comparison	**GOSTA**	**COADS SST**	**COADS Air**	**MBA E1**	**SSA**
A v B	r = 0.375*** $F_{(1,114)}$=18.5 p=0.00002	r = 0.177 *n.s.* $F_{(1,116)}$=3.7 p=0.028	r = 0.208 *n.s.* $F_{(1,114)}$=4.8 p=0.013	r = 0.110 *n.s.* $F_{(1,63)}$=0.77 p=0.19	r = 0.242 *n.s.* $F_{(1,53)}$=3.3 p = 0.04
B v A	r = 0.258 *n.s.* $F_{(1,113)}$ = 7.8 p=0.0027	r = 0.263 *n.s.* $F_{(1,115)}$ = 6.8 p=0.0048	r = 0.196 *n.s.* $F_{(1,113)}$ = 4.4 p=0.018	r = 0.185 *n.s.* $F_{(1,62)}$ = 2.2 p=0.07	r = 0.184 *n.s.* $F_{(1,52)}$ = 1.8 p=0.09

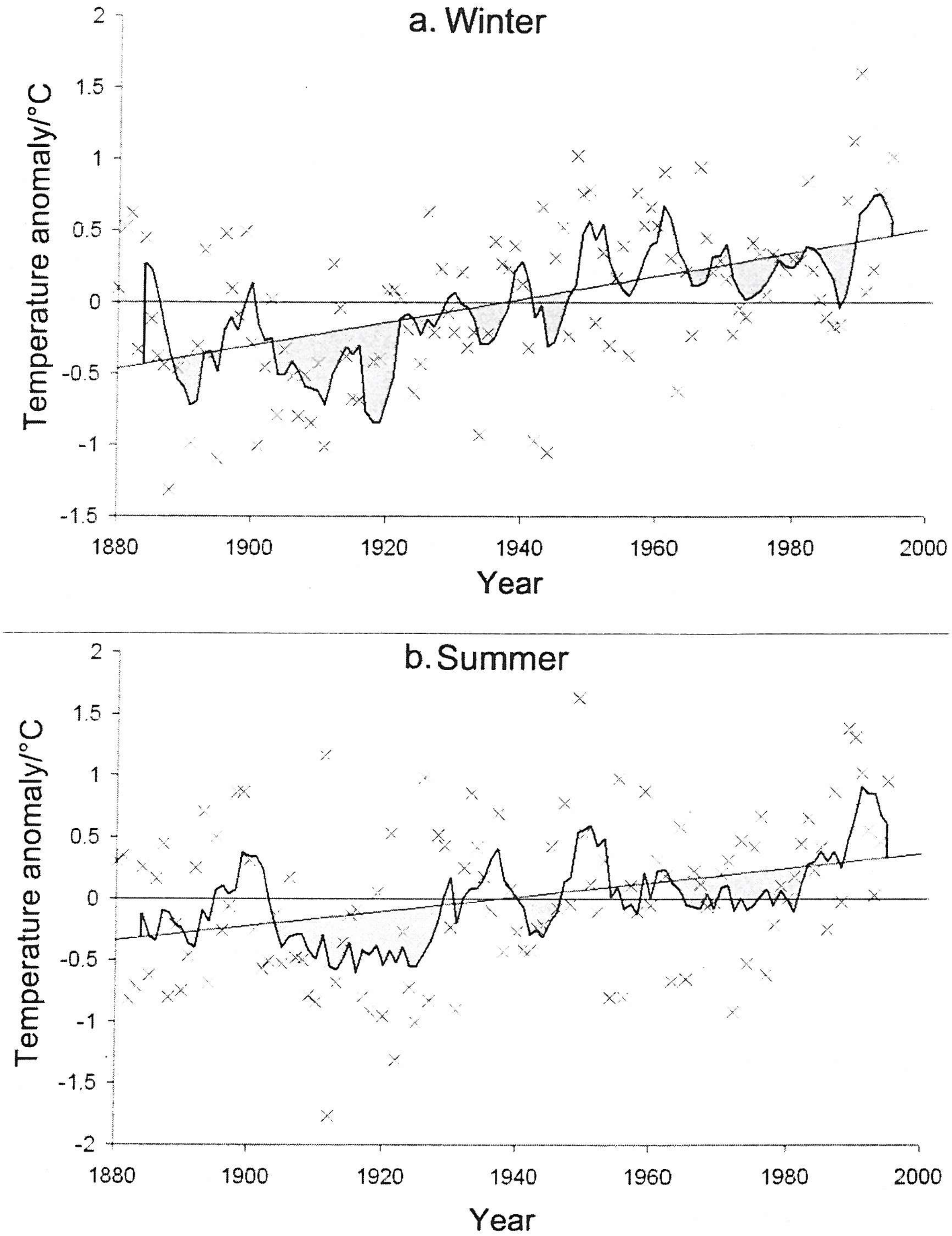


Figure 2.7. a. Winter (Jan–Mar) and b. summer (July–Sept) temperature anomalies for 1880–1995, based on the GOSTA LandSST data set (JPL/BADC, 2003; see Table 2.1). Thick lines represent 5-year running means. Thin lines are regression lines significant at $p<0.001$. (Winter: $y = 0.0082 (x–1937.5)$; $R^2=0.226$; $F_{(1,114)}=33.3$; $p<0.0001$. Summer: $y = 0.0059 (x–1937.5)$; $R^2=0.101$; $F_{(1,114)}=12.83$; $p=0.0005$.) Shading indicates cool and warm periods relative to the long-term trend.

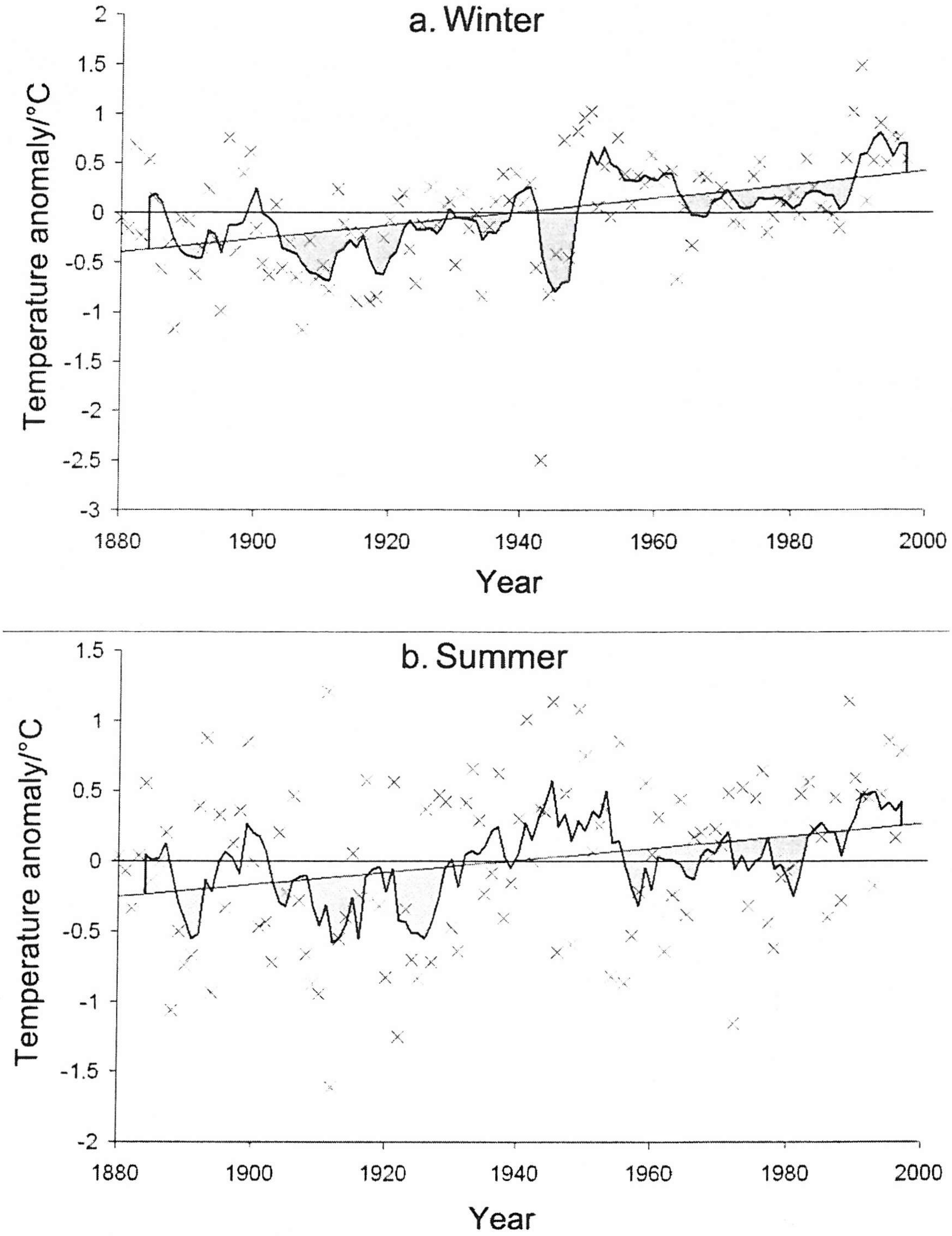


Figure 2.8. a. Winter (Jan–Mar) and b. summer (July–Sept) sea surface temperature anomalies for 1880–1997, based on the COADS data set (NOAA–CIRES, 2003; see Table 2.1). Black lines represent 5-year running means. Thin lines are regression lines significant at $p<0.01$. (Winter: $y = 0.0070\ (x - 1938.5)$; $R^2 = 0.1774$; $F_{(1,116)}=25.0$; $p<0.0001$. Summer: $y = 0.0043\ (x - 1938.5)$; $R^2 = 0.0657$; $F_{(1,115)}=8.1$, $p=0.005$). Shading indicates cool and warm periods relative to the long-term trend.

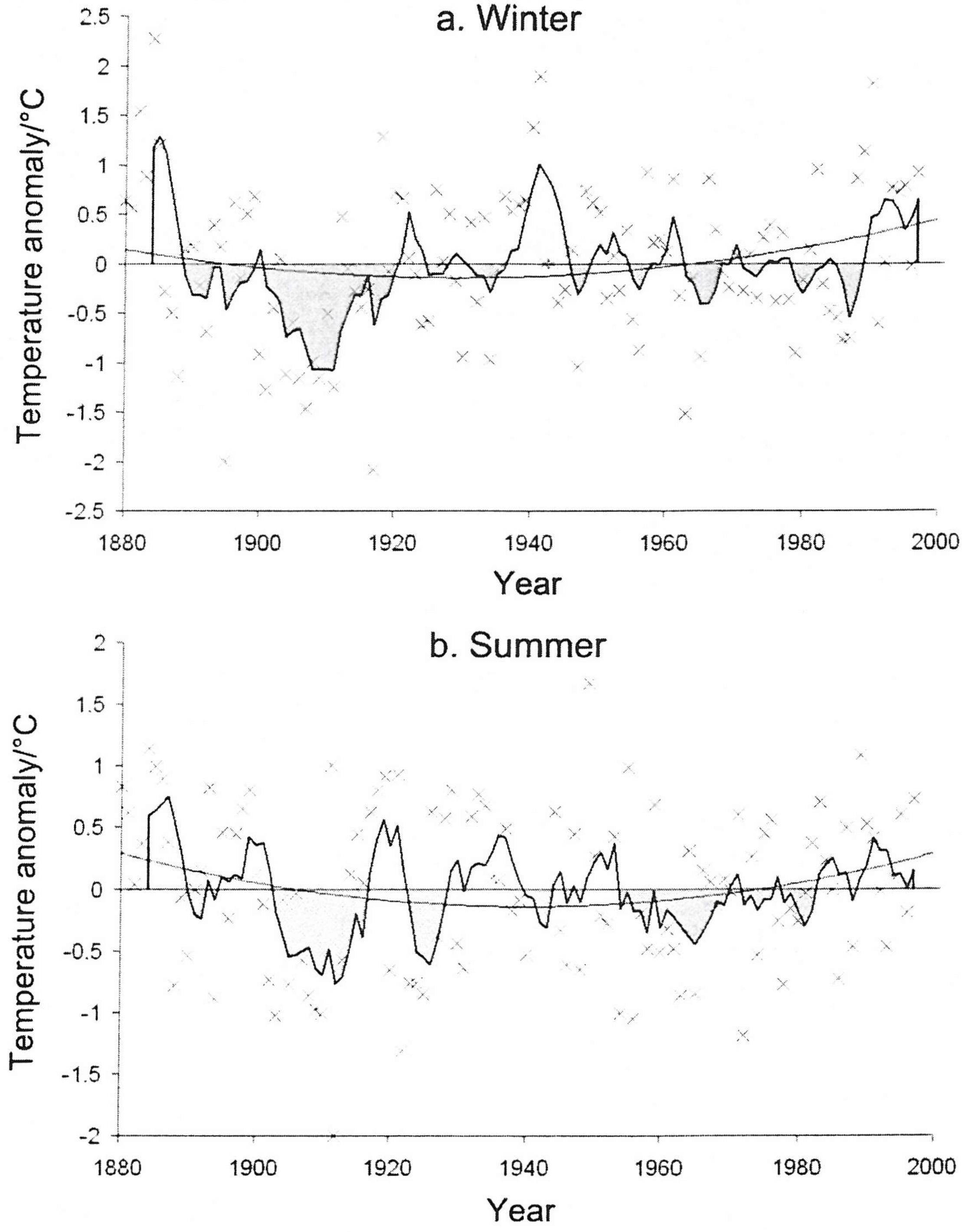
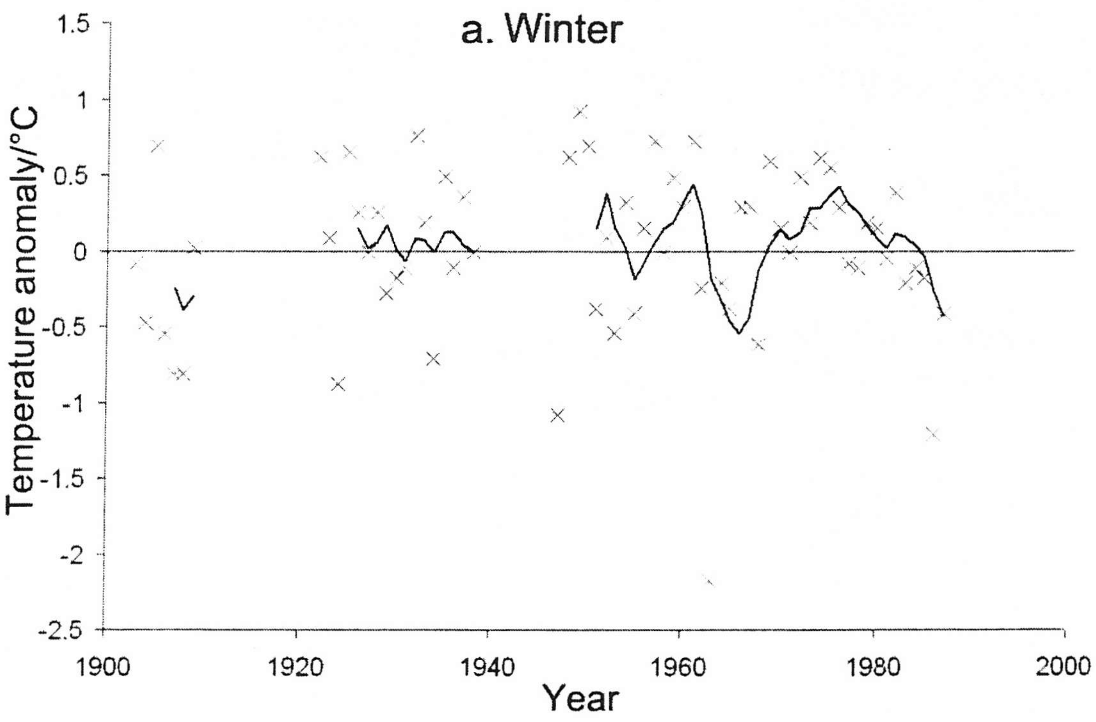


Figure 2.9. a. Winter (Jan–Mar) and b. summer (July–Sept) air temperature anomalies for 1880–1997, based on the COADS data set (NOAA–CIRES, 2003; see Table 2.1). Thick lines represent 5-year running means.
Thin curves are second-order polynomial regression curves significant at $p<0.05$.
(Winter: $y = 0.00012(x - 1929.58)^2 - 0.151$; $R^2 = 0.0342$; $F_{(1,113)} = 4.0$; $p = 0.048$.
Summer: $y = 0.00012(x - 1940.16)^2 - 0.143$; $R^2 = 0.0365$; $F_{(1,113)} = 4.3$; $p = 0.04$.)
Dark and light shading indicates cool and warm periods relative to the long-term mean.



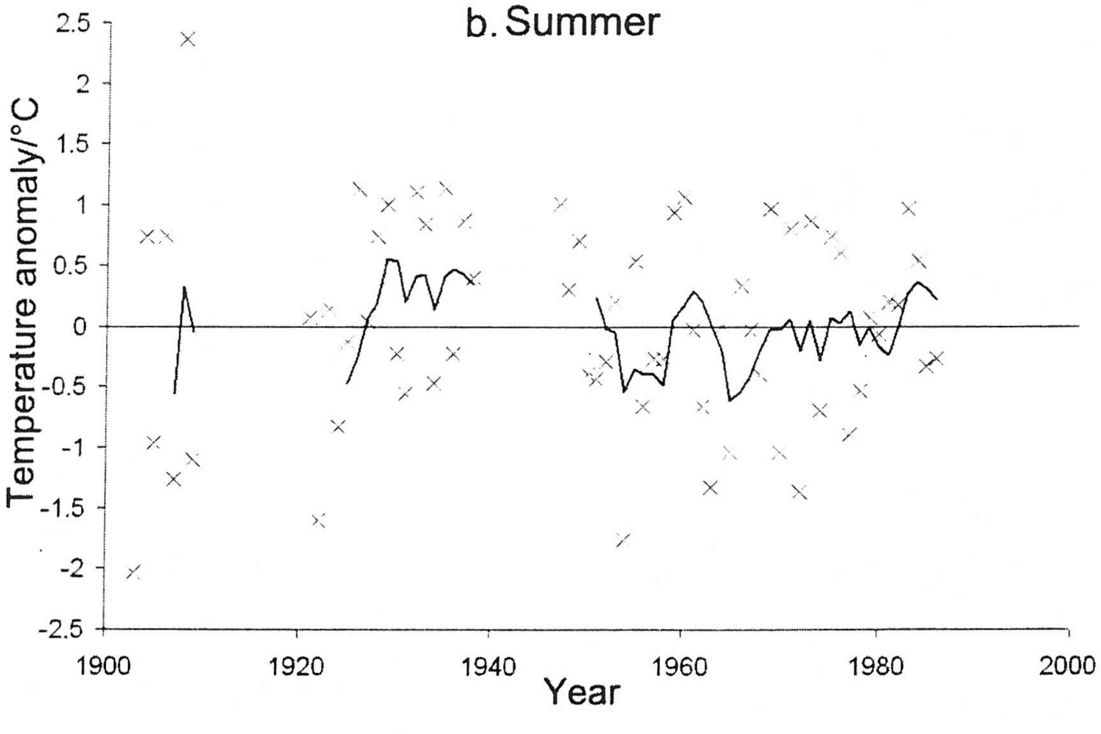


Figure 2.10. a. Winter (Jan–Mar) and b. summer (July–Sept) sea surface temperature anomalies for 1921–1987, based on data from the UK Marine Biological Association/Marine Environmental Change Network station E1 (see Table 2.1). Black lines represent 5-year running means.

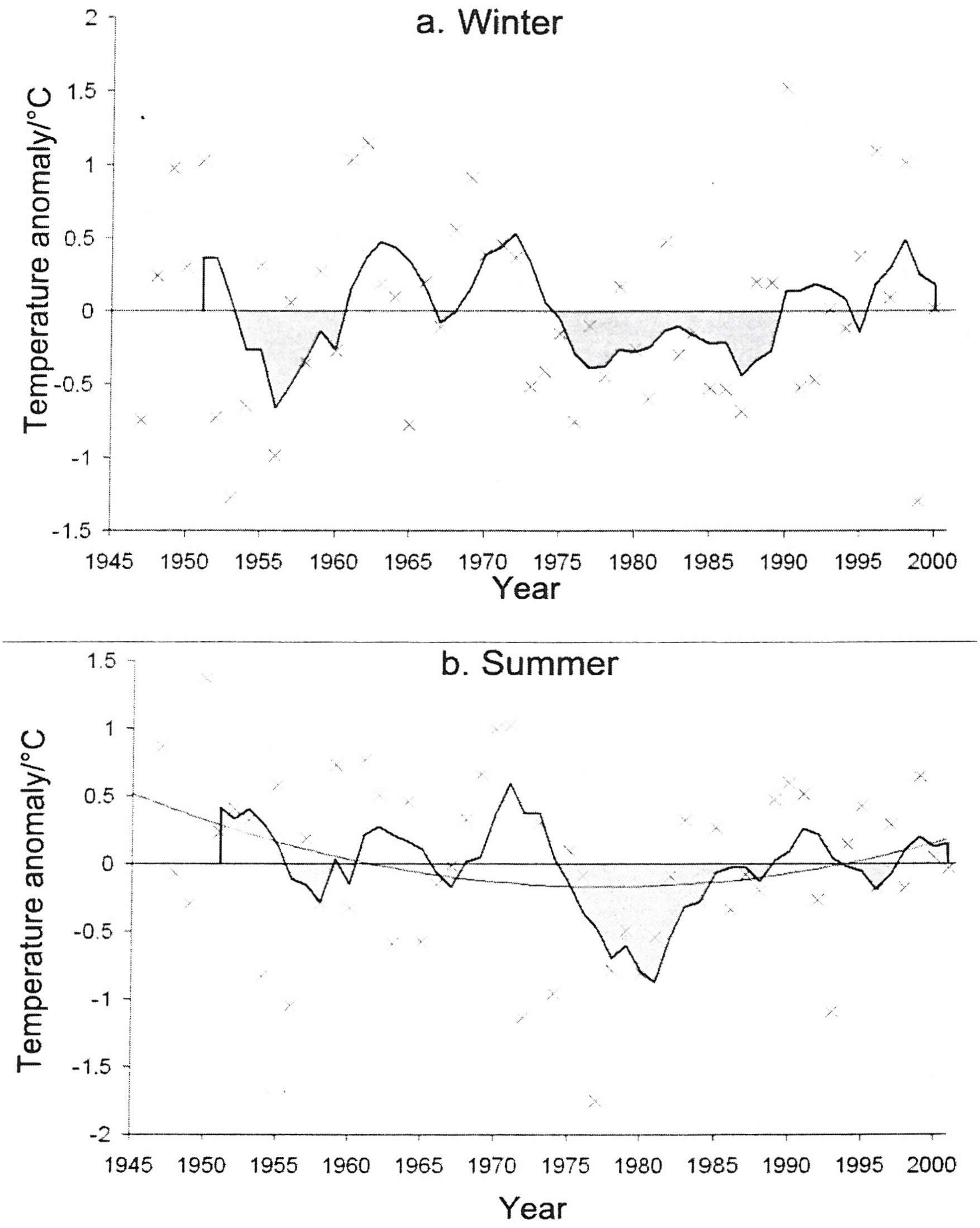


Figure 2.11. a. Winter (Jan–Mar) and b. summer (July–Sept) sea surface temperature anomalies for 1947–2001, based on data from San Sebastian Aquarium (Borja *et al.*, 2000; see Table 2.1). Black lines represent 5-year running means. Regression analysis in (a) gave no straight-line relationship ($r=0.01$, $F_{(1,53)}=0.006, p=0.94$). Thin curve in (b) is second-order polynomial regression curve significant at $p<0.05$ ($y = 0.00069 (x - 1977.07)^2 - 0.175$; $R^2 = 0.073$; $F_{(1,53)}=4.2$; $p=0.046$).
Dark and light shading indicates cool and warm periods relative to the long-term mean.

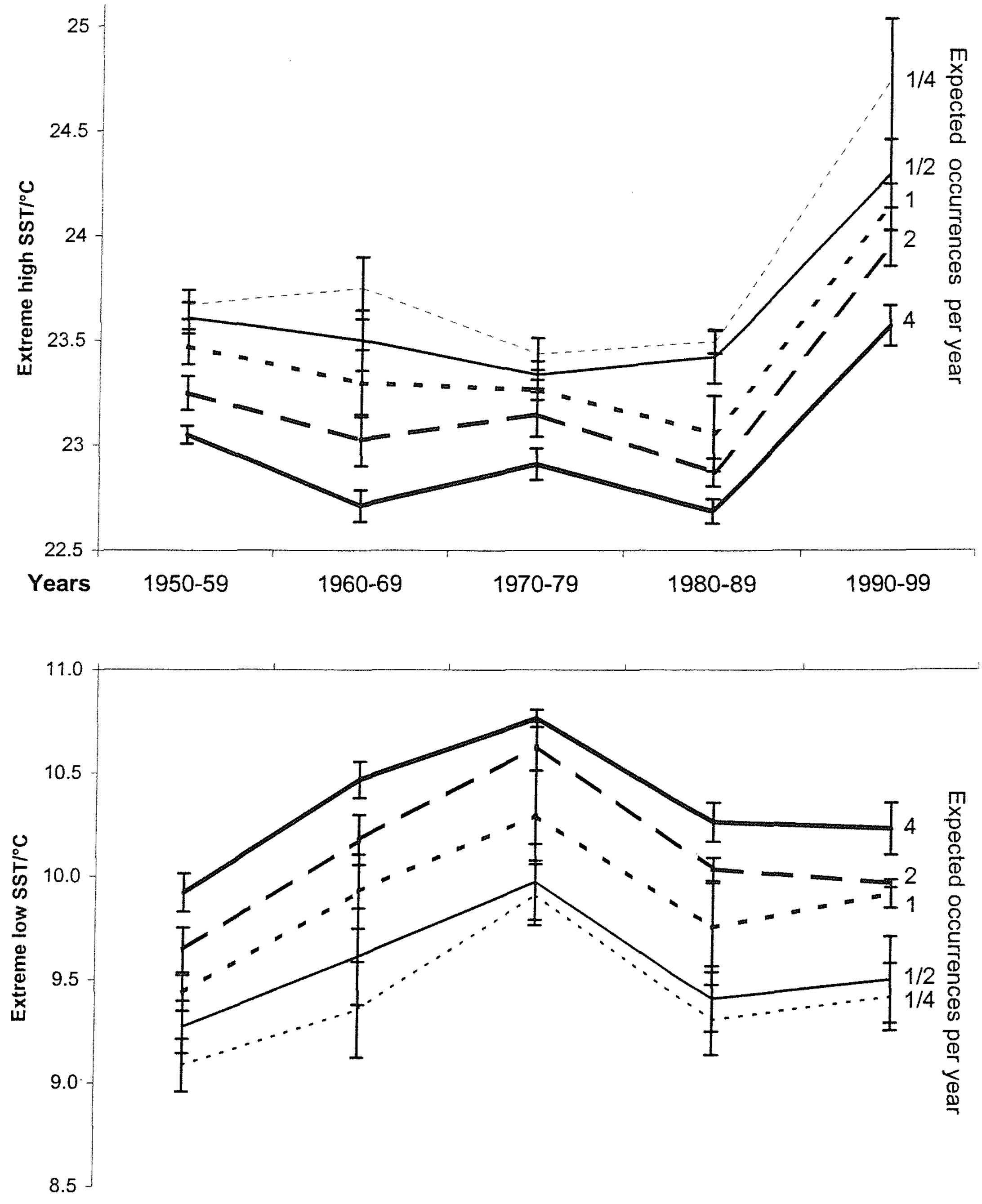


Figure 2.12. Expected frequency of extreme values of sea surface temperature in the inner Bay of Biscay during the second half of the twentieth century, by decade. Based on data from San Sebastian Aquarium (Borja *et al.*, 2000). Successive lines represent temperatures that are expected to occur 4 times a year, twice a year, once a year, once every 2 years and once every 4 years. Top graph represents maximum, and bottom graph minimum, temperatures. Error bars give standard errors determined by a bootstrap method (N=100).

2.4. Upwelling indices

2.4.1. Methods

Upwelling indices (Bakun, 1973; Johnson and Nelson, 1999) were calculated based on wind stress charts generated from the Comprehensive Ocean Atmosphere Data Set (COADS) using the website of the NOAA-CIRES Climate Diagnostics Centre (www.noaa.cdc.gov). There are two COADS series: one for 1800–1997 based on a 2° latitude x 2° longitude grid (which was used for the period 1901–1960), and one for 1960–1997 based on a 1°x1° grid. As COADS was the only long-term wind data set available, no comparisons with other data sets were made in this case.

Since coastal upwelling is the result of alongshore winds, it is necessary to calculate the component of wind stress (defined as the square of wind speed) along the coastline. Conveniently, the north coast of Spain runs almost due east-west, while the west coast of Spain and Portugal runs almost due north-south. This means that the net upwelling intensity can be estimated by considering, respectively, the easterly and northerly component of wind stress. These components are available in COADS and can be charted individually. Charts were drawn of u-wind stress (the easterly component) for the north coast, and v-wind stress (the northerly component) for the west coast, averaged from April to September for each year from 1901 to 1997. Prior to 1901 there are too many missing data to allow the index to be calculated. Example charts for the years 1994–1997 are shown in Figure 2.12 (for the west coast) and Figure 2.13 (for the north coast). The charts were used to plot time series of net upwelling index (alongshore wind stress) at six locations: on the west coast at 41°N (15km S of Porto in Portugal) and 43°N (15km N of Cabo Fisterra in Galicia, Spain), and on the north coast at 8°W (10km W of Cabo Ortegal), 6°W (15km W of Cabo Peñas), 4°W (15km W of Santander) and 2°W (near San Sebastian). These last four locations are in the four Spanish regions that border the north coast: respectively, Galicia, Asturias, Cantabria and the País Vasco.

Regression analysis was performed to identify any straight-line trends. To test whether upwelling was spatially correlated between these six locations, a correlation analysis was performed between each pair of locations.

It is important to note that the index that is being calculated here is mean net upwelling, not mean upwelling. Positive alongshore wind stress results in upwelling, leading to changes in sea surface temperatures, nutrient availability and other important environmental factors. Negative alongshore wind stress, on the other hand, does not substantially affect conditions on the rocky shore. Ideally, then, an upwelling index would sum the positive components of alongshore wind stress (on a suitable timescale, such as hourly) while discarding the negative components (Johnson and Nelson, 1999). Unfortunately, the COADS data do not permit this to be done, and consequently the index of mean net upwelling will inevitably underestimate the actual amount of upwelling. This is not a problem as long as the variance of alongshore wind stress is reasonably constant between years, because then high values of mean net upwelling will correspond to high values of mean upwelling. For the purposes of the present analysis this is assumed to be the case.

To see whether net upwelling has an effect on sea surface temperature, the correlation between net upwelling index at 2°W (near San Sebastian) and mean temperature at San Sebastian Aquarium for April–September of each year (Borja *et al.* 2000) was tested. This was the only long-term point source data set available to be tested.

2.4.2. Results

For each of the three locations in the north-west of the peninsula (Porto, Cabo Fisterra and Cabo Ortegal), a linear regression of net upwelling index against time indicated a rising trend in net upwelling throughout the 20th century ($p<0.001$). The correlation of net upwelling index against time gave no relationship at the other three locations: Cabo Peñas ($r=0.01$; $F_{(1,83)}=0.008$; $p=0.93$), Santander ($r=-0.06$; $F_{(1,82)}=0.32$; $p=0.57$), or San Sebastian ($r=-0.10$; $F_{(1,52)}=0.48$; $p=0.49$).

Table 2.3, which gives the result of the correlation matrix between each pair of locations, shows that the different locations are grouped geographically: each location shows a correlation ($p<0.000067$) with its geographical neighbour(s). All the locations except San Sebastian also show a correlation ($p<0.0033$) with their next-but-one neighbour(s). The distance between sites is approximately 150 km. Critical probability values were corrected for the number of tests performed (15).

There was a positive correlation ($p<0.05$) between upwelling index at 2°W (near San Sebastian) and mean temperature for April–September at San Sebastian Aquarium. ($r = 0.313$; $F_{(1,39)} = 4.24$; $p = 0.046$) The effect of upwelling on temperature should be negative, not positive. The result does not indicate that sufficient upwelling occurs in the inner Bay of Biscay to reduce sea temperatures.

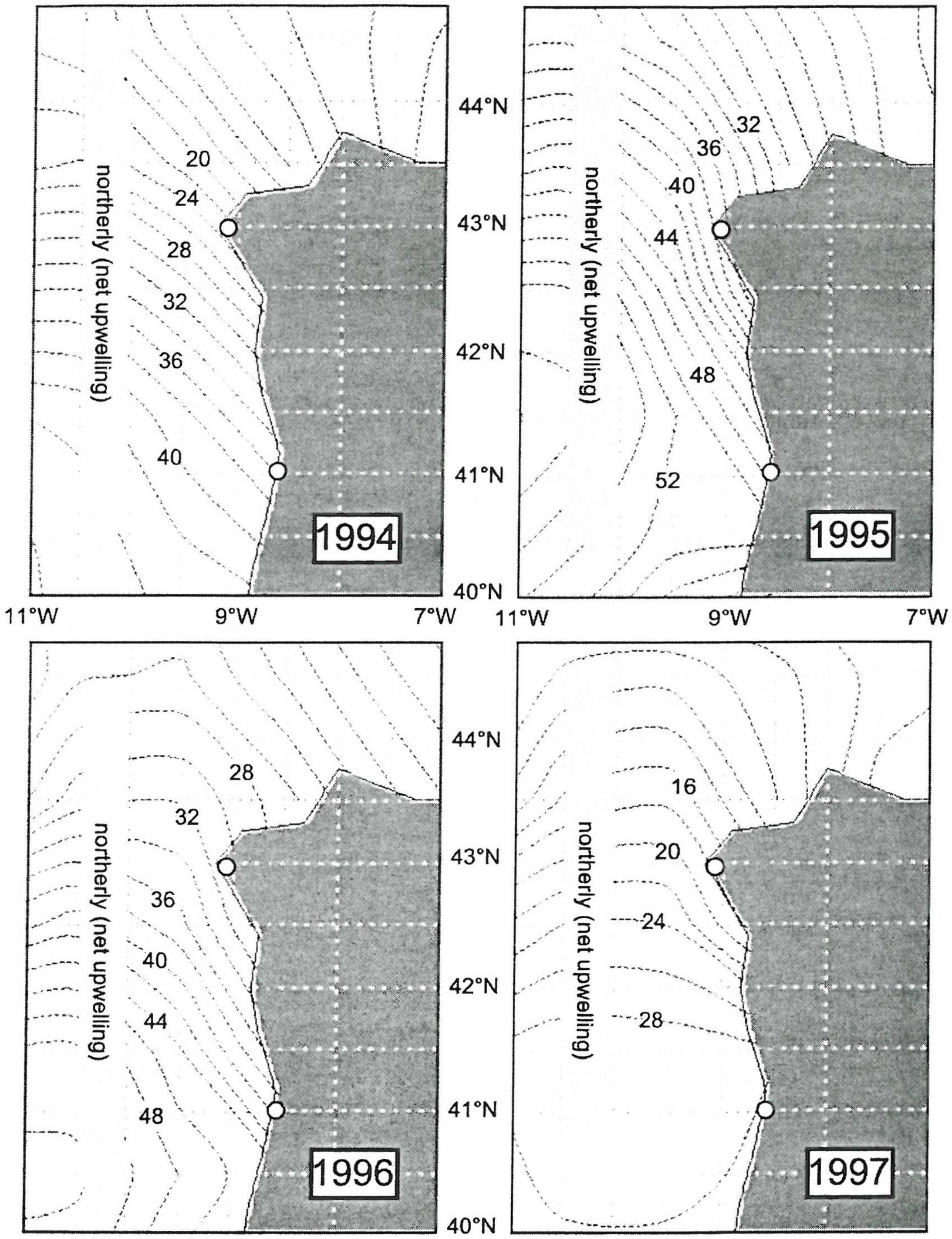


Figure 2.12. Examples of charts used to derive upwelling indices. Charts show northerly component of mean wind stress, in m^2s^{-2}, for April–September of each year 1994–1997, for the west coast of Spain and northern Portugal. Positive values indicate northerly winds and net upwelling. Circles represent points for which time series were plotted: 43°N (near Cabo Fisterra) and 41°N (near Porto): see Figure 2.14(a–b). Charts based on COADS data (NOAA-CIRES Climate Diagnostics Centre, 2003).

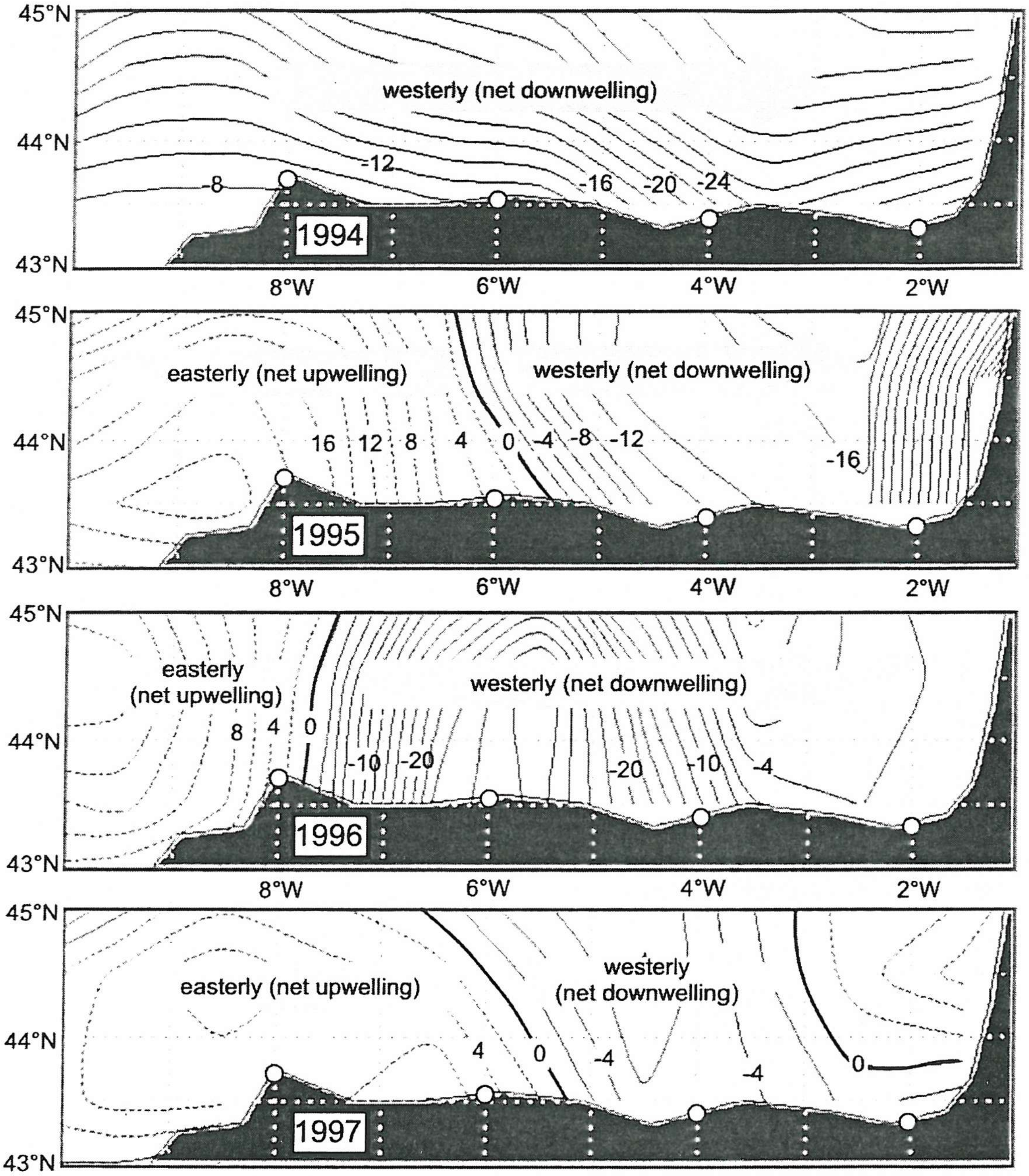


Figure 2.13. Examples of charts used to derive upwelling indices. Charts show easterly component of mean wind stress, in m^2s^{-2}, for April–September of each year 1994–1997, for the north coast of Spain. Positive values indicate easterly winds and net upwelling. Negative values indicate westerly winds and net downwelling. Circles represent points for which time series were plotted: 8°W (near Cabo Ortegal), 6°W (near Cabo Peñas), 4°W (near Santander), and 2°W (near San Sebastian): see Figure 2.14(c–f). Charts based on COADS data (NOAA-CIRES Climate Diagnostics Centre, 2003).

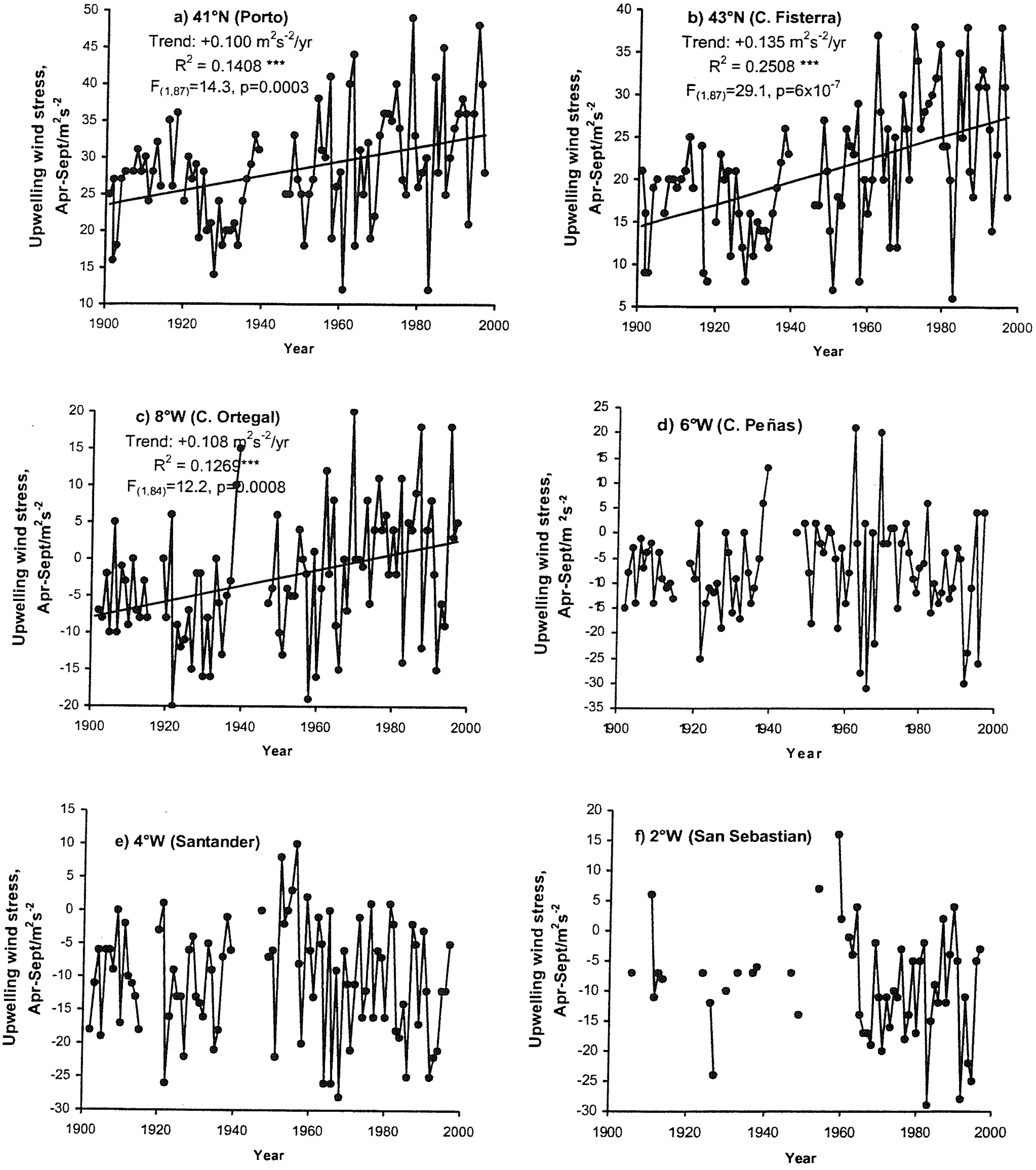

a) 41°N (Porto)
Trend: +0.100 m²s⁻²/yr
R² = 0.1408 ***
F(1,87)=14.3, p=0.0003
b) 43°N (C. Fisterra)
Trend: +0.135 m²s⁻²/yr
R² = 0.2508 ***
F(1,87)=29.1, p=6x10⁻⁷
c) 8°W (C. Ortegal)
Trend: +0.108 m²s⁻²/yr
R² = 0.1269***
F(1,84)=12.2, p=0.0008
d) 6°W (C. Peñas)
e) 4°W (Santander)
f) 2°W (San Sebastian)
Upwelling wind stress, Apr-Sept/m²s⁻²
Year
1900
1920
1940
1960
1980
2000

Figure 2.14 (prev. page). Net upwelling index (mean alongshore wind stress), in m^2s^{-2}, for April–September of each year 1901–1997, calculated for one location near Porto in Portugal (41°N 8.65°W) and five locations in northern Spain: near Cabo Fisterra, Galicia (43°N 9.3°W); near Cabo Ortegal, Galicia (8°W 43.7°N); near Cabo Peñas, Asturias (6°W 43.6°N); near Santander, Cantabria (4°W 43.4°N); and near San Sebastian, Pais Vasco (2°W 43.3°N). Regression lines are fitted by the least-squares method; *** indicates that the slope of the line is significantly different from zero ($p<0.001$). Based on COADS data (NOAA-CIRES Climate Diagnostics Centre, 2003).

Table 2.3. Pearson r-value correlation coefficients between upwelling indices for 1901–1997 for pairs of locations on the north and west coasts of Spain and Portugal. The locations are listed in geographical order from southwest (Porto) to northeast (San Sebastian). The significance of each correlation was tested. Critical probability values were corrected for the number of tests used (15). *** means significant at $p<0.000067$; ** means $p<0.00067$; * means $p<0.0033$; *n.s.* means $p\geq0.0033$.

					2°W **S.Sebastian**
				4°W **Santander**	0.599*** $F_{(1,84)}=29.2, p<0.00001$
			6°W **C. Peñas**	0.717*** $F_{(1,84)}=86.9, p<0.00001$	0.286 n.s. $F_{(1,54)}=4.6$, $p=0.04$
		8°W **C. Ortegal**	0.661*** $F_{(1,85)}=64.3, p<0.00001$	0.386** $F_{(1,84)}=14.3$, $p=0.0003$	0.346 n.s. $F_{(1,54)}=7.1$, $p=0.01$
	43°N **C. Fisterra**	0.619*** $F_{(1,83)}=50.3, p<0.00001$	0.365* $F_{(1,842}=12.3$, $p=0.0008$	0.179 n.s. $F_{(1,82)}=2.6$, $p=0.11$	0.136 n.s. $F_{(1,53)}=0.96$, $p=0.33$
41°N **Porto**	0.778*** $F_{(1,89)}=133, p<0.00001$	0.396** $F_{(1,83)}=15.0$, $p=0.0002$	0.230 n.s. $F_{(1,82)}=4.5$, $p=0.04$	0.133 n.s. $F_{(1,82)}=1.4$, $p=0.23$	0.006 n.s. $F_{(1,53)}=0.002$, $p=0.96$

2.5. Discussion

2.5.1. Spatial variation

The broad spatial patterns of distribution of warm- and cold-temperate rocky shore species in the Bay of Biscay and the surrounding region (Figure 1.2, based on Fischer-Piette, 1955a, 1958; Crisp and Fischer-Piette, 1959), have in the past been explained with reference to spatial patterns of sea surface temperature, particularly in summer (Fischer-Piette, 1955a; Ibañez, 1989, 1990). The patterns of spatial variation in climate shown in Figures 2.1 through 2.4 modify this picture somewhat.

Variations in cloud cover, associated with rainfall and humid conditions, could have a significant effect on rocky shore organisms whose survival is limited by extreme values of air temperature, insolation or elevated intensity of UV radiation (Beardall *et al.*, 1998). The relative lack of cloud cover on the west coast of France ("D" in Figure 2.4) indicates that cold-temperate species in this area are likely to be particularly susceptible to heat stress, especially in climate change scenarios where extreme high temperatures become more frequent. Similar considerations apply to the west coast of Galicia, northwest Spain. Here, despite the presence of persistent upwelling, values of cloud cover are relatively low and values of air temperature high (compared to sea temperature: "A" in Figure 2.2). This suggests that cold-temperate species, especially mid- and upper-shore species, are likely to suffer extra heat stress in this area, when compared with the coast of northeast Galicia and northwest Asturias ("C" in Figure 2.4).

Another notable feature of the latter area is the fact that both average wave height and the percentage of waves larger than 5m are lower along this section of coast (measured at 44°N, 6°W and 6.75°W) than at other points along the north coast of Spain (Figure 2.6). This section of the coast lies between Cabo Peñas (Asturias) and the headland of the north Galician coast, and may therefore be sheltered from wave action by these two promontories. The fact that relatively low wave exposure coincides with high cloud cover in this area indicates that it is likely to be unusually favourable to cold-temperate algae, relative to sea surface temperature in the area. In fact, the cold-temperate species *Fucus serratus*, which appears to respond sensitively to fluctuation in climate in northwest Spain (Fischer-Piette, 1955a; Arrontes, 1993, 2002), is more widespread and abundant on the north than the west coast of Galicia (Fischer-Piette, 1955a).

The decline in wave height along the north coast between 1972 and 1994, indicative of a reduction in storm activity, is likely to have significant effects on rocky shores, favouring brown algae, because of a reduction in wave-induced disturbance which is a main cause of damage to algal canopies (Southward, 1964; Lewis, 1964; Hawkins, 1981). Although IPCC climate models forecast an increase in stormy conditions in some areas as a result of climate change (Houghton *et al.*, 2001), this does not seem to have occurred in the region studied.

The variations in the time of low tide within the Bay of Biscay region (Figure 2.5) are probably not sufficient to give rise to major variations in the conditions experienced by rocky shore organisms.

2.5.2. Temporal variations in temperature

The two long-term data sets of sea surface temperature (GOSTA, which includes both sea and air temperatures, and COADS sea surface temperature) both show a warming trend since 1880 in the Bay of Biscay and surrounding region, with greater warming during winter than summer. The rates of warming detected, 0.68–0.82°C per century in winter and 0.43–0.59°C in summer, are close to the 0.4–0.8°C per century range for global mean warming during the 20th century estimated by the IPCC (Houghton *et al.*, 2001).

The differences between the GOSTA and COADS data sets are likely to be due to small systematic differences that especially affect the first half of the twentieth century, reflecting the fact that GOSTA includes corrections for systematic errors due to measuring methods which COADS does not (Cane *et al.*, 1997). Because the GOSTA data set is thus likely to be more accurate, and because it also combines air and sea temperatures to given an overall picture of climatic variation, this data set is used in Chapter 3 (§3.4) when calculating mean temperatures for the purpose of relating distribution of rocky shore species to climate at different times during the 20th century.

There are correlations between these data sets as well as with the San Sebastian Aquarium sea surface temperature data set (which began in 1947).

The data set show mostly similar decade-scale warm and cold periods, in both summer and winter. Similarities are especially notable between the GOSTA and COADS sea surface temperature data sets. Overall, the 1990s and the period 1945–60 were warm; the period up to 1930 was cold, and there was a cold period relative to the general upward trend between about 1960 and 1985. There was more variability, and less consistency between summer and winter patterns, in the COADS air temperature data set than in the sea surface temperature data sets. The San Sebastian Aquarium sea temperature data set broadly agrees with the GOSTA and COADS sea temperature data sets, showing high temperatures in the late 1940s and the 1990s, with a cold period between the early 1970s and 1990s. These decade-scale patterns in temperature are likely to lead to changes in the range and abundance of rocky shore species in the region.

The analysis of extreme temperatures at San Sebastian Aquarium shows that the 1990s were by far the hottest decade in terms of extreme temperatures since the 1950s, even though average summer temperatures at San Sebastian were actually warmer during the 1950s and the 1970s. This is likely to have an impact on rocky shore species, particularly those on the mid- to upper shore, which are more frequently emersed and which are liable to suffer mortality due to heat (Schonbeck and Norton, 1978, 1980; Hawkins and Hartnoll, 1985).

2.5.3. Temporal variation in upwelling

The most likely explanation for the positive correlation found between upwelling index and spring-summer sea temperature at San Sebastian is that easterly winds in the summer, instead of cooling the sea via upwelling, are warming it by transfer of heat from the continental land mass. In any case it does not support the hypothesis that upwelling is responsible for reducing sea temperatures in the inner Bay of Biscay. It may be that net upwelling indices in this area are not a true reflection of upwelling strength. Calculations of net upwelling index for the two sites on the west coast (Porto and Cabo Fisterra) probably correspond closely with the true value of upwelling index, because the prevailing winds along this coast during spring and summer are northerly (i.e. mean net upwelling index is positive). For the four locations on the north coast, on the other hand, prevailing alongshore winds are westerly, not easterly, as is shown by the negative mean values for net upwelling index. This means that true upwelling index has been substantially underestimated at all these locations. The third-order curves fitted to the data from Cabo Peñas and Santander both gave a slowly rising trend up until about 1970 followed by a falling trend. Given the lack of information about the variances of wind stress, however, it is not safe to conclude whether there is or is not a trend in upwelling over time at any of the locations studied on the north coast.

Most studies of upwelling, both of the Iberian Peninsula (Molina, 1972; Botas *et al.*, 1990; Nogueira *et al.*, 1997; Prego and Varela, 1998) and elsewhere (e.g. Johnson and Nelson, 1999), have been small-scale and short-term. The few studies spanning decades and hundreds of kilometres, show rising trends during the 20th century consistent with those observed in the northwest Iberian Peninsula in the present study. Upwelling indices calculated for 1949–1976 in four of the world's major upwelling zones, off Peru, California, North Africa and northwest Spain and Portugal (Bakun, 1973, 1990) show a rising trend, consistent with that observed in the present study.

2.5.4. Overview

As has previously been observed (e.g. Fischer-Piette, 1955; Ibañez, 1990), spatial variations in summer sea surface temperature in the Bay of Biscay region are likely to be a principal cause of the distribution of rocky shore species in the region (see §1.4). However, this chapter has highlighted other climatic factors, notably air temperature and cloud cover, which may well contribute to this distribution. Spatial variations in wave height are also likely to influence the distribution of rocky shore species. It has been seen that over most of the Bay of Biscay, spatial variations in the time of low tide are less than an hour, which is unlikely to lead to substantial changes in the conditions experienced by rocky shore organisms.

The overall trend over the last half of the 20th century in the Bay of Biscay region has been one of rising air and sea temperatures, consistent in magnitude with estimates of global warming of 0.4–0.8°C over the 20th century (Houghton *et al.*, 2001). There has been more warming in winter than in summer. In some areas, especially the west and northwest coasts of the Iberian Peninsula, increased seasonal upwelling throughout the 20th century is likely to have caused local cooling. Cold-temperate rocky shore species, especially those living on the lower shore, are likely to show expansion in these areas. Changes in interactions between species, the supply of nutrients and the conditions affecting larval stages (Connolly and Roughgarden, 1998; Menge *et al.,* 1999; Sanford, 1999, 2002a,b; see also Chapter 1) may also have profound effects on rocky shore communities in areas of enhanced upwelling. Differences in conditions between lower and upper shore and between emersion and immersion may also be enhanced in these areas. Also, the overall warming trend has been interrupted by colder periods, such as the 1920s–30s and the 1970s–80s; cold-temperate species are likely to have expanded in these periods.

Local sea temperatures on the Basque coast, inner Bay of Biscay, have also diverged from the general pattern of regional warming. Winter temperatures show no consistent trends, while summer temperatures show cooling from 1950 to 1977 and warming thereafter. Extreme summer temperatures have been much higher in the 1990s than in previous decades. Since summer temperatures appear to be limiting for many cold-water species in the inner Bay of Biscay, the net effect is likely to have been a marked retreat of these species during the 1990s. Whether this has in fact taken place is considered in the next chapter.

Thus global and regional trends in climatic conditions and their effects on rocky shore communities may be modified considerably by local variations, as has been observed in rocky shore communities in other parts of the world (Helmuth *et al.*, 2002; Denny and Paine, 1998). The next chapter will discuss the changes in rocky shore communities that have taken place over the course of the 20th century and how these changes may be related to regional variations in climate.

Chapter 3: Climate and rocky shore communities in the Bay of Biscay, 1895–2001

3.1. Introduction

This chapter investigates spatial patterns and temporal variations in the distribution of selected rocky shore species in the Bay of Biscay. This is an area where there are relatively steep spatial gradients in temperature and other climatic factors (see §1.4 and §2.2), and where considerable changes in climate have take place during the 20th century (see §2.3–§2.5). This chapter integrates published and unpublished data collected since 1895 with data from new surveys carried out in 2000–01 in order to evaluate how the distribution of rocky shore species has responded to these variations in climate.

3.1.1. Studying long-term variation on rocky shores

The main ecological processes affecting the spatial distribution of rocky shore species, and the effects of climate on these processes, have already been reviewed in Chapter 1. Ecologists have devoted a great deal of time to describing and explaining spatial patterns in species abundance in response to environmental gradients (vertical, horizontal and latitudinal). In contrast, there have been far fewer studies of long-term temporal variation – either using repeated surveys separated by time intervals or continuous time series – mainly because this type of study is so much more difficult to undertake. Relevant studies can be summarised briefly.

One of the few examples of a long continuous time series of data on populations of rocky shore organisms has been collected in south-west Britain since 1951 (Southward and Crisp, 1952, 1954; Southward, 1967, 1980, 1991; Southward *et al.*, 1995). Southward and co-workers have found that the abundances of three common rocky shore barnacles show correlations with sea temperature. *Chthamalus montagui* and *C. stellatus* are warm-water species that reach their northern limits in Britain, and show positive correlations with temperature. *Semibalanus balanoides*, a boreo-arctic barnacle species, shows a negative correlation. A relationship with temperature was also found in less extensive time series of the warm-water limpet species *Patella depressa* when compared with the total abundance of all limpets (Southward *et al.*, 1995; Hawkins, pers. comm.). In southern Britain and France, broad-scale studies of geographical distribution of rocky shore species made using semi-quantitative abundance scales (Crisp and Southward, 1958; Crisp and Fischer-Piette, 1959) have been used to provide a baseline for subsequent studies of climate-related change, such as the effects of an extremely cold winter (Crisp, 1964) and more recent responses to warming (Herbert *et al.*, 2003).

In the Bay of Biscay, Fischer-Piette (1957c) and Fischer-Piette and Dupérier (1966) investigated changes in species distribution in the late 1940s, 1950s and 1960s, and related them with climate in a descriptive, non-quantitative way. The methods used can, however, be crucial to the success of long-term studies: a repeat study of communities in a Danish estuary after an interval of 50 years (Middelboe and Sand-Jensen, 2000) found significant changes using quantitative methods which would not have been detected with non-quantitative methods alone.

Foster *et al.* (1988) review studies of fluctuations over time in rocky shore communities in central and northern California. They emphasize that most such studies are related to specific events which provide a pretext for a focused study lasting a few years: examples include pollution (Widdowson, 1971; Harris, 1983), introduction of exotic species (DeWreede, 1983) or extreme weather events (e.g. winter storms in 1982–83: PGE, 1984; El Niño: Dayton and Tegner, 1991). These studies are thus of limited use in monitoring long-term change.

In the absence of long time series, it is only possible to compare a few points in time, which can lead to difficulties in interpreting the results. A study of this type in central California (Sagarin *et al.*, 1999) repeated, between 1993 and 1996, a survey of abundance of intertidal organisms in fixed quadrats at a single site originally carried out between 1931 and 1933. The change in quantitative abundances of species at this site was found to be correlated with the extent of the geographical range of each species: most species classified as relatively "northern" declined, while those classified as relatively "southern" mostly increased. The authors concluded that this constituted evidence of an overall shift towards communities of a more southern character. However, the high variability of rocky shore communities in time and space means that comparisons between small numbers of sites and years cannot readily be extrapolated to large-scale, long-term trends (Denny and Paine, 1998; Underwood and Chapman, 2000; Thompson *et al.*, 2002).

3.1.2. Objectives

The overall aim of this chapter is to investigate spatial and temporal patterns of distribution of selected rocky shore species in the Bay of Biscay, with specific reference to climatic factors.

The specific objectives are as follows:

1. To review and synthesise, in a historical context, existing studies carried out since the 1890s of rocky shore communities in the Bay of Biscay, both those published in the scientific literature, in limited circulation reports, and unpublished material.
2. To describe and report the results of my broad-scale re-survey (during 2000–01) of the distribution of key rocky shore species in the Bay of Biscay, with the aim of establishing a baseline for studying subsequent variations in both space and time.
3. To present a comparative analysis of the results of this survey together with those of past studies so as to assess change over time.
4. To relate any changes observed to fluctuations in climatic conditions in the region during the 20th century, especially temperature, and to test whether significant temperature-related changes in species distribution can be detected.

3.2. Synthesis of studies of rocky shores in the Bay of Biscay, 1890–2001

The main questions this chapter seeks to answer are how the distribution and abundance of rocky shore species in the Bay of Biscay have varied since the 1890s when the first studies were made (Sauvageau, 1897; Dautzenberg, 1894; Fischer, 1899), and whether this variation can be related to temperature. I have attempted to review all relevant studies of distribution of rocky shore species in the area from Biarritz in southwest France (43.5N 1.5W) to Cabo Ortegal in northwest Spain (43.8N 7.9W). Most of the studies reviewed are in Spanish (some are in French); some are from unpublished reports, theses or journals not readily available outside Spain.

The first large-scale study of distribution of rocky shore species along the north coast of Spain was by Sauvageau (1897) on algae. Quantitative methods were not used, but distribution was assessed using descriptive methods. Faunistic studies of invertebrates during this period were restricted to a few locations, mainly in the French Basque country (Dautzenberg, 1894; Fischer, 1899; de Beauchamp, 1907). Descriptive methods continued to be used in later floristic studies such as that of Miranda (1931) on algae in central Asturias. Fischer-Piette (1955a) studied selected rocky shore taxa on the north coast of Spain using descriptive methods, and together with other researchers looked at selected species over wide areas: Fischer-Piette and Gaillard (1959) at *Patella* from the Basque coast to Morocco, and Fischer-Piette (1957a) at *Pelvetia canaliculata* from the English Channel to Portugal.

In the 1940s Fischer-Piette began to study spatial variation and change over time in species distribution along the north coast of Spain (Fischer-Piette, 1955b, 1956, 1957b, 1957c). He concluded that between 1900 and 1949 there had been a shift towards warm-temperate communities along the whole north coast, equivalent to a westward shift in species limits of some 300km. The trend from 1949 to 1957, on the other hand, was towards more cold-temperate communities, particularly in Galicia. Later studies of change over time concentrated on fucoid algae on the French and Spanish Basque coast (Fischer-Piette and Dupérier, 1960, 1961, 1963, 1965, 1966), where similar patterns of change over time were observed, with retreat of cold-temperate species from 1900 to 1949 and subsequent advance.

Semi-quantitative methods using formal abundance scales (Southward and Crisp, 1954b; Crisp and Southward, 1958) began to be employed around this time, in surveys such as that of Crisp and Fischer-Piette (1959) which studied rocky shore species along the French Atlantic coast.

Studies in the region since 1970 have tended to use more quantitative methods, but with a narrower focus. These more recent studies are typically oriented less towards building general understanding and more towards solving a specific problem. Hence they are not usually focussed on large-scale or long-term change and relationships with climate. Most studies have been of limited geographical extent and/or restricted to particular taxonomic groups, including intertidal fish (Ibañez and Miguel, 1990; Ibañez *et al.*, 1992); molluscs (Borja, 1987); *Saccorhiza polyschides* (Gorostiaga, 1986; Fernandez *et al.*, 1988; Borja and Gorostiaga, 1990); *Fucus serratus* (Arrontes, 1993, 2002); *Fucus vesiculosus* (Viejo and Arrontes, 1992). Nonetheless general surveys of parts of the coast have also been carried out (Anadon and Neill, 1981; Anadon, 1983). New methods of data analysis have been employed, such as multivariate analysis of species distribution, and "R/F ratios", defined as the ratio between the number of species of red and brown algae in an area (Ibañez, 1990). In general these studies have served to underline the general impression of species distribution that was already known in the late 19th century, but have contributed much less to understanding change over time, with a few exceptions such as the work of Arrontes (1993, 2002) on range shifts in *Fucus serratus*. Reviews by Ibañez and others (Ibañez, 1988, 1989, 1990; Fernandez *et al.*, 1988) have updated Fischer-Piette's studies of change over time on the Basque coast, concluding that the cooling trend that began around 1949 lasted until the 1980s. During the early 1980s the arrival of *Saccorhiza polyschides* on the Basque coast was seen as an indicator of unusually cool conditions (Gorostiaga, 1986; Fernandez *et al.*, 1988; Borja and Gorostiaga, 1990). This trend then reversed and warming began, leading to overall patterns of distribution in the 1990s similar to those of the 1950s.

On the whole, research on rocky shores in the area during 1890–2000 has been sporadic, with intensive work during certain years, followed by long gaps. More studies have looked at algae than at invertebrates. Few studies have been designed with the intention of looking at long-term change. To study change over time, it is therefore necessary to combine data from studies with different locations, aims and methods. Because of the dangers in comparing small geographical areas, it is also important to focus on those time periods during which there are data for an extensive area of coast, if necessary combining results from different studies carried out in the same or successive years. For the purposes of this chapter, analysis was limited to those years for which data are available for at least 200km of coast, in studies carried out no more than three years apart (summarised in Table 3.1).

Table 3.1. Studies of rocky shore communities in the Bay of Biscay carried out in selected years between 1890 and 2000. Years are when surveys were carried out, not publication date. Numbers of sites are approximate because the definition of a site varies from study to study; n/s means sites studied were not specified in the published work. First site and last site refer to the locations of the geographical extremes (northeast and southwest) at which data are available. Biota refers to the groups covered by the study (Invert. = invertebrates, Algae = macroalgae, *Fucus* = *Fucus* spp.).

Years	No. Sites	First site (NE)	Last site (SW)	Biota	References
1895	8	Biarritz (43.5N 1.5W)	La Coruña (43.3N 8.4W)	Algae	Sauvageau, 1897
1949	>25	S. Sebastian (43.3N 2.00W)	Galicia	Algae Invert.	Fischer-Piette, 1955a
1954–55	>100	Brittany	Hendaye (43.4N 1.7W)	Algae Invert.	Crisp and Fischer-Piette, 1959
1960–66	20	Biarritz (43.5N 1.5W)	Bermeo (43.4N 2.70W)	*Fucus*	Fischer-Piette and Dupérier, 1960, 1961, 1963, 1965, 1966; Hoek and Donze, 1966
1979–81	35	Cabo Higuer (43.4N 1.75W)	S. Cipriano (43.7N 7.5W)	Algae Invert.	Anadon *et al.*, 1979; Anadon and Neill, 1981; Angulo, 1979; Villar *et al.*, 1981; Gorostiaga, 1981
1994–96	17	Mundaka (43.4N 2.7W)	Figuera (43.6N 7W)	Algae Invert.	Gutiérrez Moran, 1994; Borja *et al.*, 1995, 1996

3.3. Survey of rocky shore communities in the Bay of Biscay, 2000–01

The survey of rocky shore communities was carried out in two phases: the first in spring 2000 and the second in spring and summer 2001. Surveys were carried out at a total of 36 sites on the north coast of Spain (21) and the west coast of France (15) (Figure 3.2, Table 2.3). Where possible, pairs of nearby sites were chosen, no more than about 10km apart, representing two different rocky shore habitats: the open coast (moderately to very exposed) and an unpolluted port or estuarine environment (very sheltered). In some areas, however, this was not possible because of a lack of sheltered habitat (or, rarely, a lack of exposed habitat). Sites were based on those used in previous surveys (specifically those of Fischer-Piette, 1955a, and Crisp and Fischer-Piette, 1959).All surveys were carried out as far as possible on areas of smooth, seaward-sloping rock so as to minimize the influence of topographical heterogeneity. Overhangs, crevices and rock pools greater than 2cm across were excluded from the survey. Slope of areas surveyed, however, varied from almost vertical to almost horizontal.

The first phase of the survey (April–June 2000) surveyed all macrobenthic species identifiable with the naked eye within a 10m^2 area, and estimated their abundance in upper, mid and lower shore zones, using the SACFOR scale (based on Hawkins and Jones, 1992, adapted from Crisp and Southward, 1958; see Appendix A, Table A.1.) The second phase (March–July 2001) covered more sites and a larger area at each site (approximately 100 m^2) but only included a limited range of species (see Table 3.2), chosen on the basis of their abundance and their value as indicators of climate. Search effort was standardised in this second phase by timing each survey of a site to 30 minutes. The SACFOR scale was again used. For algae, visual estimates of percentage cover were also made in this phase.

The survey design is evaluated and potential problems with it are discussed in §3.6.1. Raw data, locations and survey dates from both phases of the survey are given in Appendix A.

Table 3.2. Species surveyed during the second phase (March–July 2001) of the survey of rocky shores in the Bay of Biscay. (N) and (S) indicate species with relatively northern and southern distributions.

Phylum	Species
Phaeophyta	*Fucus spiralis* (N), *Fucus vesiculosus* (N), *Fucus serratus* (N) *Ascophyllum nodosum* (N), *Pelvetia canaliculata* (N), *Himanthalia elongata* (N), *Saccorhiza polyschides* (N), *Bifurcaria bifurcata* (S)
Mollusca	*Patella vulgata* (N), *Patella depressa* (S), *Patella rustica* (S) *Osilinus lineatus* (S), *Gibbula umbilicalis* (S), *Nucella lapillus* (N)

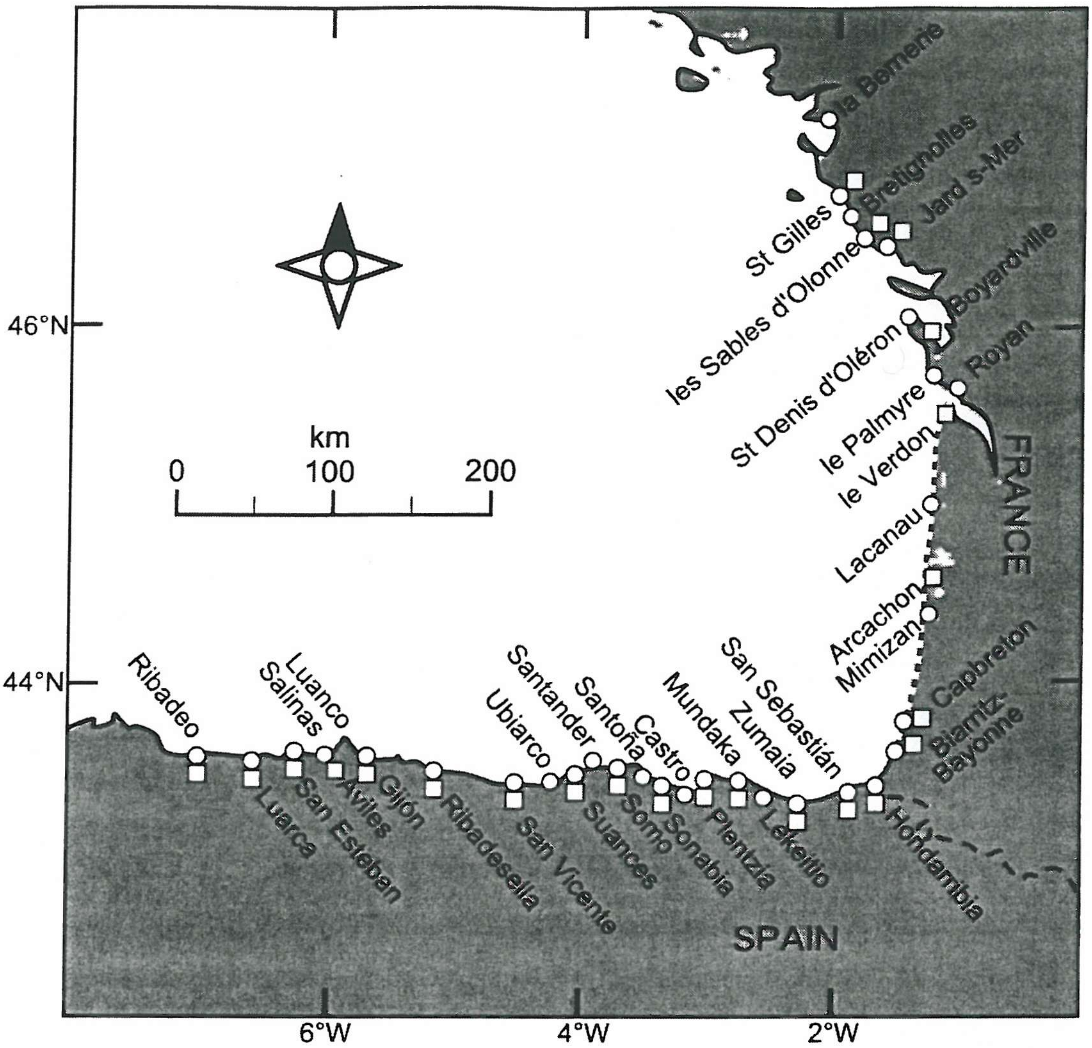


Figure 3.1. Rocky shore sites in the Bay of Biscay surveyed by the author in 2000–1. Sites on the open coast (moderately to very exposed) are represented by circles (○) and sites in estuaries/ports (very sheltered) by squares (☐). The dotted coastline indicates the area of predominantly sandy coast with little rocky shore habitat between Biarritz and the Gironde.

3.4. Synthesis of new surveys and past studies

The results of my 2000–01 surveys were compared with past studies since 1895 (Table 3.1), for eight species of algae and six species of invertebrates (Table 3.2).

None of the studies listed in Table 3.1 were designed with the aim of studying long-term change, with the exception of the work of Fischer-Piette and Dupérier (1960, 1961, 1963, 1965, 1966), which was limited to a few species and only covered the French Basque country. Four distinct time periods were compared: 1895 (French Basque country and Spain); 1949 (Spain) and 1954–55 (France); 1979–81 (Spain); and 1994–96 (Spain). From analysis of climatic data (Chapter 2; see also Table 3.3 below) it can be seen that 1895 and 1980 were cool periods while 1949–54 and the

1990s were warm periods. All the studies listed in Table 3.1 studied the distribution of macroalgae, but only a few, notably Fischer-Piette (1955a) and Crisp & Fischer-Piette (1959) also studied invertebrates.

Data on distribution of each species selected were obtained from the studies listed in Table 3.1. Sites were classified as either open coast (moderately to very exposed) or very sheltered (estuaries and ports), and for the purpose of making clear maps, data from nearby sites were combined. To compare studies with different methods, a simplified semi-quantitative scale was used, classifying species as abundant (25% or greater cover for algae, at least 10 individuals per square metre for invertebrates), present (less than 25% cover or 10 per square metre), or absent (none observed during the survey) at each site. The results are plotted in Figures 3.2 to 3.13.

In order to simplify comparison between studies with different methods, the analysis of species distribution was made principally on the basis of range limits. For cold-temperate species there potentially exist two range limits in the Bay of Biscay: a southern limit on the west coast of France, and an eastern limit on the north coast of Spain. Since many northern species extend their range further south and east in sheltered conditions (estuaries, ports) than in exposed conditions on the open coast, it is also possible to identify different limits in different types of habitat. Each species therefore potentially has a "limit in sheltered conditions" as well as a "limit on the open coast". The observed positions of the limit of each species in Spain and France in each type of habitat are plotted in Figures 3.2 to 3.9(f–g).

3.5. Results

This section presents and compares the results of the past studies listed in Table 3.1 together with those of my own surveys in 2000–01.

3.5.1. Algae: Phaeophyta

3.5.1.1. Fucus spiralis

Fucus spiralis (Figure 3.2) has the most southern distribution of the eight species of algae studied in this chapter. It extends as far south as Morocco and the Canaries (Crisp and Fischer-Piette, 1959). During the first half of the 20th century it was found throughout the Bay of Biscay, including the Basque coast (Fischer-Piette, 1955; Crisp and Fischer-Piette, 1959). In the 1950s and early 1960s considerable variations in the abundance of this species were observed on the French and Spanish Basque coast (Fischer-Piette and Dupérier, 1960, 1961, 1963, 1965, 1966), but it was never completely absent from any significant areas of the coast. In 1979–81 it was found all along the Spanish Basque coast (Angulo, 1979; Villar et al., 1981; Gorostiaga, 1981).

In my 2000–01 survey *F. spiralis* was not found at 9 sites (five open coast and four estuary/port) between its observed limits (Capbreton and Mundaka), a gap of 120km.

3.5.1.2. Fucus vesiculosus

Fucus vesiculosus (Figure 3.3) is a more boreal species than *F. spiralis*. It extends from the Arctic as far south as Morocco, but is restricted to estuaries in the southern part of its range (Fischer-Piette, 1955; Ladah *et al.*, 2003). In the Bay of Biscay, similarly, its range extends considerably further in estuaries and highly sheltered sites than on the open coast. In 1895 it was recorded in the estuary of Pasajes, east of San Sebastian (Sauvageau, 1897), but subsequent surveys have recorded its eastern limit in Spain to be in the Mundaka Estuary (Fischer-Piette, 1955; Angulo, 1979). In contrast, on the open coast it has been found no further east than San Vicente (Fischer-Piette, 1955) and Llanes (Anadon and Neill, 1981), approximately 130–160km to the west of Mundaka. In France, the same pattern is found. On the open coast *F. vesiculosus* did not extend beyond the Gironde in 1954–55, but in the same years it was actively reproducing in the Arcachon Basin, and was even present in estuaries on the French Basque coast (Crisp and Fischer-Piette, 1959), some 200km beyond its limit on the open coast.

My 2000–01 survey found the range of *F. vesiculosus* to be somewhat reduced compared with the 1950s and 1980s. In France the limit on the open coast (Royan) was unchanged compared with 1954–55 (Crisp and Fischer-Piette, 1959) but the species was not found on the French Basque coast, even in estuaries. In Spain, the limit in estuaries was still found at Mundaka, but the limit on the open coast was at Gijon, some 100km west of its 1949 observed limit at San Vicente (Fischer-Piette, 1955). Gutiérrez Moran (1994) found the limit of this species on the open coast at Cazonera, 25km to the west of Cabo Peñas, which represents a retreat of over 100km compared with 1949 or 1981; this corroborates my observation of a substantial retreat on the open coast.

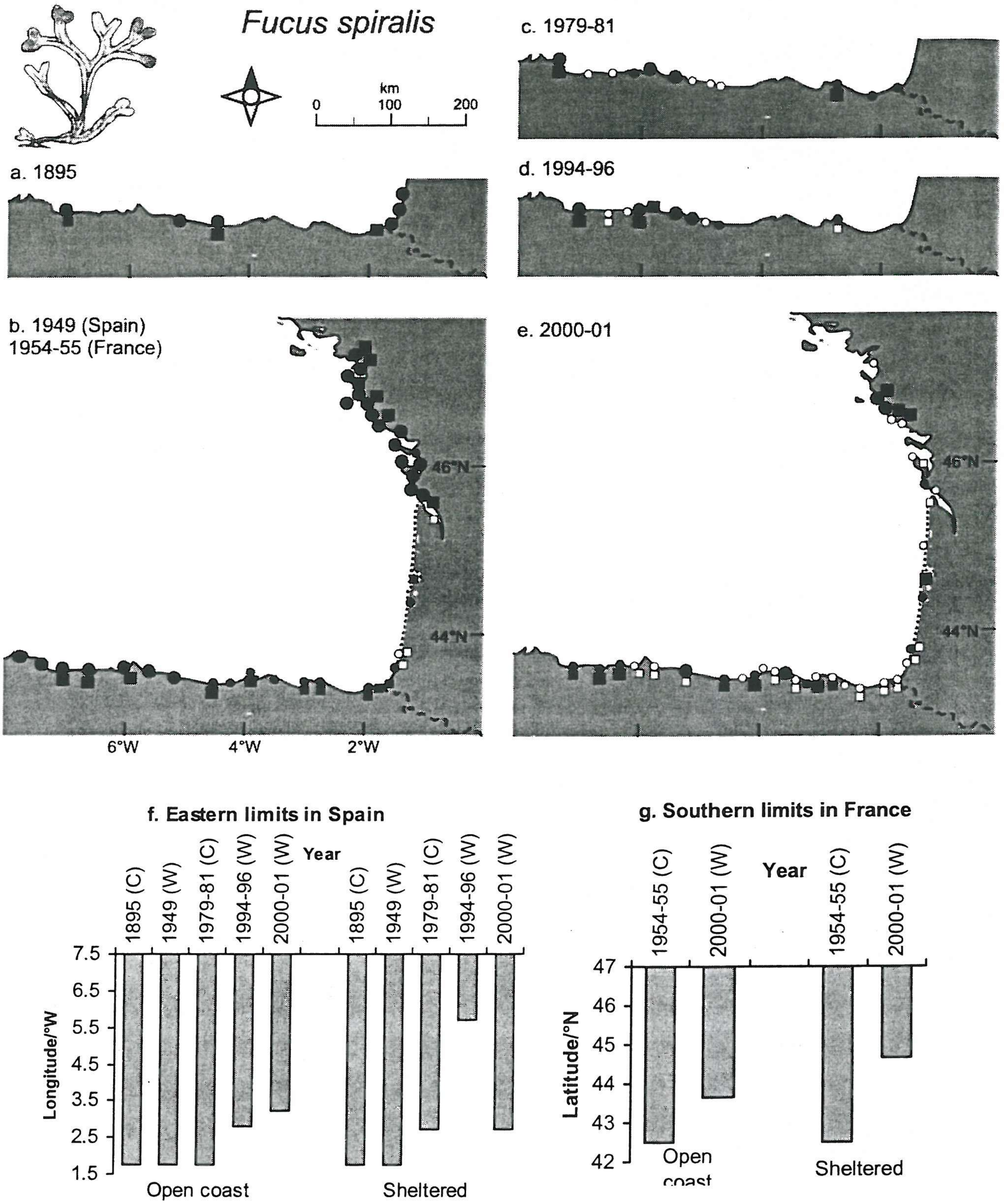


Figure 3.2. (a–e) Distribution of *Fucus spiralis* in the Bay of Biscay in 1895, 1949–55, 1979–81, 1994–96, and 2000–01. Symbols represent maximum cover at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <25% cover. Large closed (●■): ≥ 25% cover. Dotted coastline indicates area with little rocky shore habitat. (f–g) Positions of range limits in Spain and France in the same years. "C" and "W" indicate broadly cold and warm periods (see Table 3.4). See Table 3.1 for references. Illustration adapted from Fish and Fish, 1996.

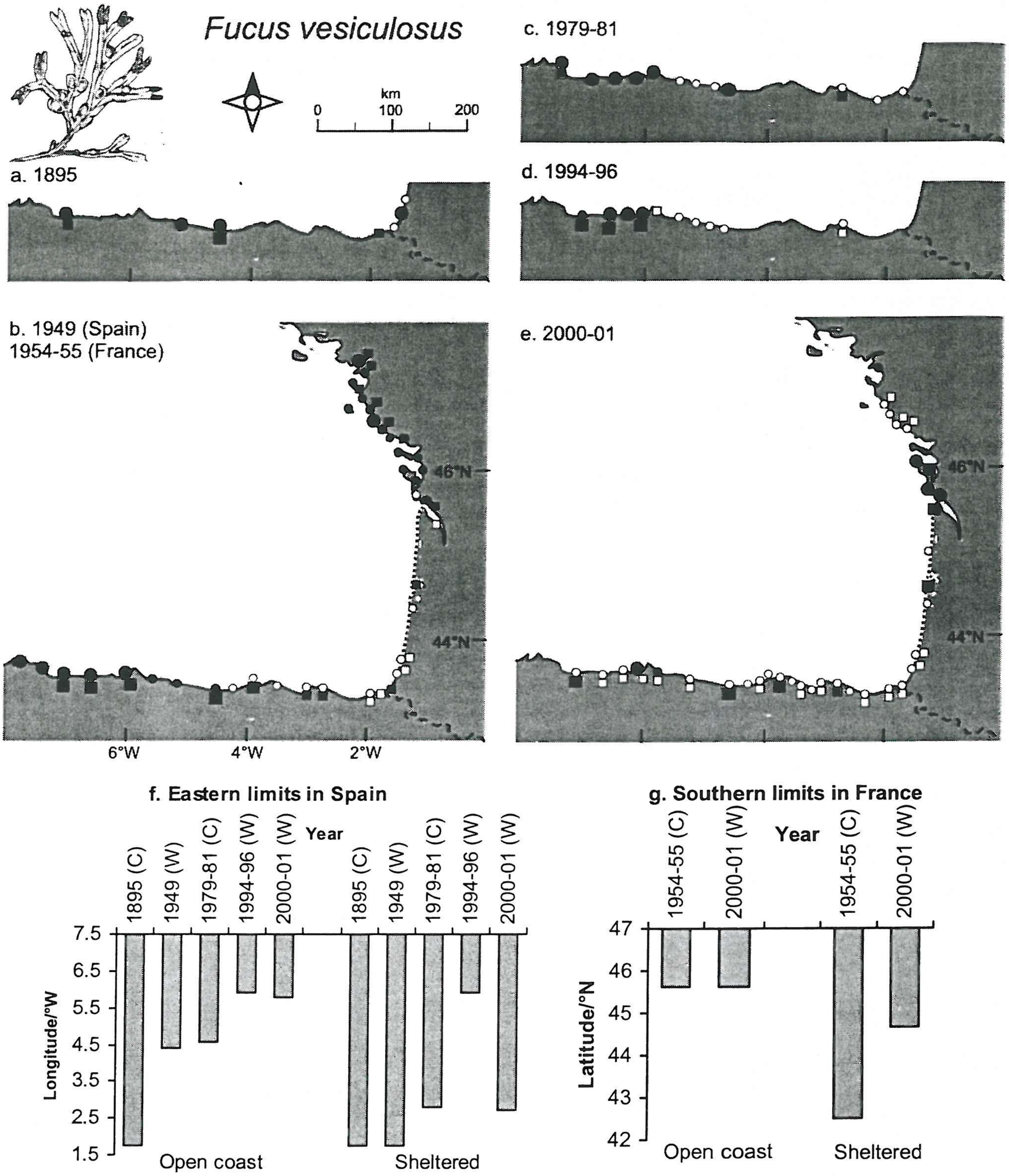


Figure 3.3. (a–e) Distribution of *Fucus vesiculosus* in the Bay of Biscay in 1895, 1949–55, 1979–81, 1994–96, and 2000–01. Symbols represent maximum cover at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <25% cover. Large closed (●■): ≥ 25% cover. Dotted coastline indicates area with little rocky shore habitat. (f–g) Positions of range limits in Spain and France in the same years. "C" and "W" indicate broadly cold and warm periods (see Table 3.4). See Table 3.1 for references. Illustration adapted from Fish and Fish, 1996.

3.5.1.3. Fucus serratus

Fucus serratus (Figure 3.4) is the most northern of the eight species algae studied in this chapter. Its southern limit is near the northern border of Portugal (Fischer-Piette, 1959). It has not been found on the French or Spanish Basque coast since studies began. As with *F. vesiculosus,* its range in the 1950s extended further east and south into the Bay of Biscay in estuaries than on the open coast (Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959). However, the difference between limits in the two habitats was not as great as with *F. vesiculosus*, and none of the studies carried out since then have found a clear difference between the species' limit in estuaries and on the open coast.

In France, the range of *F. serratus* on the open coast in 1954–55 extended as far as the Gironde; beyond this limit it was found in the Arcachon Basin (Crisp and Fischer-Piette, 1959). My 2000–01 surveys observed its limit on the open coast at Royan, close to its position in 1954–55, but it was not found in estuaries beyond this limit.

In Spain, *F. serratus* has retreated during the course of the 20th century. In 1895, it was found at San Vicente both in the estuary and on the open coast (Sauvageau, 1897); by 1949 its observed limit on the open coast had retreated 100km to Gijon. In the early 1980s its limit was observed in Cartavio, western Asturias, about another 90km further to the west (Anadon and Neill, 1981). Since then its range has extended back again as far as Novellana, an extension of about 40km (Arrontes, 1993, 2002).

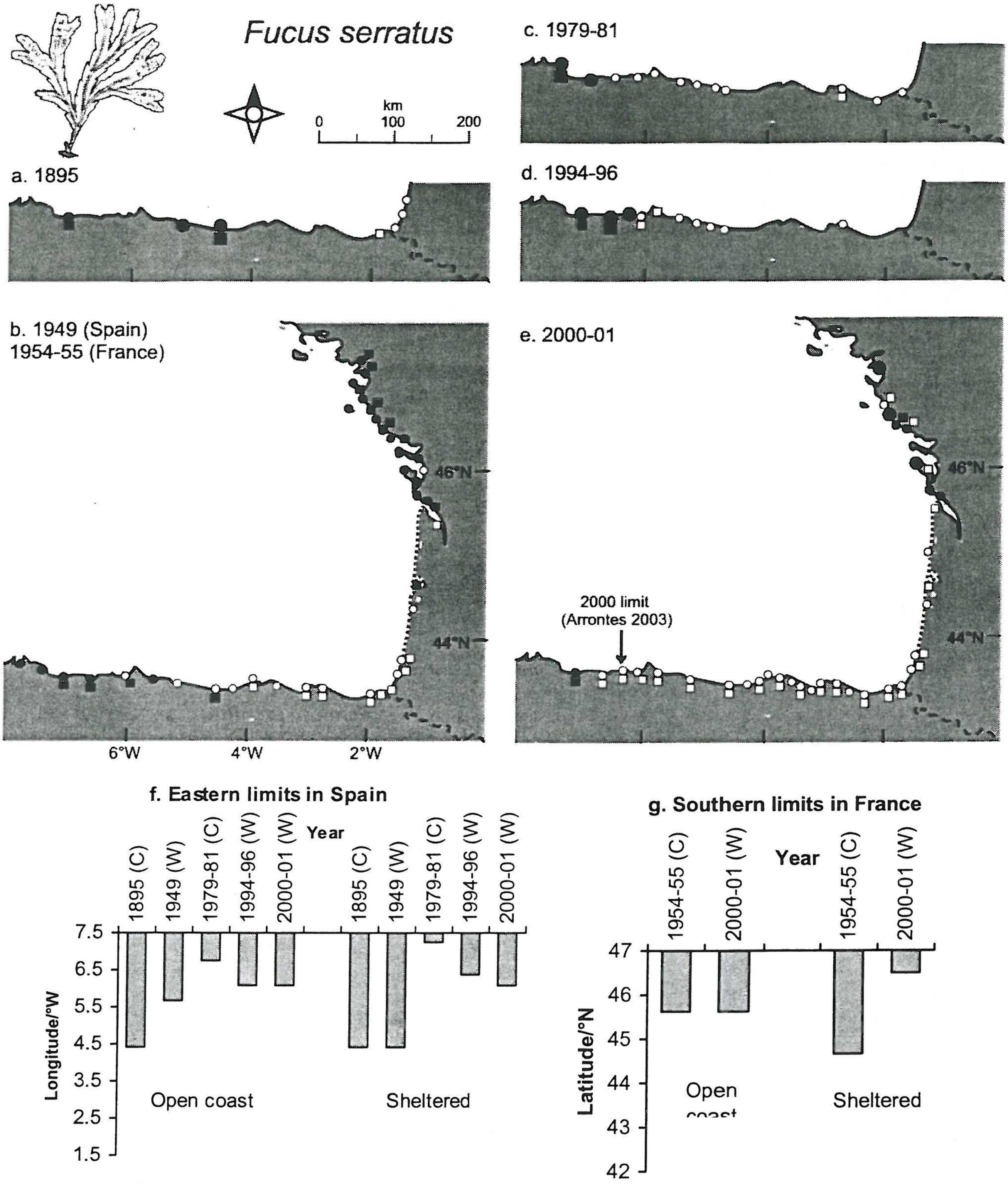


Figure 3.4. (a–e) Distribution of *Fucus serratus* in the Bay of Biscay in 1895, 1949–55, 1979–81, 1994–96, and 2000–01. Symbols represent maximum cover at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <25% cover. Large closed (●■): ≥ 25% cover. Dotted coastline indicates area with little rocky shore habitat. (f–g) Positions of range limits in Spain and France in the same years. "C" and "W" indicate broadly cold and warm periods (see Table 3.4). See Table 3.1 for references. Illustration adapted from Fish and Fish, 1996.

3.5.1.4. *Pelvetia canaliculata*

Pelvetia canaliculata (Figure 3.5) forms the uppermost band in the typical vertical zonation pattern of fucoid algae on cold-temperate rocky shores (Lewis, 1964; Raffaelli and Hawkins, 1999). It is the fucoid species that is most tolerant of desiccation stress (Dring and Brown, 1982; Pfetzing *et al.*, 2000). Nonetheless, the range of *P. canaliculata* does not extend as far south as that of *Fucus spiralis* or *F. vesiculosus*. Its southern limit in the first half of the 20th century was near Porto in northern Portugal (Fischer-Piette, 1957a). At the same time the species was present but extremely rare (Fischer-Piette, 1957a) over a large area of the inner Bay of Biscay, between the Île de Ré in France and Mundaka in the Spanish Basque country. The distribution map in Crisp and Fischer-Piette (1959) gives the species as being absent in the inner Bay of Biscay, with it southern limit in France at La Rochelle. However, the more detailed discussion by Fischer-Piette (1957a) clearly indicates that it was present in scattered locations throughout the Bay of Biscay, albeit exceedingly rare.

Records from Capbreton in 1992 (a few isolated plants under a bridge in a canalised entrance to a lagoon: Hawkins, pers. comm.) and San Sebastian in 2000–01 (my survey) indicate that it was still present in the inner Bay of Biscay at the end of the 20th century. Thus there appears to have been no change in the absolute limits of distribution of *P. canaliculata* in the Bay of Biscay during the 20th century. However, there have been marked changes in its abundance. In my 2000–01 survey it was not found at 47 sites and present at only 8 throughout the area studied. In mid-century it was present but not abundant at most sites in northern Spain and many in France north of the Gironde, and rare only in the area dominated by sandy beaches south of the Gironde (Fischer-Piette 1955a, 1957a; Crisp and Fischer-Piette, 1959). In contrast, Anadon and Neill (1981) found the species to be relatively abundant at Bañugues near Cabo Peñas in central Asturias, whereas in mid-century it was not abundant on the open coast until Galicia, some 100km further west (Fischer-Piette, 1955a, 1957a). Sauvageau (1895) found the species to be relatively abundant on the open coast at San Vicente, another 100km further east of the area studied by Anadon and Neill (1981). The relative abundance of *P. canaliculata* in the Bay of Biscay at different times in the 20th century, therefore, can be expressed as follows: $1895 \geq 1980 > 1950 > 2000$.

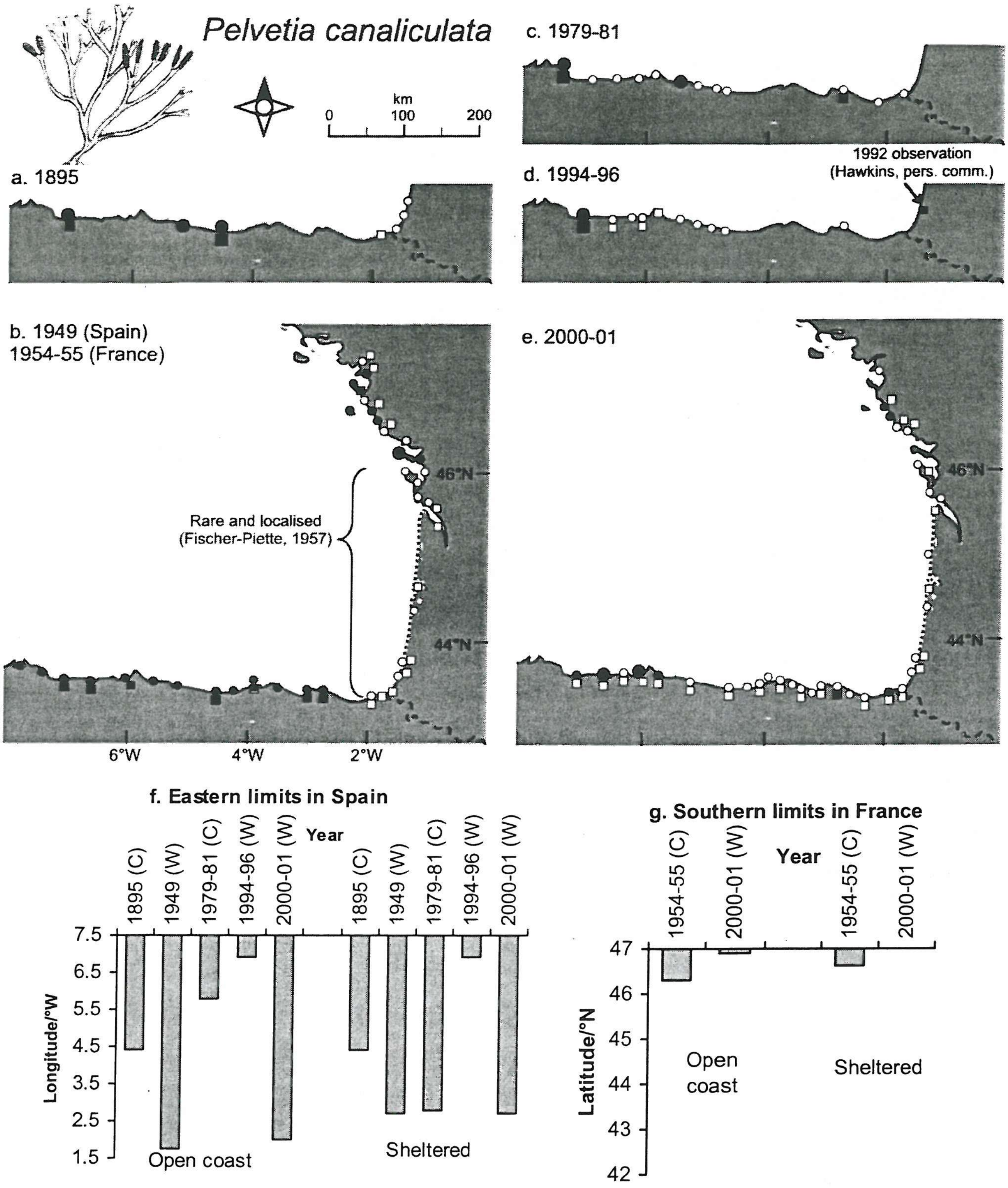


Figure 3.5. (a–e) Distribution of *Pelvetia canaliculata* in the Bay of Biscay in 1895, 1949–55, 1979–81, 1994–96, and 2000–01. Symbols represent maximum cover at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <25% cover. Large closed (●■): ≥ 25% cover. Dotted coastline indicates area with little rocky shore habitat. (f–g) Positions of range limits in Spain and France in the same years. "C" and "W" indicate broadly cold and warm periods (see Table 3.4). See Table 3.1 for references. Illustration adapted from Fish and Fish, 1996.

3.5.1.5. *Ascophyllum nodosum*

Ascophyllum nodosum (Figure 3.6) shows a strong preference for sheltered, often muddy, habitats. On the north coast of Spain it has been mainly restricted to estuaries throughout the 20th century (Sauvageau, 1897; Fischer-Piette, 1955a; Villar *et al.*, 1981; Anadon and Neill, 1981). In France it is found in sheltered areas on the open coast to the north of the Gironde (Crisp and Fischer-Piette, 1959). It is very long-lived (more than 20 years) and slow-growing (Aberg, 1992) and proliferates vegetatively. It is therefore likely to exhibit a time lag in responding to environmental changes when compared with faster-growing, less long-lived species.

Between 1955 (Crisp and Fischer-Piette, 1959) and 2000 (my survey) *A. nodosum* appears to have retreated northwards on the French west coast (north of the Gironde) by about 100km at both estuarine and open coast sites. However, this is based on observations at a few sites only; I did not visit the sheltered Anse de l'Aguillon between the Île d'Oléron and Jard-sur-Mer, where *A. nodosum* was present in 1954–55. I have also not observed whether the estuarine population at St Jean de Luz (French Basque coast) noted by Crisp and Fischer-Piette (1959) is still present.

There has been a small colony of *A. nodosum* in the Mundaka Estuary since at least 1949 (Fischer-Piette, 1955a; Villar *et al.*, 1981). This is the eastern limit of the species in Spain at the time of writing. In 1895 it was present in the estuary at Pasajes, some 60km further east, (Sauvageau 1897), but Fischer-Piette (1955a) did not find it there in 1949, and speculated that it had perhaps been killed by oil pollution.

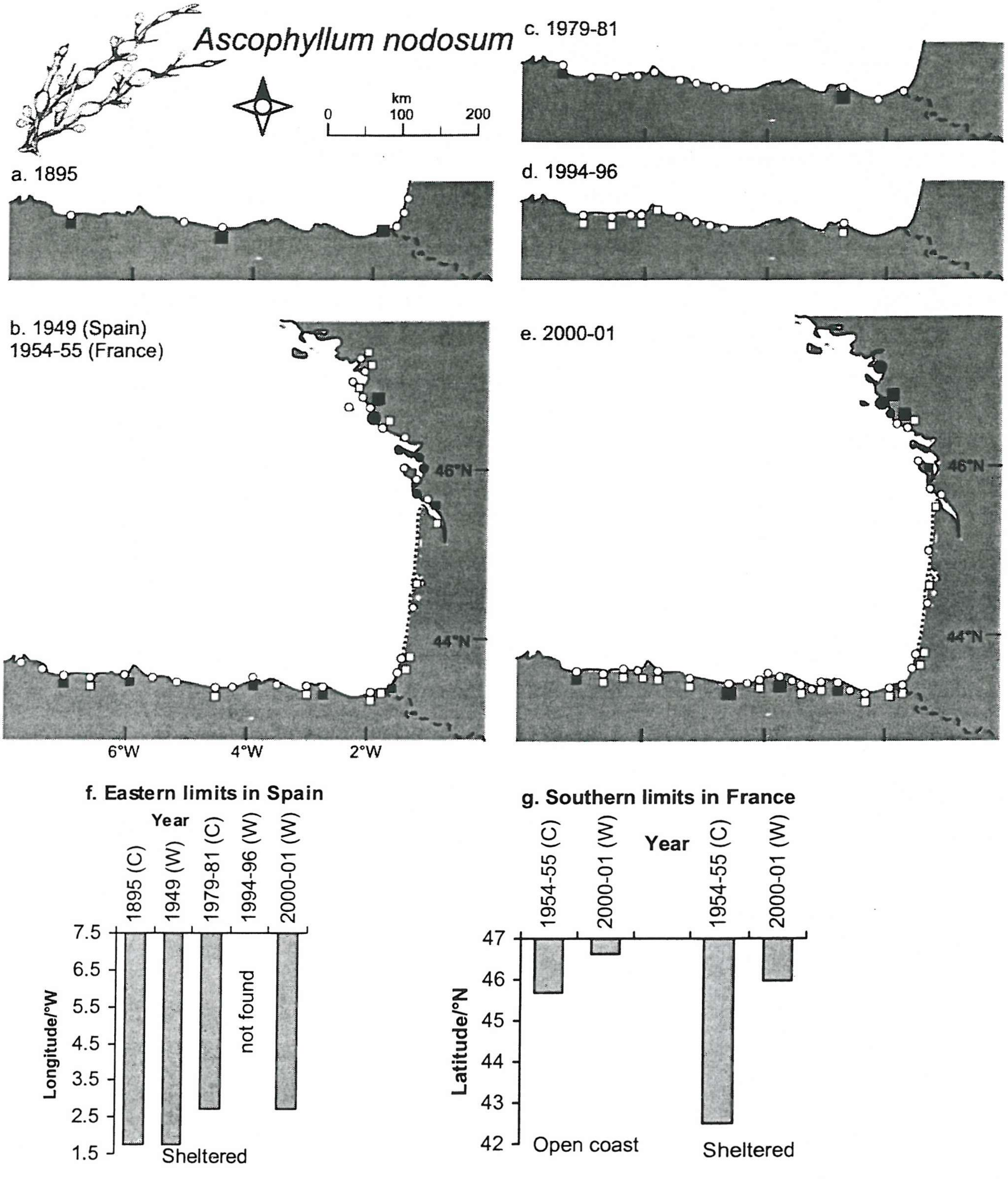


Figure 3.6. (a–e) Distribution of *Ascophyllum nodosum* in the Bay of Biscay in 1895, 1949–55, 1979–81, 1994–96, and 2000–01. Symbols represent maximum cover at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <25% cover. Large closed (●■): ≥ 25% cover. Dotted coastline indicates area with little rocky shore habitat. (f–g) Positions of range limits in Spain and France in the same years. "C" and "W" indicate broadly cold and warm periods (see Table 3.4). See Table 3.1 for references. Illustration adapted from Fish and Fish, 1996.

3.5.1.6. *Himanthalia elongata*

Himanthalia elongata (L.) Gray (Figure 3.7) is a cold-water, lower-shore fucoid alga whose range extends from the Arctic (including Iceland) to mid-Portugal (Fischer-Piette, 1951; Crisp and Fischer-Piette 1959; Santos, 2000). In 1895 it was abundant along the north coast of Spain as far as San Vicente, and occasional plants were found on the French Basque coast. These were thought to be the result of large annual inputs of propagules and did not constitute a self-reproducing population (Sauvageau, 1897; Crisp and Fischer-Piette, 1959). By 1950 its limit had retreated westward by about 130km, to between Luarca and Salinas (Fischer-Piette, 1951, 1955a), where it remained for the rest of the century (Anadon and Neill, 1981; Gutierrez Moran, 1994). In May 2000 I found a few buttons of *H. elongata* at Gijon, but these were likely to be the result of transport of propagules from the main population some 80km to the west, and did not constitute a reproductively active population. *Himanthalia* is evidently able to disperse considerable distances by means of detached, fertile reproductive straps, which float and can drift far out to sea (Hawkins, pers. comm.). It can thus be considered as a "volatile" species (Hiscock *et al.* 2001, 2004), likely to respond rapidly to climate change.

In France, *H. elongata* was rare south of the Loire in 1954–55 (Crisp and Fischer-Piette, 1959). I did not observe this species in France in 2001 but there is no clear indication that it has retreated during that time.

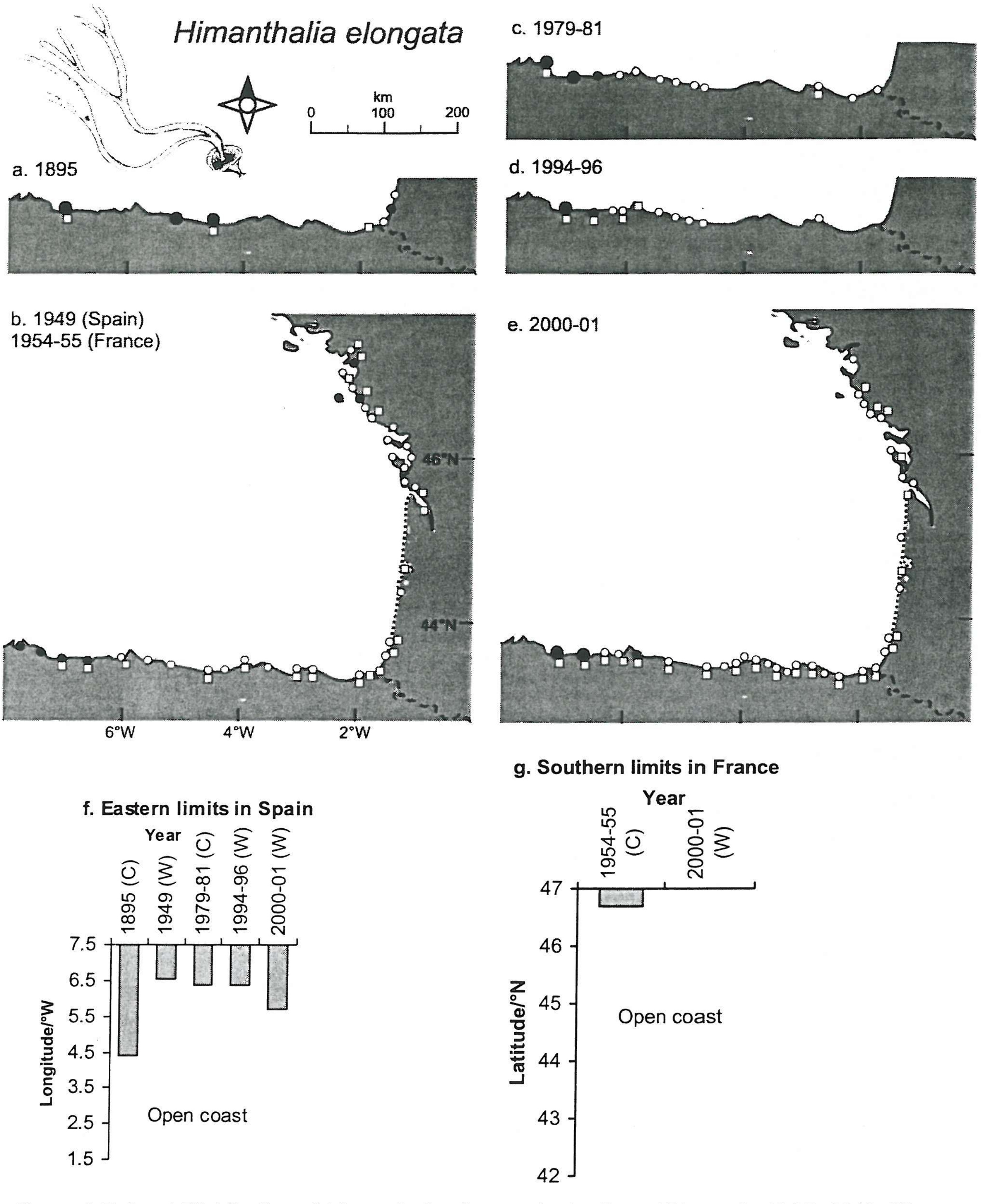


Figure 3.7. (a–e) Distribution of *Himanthalia elongata* in the Bay of Biscay in 1895, 1949–55, 1979–81, 1994–96, and 2000–01. Symbols represent maximum cover at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <25% cover. Large closed (●■): ≥ 25% cover. Dotted coastline indicates area with little rocky shore habitat. (f–g) Positions of range limits in Spain and France in the same years. "C" and "W" indicate broadly cold and warm periods (see Table 3.4). See Table 3.1 for references. Illustration adapted from Fish and Fish, 1996.

3.5.1.7. *Bifurcaria bifurcata*

Bifurcaria bifurcata (Figure 3.9) is a warm temperate, lower shore fucoid alga found from Morocco (Fischer-Piette, 1955a) and which just reaches southwest Britain and western Ireland (Southward and Crisp, 1954b; Crisp and Southward, 1958). Thus it has the most southern distribution of the eight algal species studied in this chapter, and is near the middle of its range in the Bay of Biscay.

It has been absent from the French Basque coast since 1895 (Sauvageau, 1897; Crisp and Fischer-Piette, 1959), and in 1954–55 was absent from the whole west coast of France south of the Loire, apart from a few offshore islands and one population on the mainland at the exposed Point St-Gildas. My 2000–01 survey, likewise, did not find *B. bifurcata* on the French coast (the Loire was the northern limit of my survey).

In Spain *B. bifurcata* is, comparatively, much more widespread than it is in France. In 1933–34 and also in 1949 its observed eastern limit on the Spanish Basque coast was at Zumaya, just 40km from the French border (Fischer-Piette, 1955a), and it was relatively common throughout the north coast. This distribution pattern was maintained throughout the 20th century. My 2000–01 survey again found the eastern limit of *B. bifurcata* at Zumaya, and observed a very similar pattern of distribution along the coast to that seen in 1949.

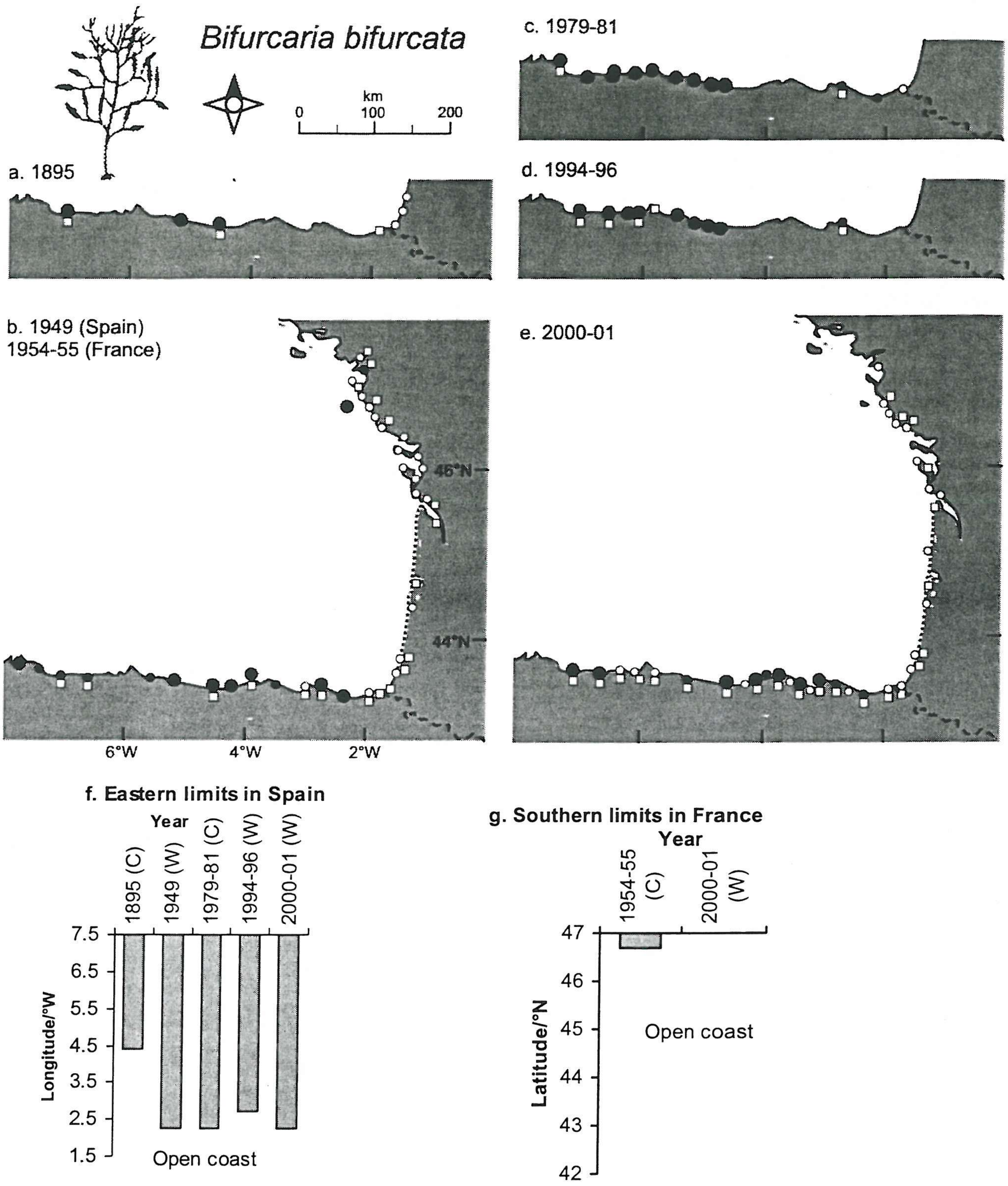


Figure 3.8. (a–e) Distribution of *Bifurcaria bifurcata* in the Bay of Biscay in 1895, 1949–55, 1979–81, 1994–96, and 2000–01. Symbols represent maximum cover at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <25% cover. Large closed (●■): ≥ 25% cover. Dotted coastline indicates area with little rocky shore habitat. (f–g) Positions of range limits in Spain and France in the same years. "C" and "W" indicate broadly cold and warm periods (see Table 3.4). See Table 3.1 for references. Illustration adapted from Southward *et al.*, 1995.

3.5.1.8. *Saccorhiza polyschides*

Saccorhiza polyschides (Light.) Batt. (Figure 3.9) is a kelp with a cold-temperate distribution. Its range extends from western Norway as far as southern Morocco (Crisp and Fischer-Piette, 1959; Norton, 1970). It is a very fast-growing annual, reaching lengths of about two metres in a single growing season, and can thus be expected to respond rapidly to variations in environmental conditions.

In 1895 it was abundant throughout the north coast of Spain and the French Basque coast (Sauvageau, 1897). In the 1950s, by contrast, it was rare on the French Basque coast (Crisp and Fischer-Piette, 1959) and absent from the Spanish Basque coast (Fischer-Piette, 1955a). At the same time it was absent from the Gironde to the Basque coast, an area dominated by sandy shores. North of the Gironde it was relatively uncommon as far as St Gilles. In northern Spain, its 1949 eastern limit was at Santander.

In the early 1980s *S. polyschides* recolonised the Spanish Basque coast and quickly became widespread (Gorostiaga, 1986; Fernandez *et al.*, 1988; Borja and Gorostiaga, 1990). In 2000–01 (my survey) *S. polyschides* was rare and localised, but still widespread (appearing as far east as Mundaka), on the Spanish coast. In most cases it was found in especially damp and shady places. On the French coast it was only observed at one site, les Sables d'Olonne, indicating a considerable retreat since 1955.

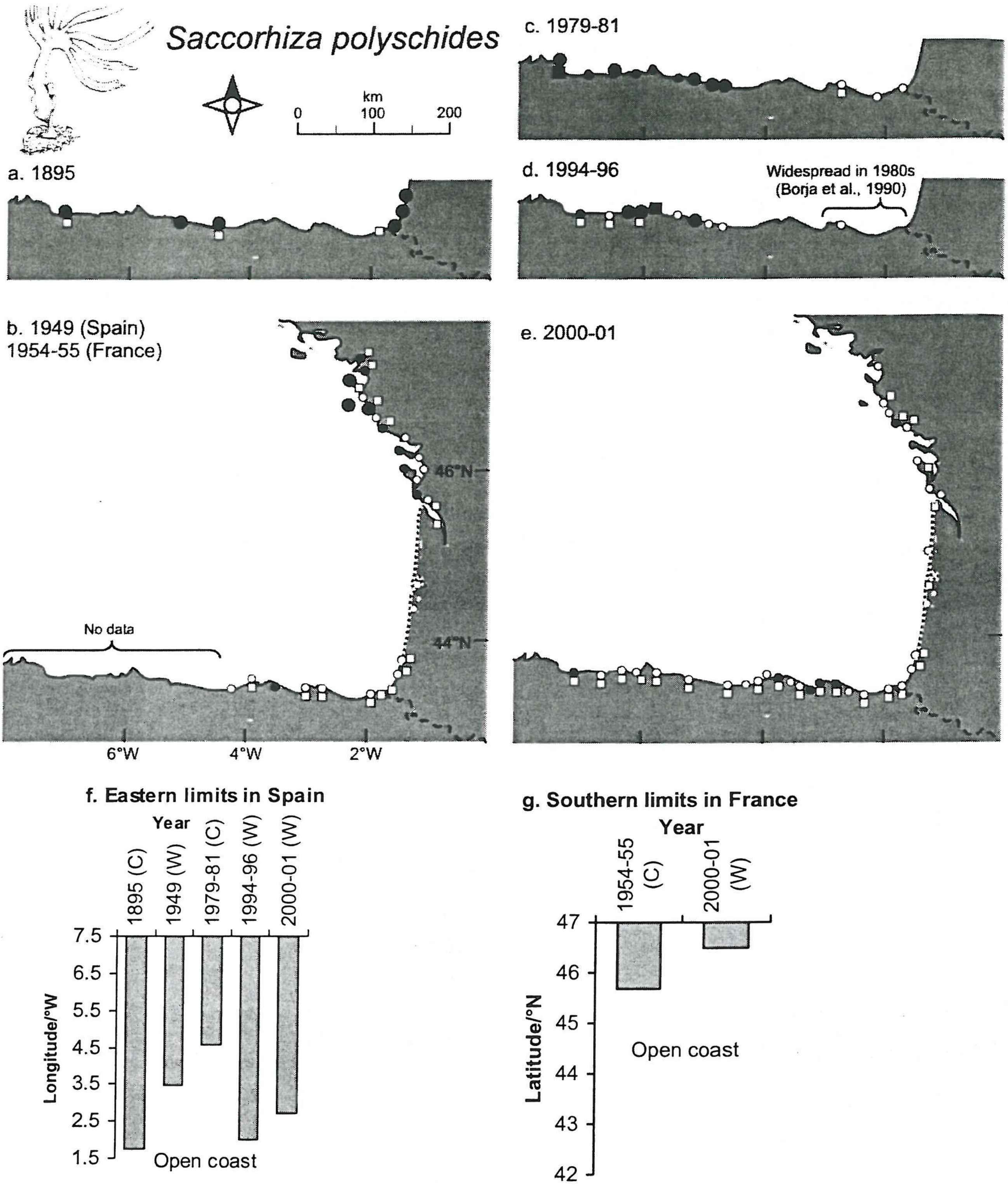


Figure 3.9. (a–e) Distribution of *Saccorhiza polyschides* in the Bay of Biscay in 1895, 1949–55, 1979–81, 1994–96, and 2000–01. Symbols represent maximum cover at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <25% cover. Large closed (●■): ≥ 25% cover. Dotted coastline indicates area with little rocky shore habitat. (f–g) Positions of range limits in Spain and France in the same years. "C" and "W" indicate broadly cold and warm periods (see Table 3.4). See Table 3.1 for references. Illustration adapted from Fish and Fish, 1996.

3.5.2. Invertebrates: Mollusca

3.5.2.1. Gibbula umbilicalis

The grazing trochid *Gibbula umbilicalis* (Figure 3.10), a southern species found from Mauritania (Crisp and Fischer-Piette, 1959) to northern Scotland (Lewis, 1986), has in the past been abundant throughout the Bay of Biscay region, except in places that are either too exposed or with too much sand or mud (Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959). On the predominantly sandy French coast between the Gironde and Biarritz it was common, but not abundant, in 1954–55 (Crisp and Fischer-Piette, 1959). In 2001, by contrast, I did not find this species between Biarritz and the Île d'Oléron, and it was only present in moderate quantities on the rest of the French coast, indicating an overall decline (which, however, may be an artefact of the survey methods: see *Osilinus lineatus* below). It was, however, still abundant along the north coast of Spain.

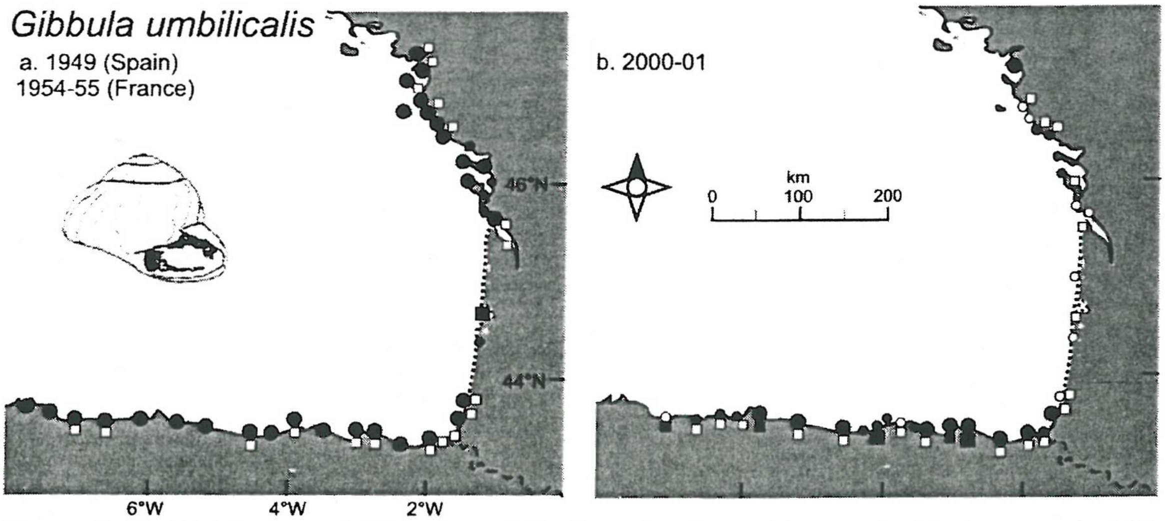


Figure 3.10. Distribution of *Gibbula umbilicalis* in the Bay of Biscay in 1949–55 and 2000-01. Symbols represent maximum abundance at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <10 individuals/m^2. Large closed (●■): ≥10 individuals/m^2. Dotted coastline indicates area with little rocky shore habitat. See Table 3.1 for references. (Illustration adapted from Southward *et al.*, 1995).

3.5.2.2. *Osilinus lineatus*

The grazing trochid *Osilinus lineatus* (Figure 3.11), a southern species found from Morocco (Crisp and Fischer-Piette, 1959) to north Wales and Northern Ireland (Lewis, 1986), was not studied by Fischer-Piette in Spain in 1949 (Fischer-Piette, 1955a). Its distribution in France in 1954–55 (Crisp and Fischer-Piette, 1959) was similar to that of *Gibbula umbilicalis* (see Figure 3.10), but more restricted: it was rare to absent between the Île d'Oléron and the French Basque coast, due to the sandy nature of the mainland coast, but common on the islands. In 2001 it was not found at all on the French coast south of St Denis d'Oléron, and was notably less common further north than in 1954–55, again indicative of an overall decline, as with *G. umbilicalis*. The decline observed in both species could have been related to the type of habitat surveyed, however: trochids generally prefer moderately exposed boulder shores (Bode *et al.*, 1986), and few of the sites I surveyed in France in 2001 were of this type.

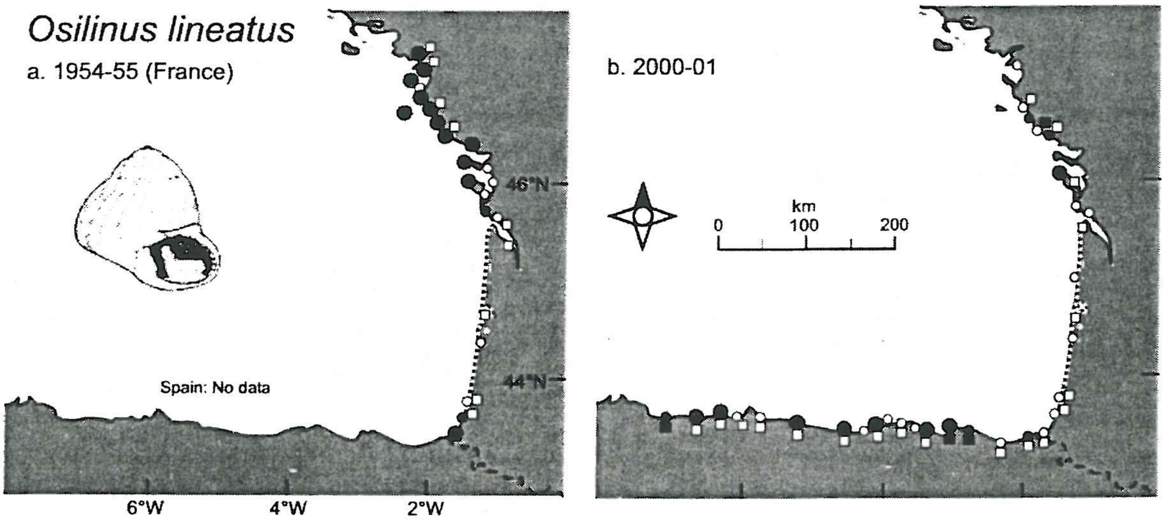


Figure 3.11. Distribution of *Osilinus lineatus* in the Bay of Biscay in 1954–55 and 2000-01. Symbols represent maximum abundance at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <10 individuals/m^2. Large closed (●■): ≥10 individuals/m^2. Dotted coastline indicates area with little rocky shore habitat. See Table 3.1 for references. (Illustration adapted from Southward *et al.*, 1995).

3.5.2.3. *Nucella lapillus*

Nucella lapillus (Figure 3.12), the common dog-whelk, is a cold-water species that in the 1950s reached as far south as the Gironde in France (Crisp and Fischer-Piette, 1959) and reappeared in northwest Spain (Fischer-Piette, 1955a). It was rare at Luarca and Ribadeo in 1949, becoming more common further west in Galicia.

In 2001 one individual was found at San Esteban de Pravia, some 35km east of Luarca, its observed limit in 1949 (Fischer-Piette did not visit San Esteban). A few individuals were also found on the open coast at Ribadeo. The species was absent from all other sites. There was thus little obvious difference in its abundance or distribution between 1949 and 2001 in the area of Spain studied. In France, however, the species has declined remarkably since 1955. I did not observe it at any of the sites visited in 2001. This change can probably be ascribed to the effects of tributyltin (TBT) pollution, from which many European populations are still recovering (Gibbs *et al.*, 1987, 1991; Huet *et al.*, 1996; Evans *et al.*, 1998; Morgan *et al.*, 1998; Barreiro *et al.*, 1999; Spence *et al.*, 1990; Barroso and Moreira, 2002; Birchenough *et al.*, 2002; Santos *et al.*, 2002). Climatic factors may, however, have contributed additional stress to an already threatened population and perhaps prevented repopulation of this area.

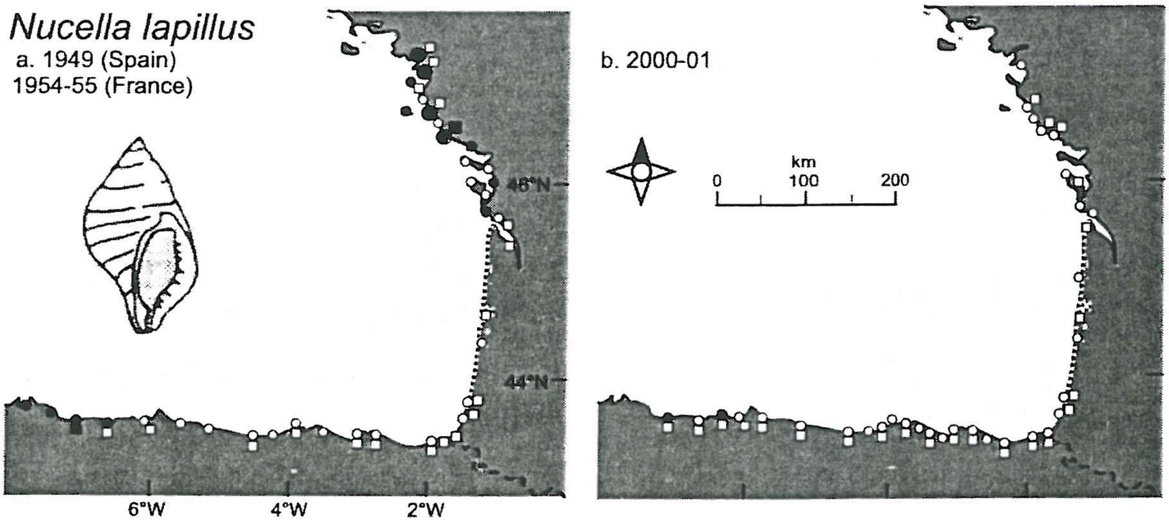


Figure 3.12. Distribution of *Nucella lapillus* in the Bay of Biscay in 1949–55 and 2000-01. Symbols represent maximum abundance at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <10 individuals/m^2. Large closed (●■): ≥10 individuals/m^2. Dotted coastline indicates area with little rocky shore habitat. See Table 3.1 for references. (Illustration adapted from Southward *et al.*, 1995)

3.5.2.4. *Patella depressa*

The black-footed limpet *Patella depressa* (Figure 3.13a) is a warm-water species whose range extends from Senegal (Fischer-Piette and Gaillard, 1959) to north Wales (Lewis, 1964) and the Isle of Wight (Crisp and Southward, 1958). It is present throughout the Bay of Biscay, but more common on exposed shores and relatively rare in estuaries.

On the north coast of Spain, the abundance of *P. depressa* decreases from east to west. It is the dominant species of limpet at mid-tide level on moderately exposed to exposed shores from the French Basque coast as far as about 6°W, near Cabo Peñas (see Chapter 4). Further west, in Galicia, *Patella vulgata* becomes the dominant species.

Its distribution in France in the 1950s (Crisp and Fischer-Piette, 1959; Fischer-Piette and Gaillard, 1959) was similar to that observed in 2000–01. On the north coast of Spain in 1949 (Fischer-Piette, 1955a; Fischer-Piette and Gaillard, 1959), although it was present at moderately exposed to exposed sites throughout, it was the dominant species only on the Basque coast. *Patella depressa* has clearly increased in abundance in northern Spain between 1949 and 2000–01.

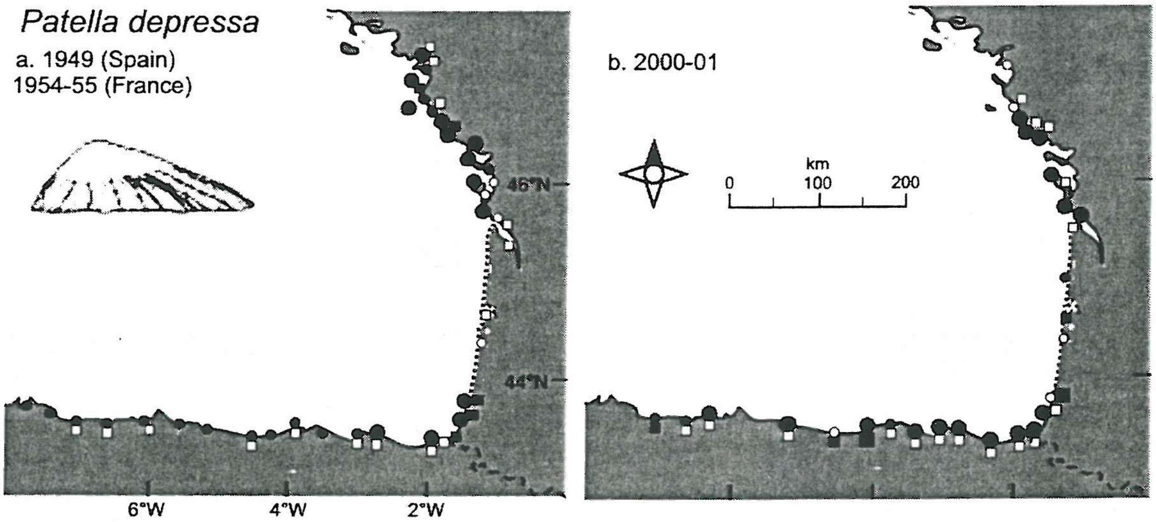


Figure 3.13. Distribution of *Patella depressa* in the Bay of Biscay in 1949–55 and 2000-01. Symbols represent maximum abundance at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <10 individuals/m^2. Large closed (●■): ≥10 individuals/m^2. Dotted coastline indicates area with little rocky shore habitat. See Table 3.1 for references. (Illustration adapted from Southward *et al.*, 1995).

3.5.2.5. Patella vulgata

The common limpet *Patella vulgata* (Figure 3.13b) is a boreal species whose range extends from northern Norway to southwest Spain (Fischer-Piette, 1958; Guerra and Gaudencio, 1986). As with *P. depressa,* it is present throughout the Bay of Biscay, but the distribution of the two species is almost opposite: *P. vulgata* is typically less common in the inner Bay than in Brittany and northwest Spain, and less common on the open coast than in estuaries. Like *P. depressa,* however, it is also less common between the Gironde and the French Basque coast, an area dominated by sandy shores.

Since the 1950s (Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959; Fischer-Piette and Gaillard, 1959) *P. vulgata* has evidently decreased in abundance throughout the Bay of Biscay. In 1949 it was abundant on moderately exposed shores throughout the north coast of Spain, with the possible exception of the Basque coast (Fischer-Piette, 1955a; Fischer-Piette and Gaillard, 1959).

Both *P. depressa* and *P. vulgata* are discussed in greater detail in Chapters 4 and 5.

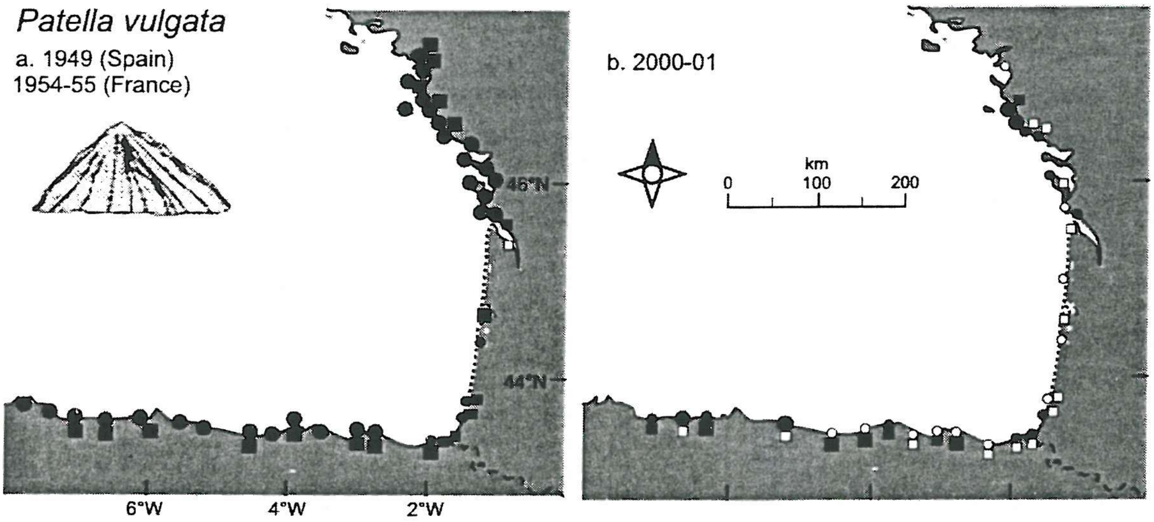


Figure 3.14. Distribution of *Patella vulgata* in the Bay of Biscay in 1949–55 and 2000-01. Symbols represent maximum abundance at moderately to very exposed coastal sites (circles) and in estuaries and ports (squares). Open symbols (○□): absent. Small closed (●■): <10 individuals/m^2. Large closed (●■): ≥10 individuals/m^2. Dotted coastline indicates area with little rocky shore habitat. See Table 3.1 for references. (Illustrations adapted from Southward *et al.*, 1995).

3.5.2.6. *Patella rustica*

P. rustica (distribution not shown) is a warm-water species found mainly on the high shore, and is particularly common in exposed areas. It reaches its northern limit on the French Basque coast (Fischer-Piette, 1955a). In 1949 its abundance decreased progressively westward from the Basque coast to western Galicia, where it was rare and very localised (Fischer-Piette, 1955a). In the present study, it was found occasionally at exposed sites along the north coast of Spain, extending as far west as Cariño in the extreme north-west of Galicia, the observed limit. It was absent from all the sites visited on the west coast of Galicia. As no very exposed sites were surveyed, however, it is not possible to say with certainty whether this species has retreated since 1949.

3.6. Analysis

The species distribution data synthesized in §3.5 were analysed with the aim of detecting climate-related shifts in distribution of rocky shore species during the course of the twentieth century. The first step in the analysis (§3.6.1) was to examine temperature data so as to rank the time periods to be compared from warmest to coolest in terms of their average climate. For distribution data from northern Spain, the time periods to be compared were 1895, 1949, 1979–81 and 2000–01. For data from western France, the periods to be compared were 1954–55 and 2000–01.

The analysis of species distribution was done in three stages. To obtain a preliminary impression of overall changes in species distribution and their relation with climate, rankings were made of both range and overall abundance for 14 selected species during each of the time periods for which data were available (§3.6.2; see Table 3.4). For the eight species of algae, the rankings for the four time periods 1895, 1949, 1980 and 2000 were plotted against corresponding temperature ranks in order to give a visual picture of the broad relationship between climate and species distribution.

The second stage (§3.6.3) was statistical testing of overall changes in distribution for the 14 species (Table 3.2). This comparison was made between the time periods 1949–55 and 2000–01 in both Spain and France; distribution data for the other periods were less reliable and were only available for algae, not invertebrates. Based on the rankings derived in §3.6.2, a sign test was used to test whether significantly more species had moved in the direction predicted by the change in climate (i.e. northern species contracting in range or becoming less abundant, southern species expanding in range or becoming more abundant) than in the opposite direction.

The third stage (§3.6.4) was statistical testing of changes in abundance of particular species. This was carried out based on two time periods in Spain (1949 and 2000–01) for which abundance data were available for algae at the same or similar sites. Abundances at 20 sites were compared. A sign test was again used to test whether each species had changed in abundance in the direction predicted by the change in temperature (i.e. northern species becoming less abundant, southern species more abundant) at significantly more sites than those at which it changed in the opposite direction.

3.6.1. Ranking of temperature for time periods to be compared

Temperature data were analysed based on two data sets (described in Chapter 2): regional air-sea temperatures for the area 40–50°N, 0–10°W based on the Global Surface Temperature Atlas (GOSTA) data set (Jet Propulsion Laboratory/British Atmospheric Data Centre, 2003); and local temperatures in the inner Bay of Biscay based on daily measurements of sea surface temperature taken at San Sebastian Aquarium since 1947 (Borja *et al.*, 2000). The GOSTA data set was used rather than the other long-term data set (COADS) described in Chapter 2 because GOSTA includes corrections for bucket temperatures, making it more accurate than COADS prior to 1950 (Cane *et al.*, 1997).

Seasonal temperature anomalies for summer (July–September) and winter (January–March) were calculated from both data sets as described in §2.3.1. For each of the time periods to be compared (1895, 1949, 1954–55, 1979–81, and 2000–01), mean summer and winter temperature anomalies were calculated for the five years preceding the periods to be compared. Thus the ranking for 1949 was based on temperatures for 1945–49. For the period 1979–81, two five-year mean periods were compared: 1975–79 and 1980–84; the latter period was included in order to use distribution data for *Saccorhiza polyschides* from the mid-1980s (Gorostiaga, 1986). Because the GOSTA data set only goes up to 1995, data from the years 1991–95 were used to generate the ranking for the period 2000–01. The seasonal temperature anomalies and the resulting rankings are given in Table 3.3.

The rankings between the four periods which were to be compared in Spain proved to be identical for summer and winter temperature: 1895 was the coldest period, followed by the 1980s, then 1949, with 2000–01 being the warmest period. Of the two periods to be compared in France, 1954–55 was cool and 2000–01 was warm.

Table 3.3. (top) Summary of variation in key climatic factors in the Bay of Biscay during selected ten-year periods since 1886. Values of mean **summer** (July–Sept) and **winter** (Jan–March) temperature are anomalies (long-term mean removed). **GOSTA** values are regional averages of sea and air temperatures for the Bay of Biscay region (40–50°N, 0–10°W), based on the Global Surface Temperature Atlas data set (Jet Propulsion Laboratory/British Atmospheric Data Centre, 2003). **SSA** values are based on daily measurements of sea surface temperature taken at San Sebastian Aquarium since 1947 (Borja *et al.*, 2000). Calculation of seasonal anomalies described in §2.3.1.
–: Data not available. #: Data for 1947–49.
(bottom) Overall temperature ranking for time periods to be compared.

	Winter		**Summer**	
Years	**GOSTA**	**SSA**	**GOSTA**	**SSA**
1891–95	-0.69	–	-0.22	–
1945–49	0.28	0.22#	0.26	0.16#
1950–54	-0.03	-0.20	-0.27	0.30
1975–79	0.05	-0.19	-0.21	-0.61
1980–84	0.05	-0.15	0.11	-0.07
1991–95	0.34		0.32	
1996–2000	–	0.25	–	0.23

	Ranking	
Variable	**Spain**	**France**
Winter T	2000 > 1949 > 1980s > 1895	2000 > 1955
Summer T	2000 > 1949 > 1980s > 1895	2000 > 1955

3.6.2. Ranking of species range and abundance

As an initial comparison between the various studies of species distribution, a ranking system was adopted, based on two criteria: range (i.e. position of observed range limit) and overall abundance throughout the species' range. For each of the species listed in Table 3.2, comparisons were made between the four periods for which data were available (1895, 1980s, 1949 and 2000–01) in order to establish rankings.

Differences in the number and location of sites were taken into account when assessing whether definite changes in species range had occurred. The resulting ranks are given in Table 3.4. For the eight species of algae for which data were available from N Spain for all four time periods, the resulting ranks are plotted in Figure 3.14 against the corresponding ranks of temperature (Table 3.3).

Table 3.4. Qualitative summary of range shifts and changes in abundance for eight species of brown algae and six species of molluscs in the Bay of Biscay, between 1895 and 2000. Within each phylum the species are listed in rough order of vertical position on the shore, with upper shore species at the top of the table. The range and overall abundance within its range of each species (see Figures 3.2–3.12) are compared in the different years for which widespread data are available. >* indicates a decline that may be primarily due to pollution. >? indicates an apparent decline that may be an artefact of the survey methods.

		Ranking of range		**Ranking of abundance**	
	Species	**N Spain**	**W France**	**N Spain**	**W France**
Phaeophyta	*P. canaliculata* (N)	1895≈1980≈1949≥2000	1955>2000	1895≥1980>1949>2000	1955>2000
	F. spiralis (N)	1895≈1949≈1980>2000	1955>2000	1895>1949≈1980>2000	1955>2000
	F. vesiculosus (N)	1895>1949≈1980>2000	1955≈2000	1895≥1980≥1949>2000	1955>2000
	A. nodosum (N)	1895>*1949≈1980≈2000	1955>2000	1895≥1949≈1980≈2000	1955≈2000
	F. serratus (N)	1895>1949>2000>1980	1955≈2000	1895≈1980≥1949≈2000	1955≈2000
	B. bifurcata (S)	1895≈1949≈1980≈2000	1955≈2000	1895≈1949≈1980≈2000	1955≈2000
	H. elongata (N)	1895>1949≈1980≈2000	1955≈2000	1895≈1980≈2000≥1949	1955≈2000
	S. polyschides (N)	1895>1980s>2000>1949	1955>2000	1895≥1980s>2000≥1949	1955>2000
Mollusca	*P. rustica* (S)	1949≈2000	Absent	1949≈2000	Absent
	P. depressa (S)	1949≈2000	1955≈2000	2000>1949	1955≈2000
	P. vulgata (N)	1949≈2000	1955≥2000	1949>2000	1955>2000
	G. umbilicalis (S)	1949≈2000	1955>?2000	1949≈2000	1955>?2000
	O. lineatus (S)	No data	1955>?2000	No data	1955>?2000
	N. lapillus (N)	1949≈2000	1955>*2000	1949≈2000	1955>*2000

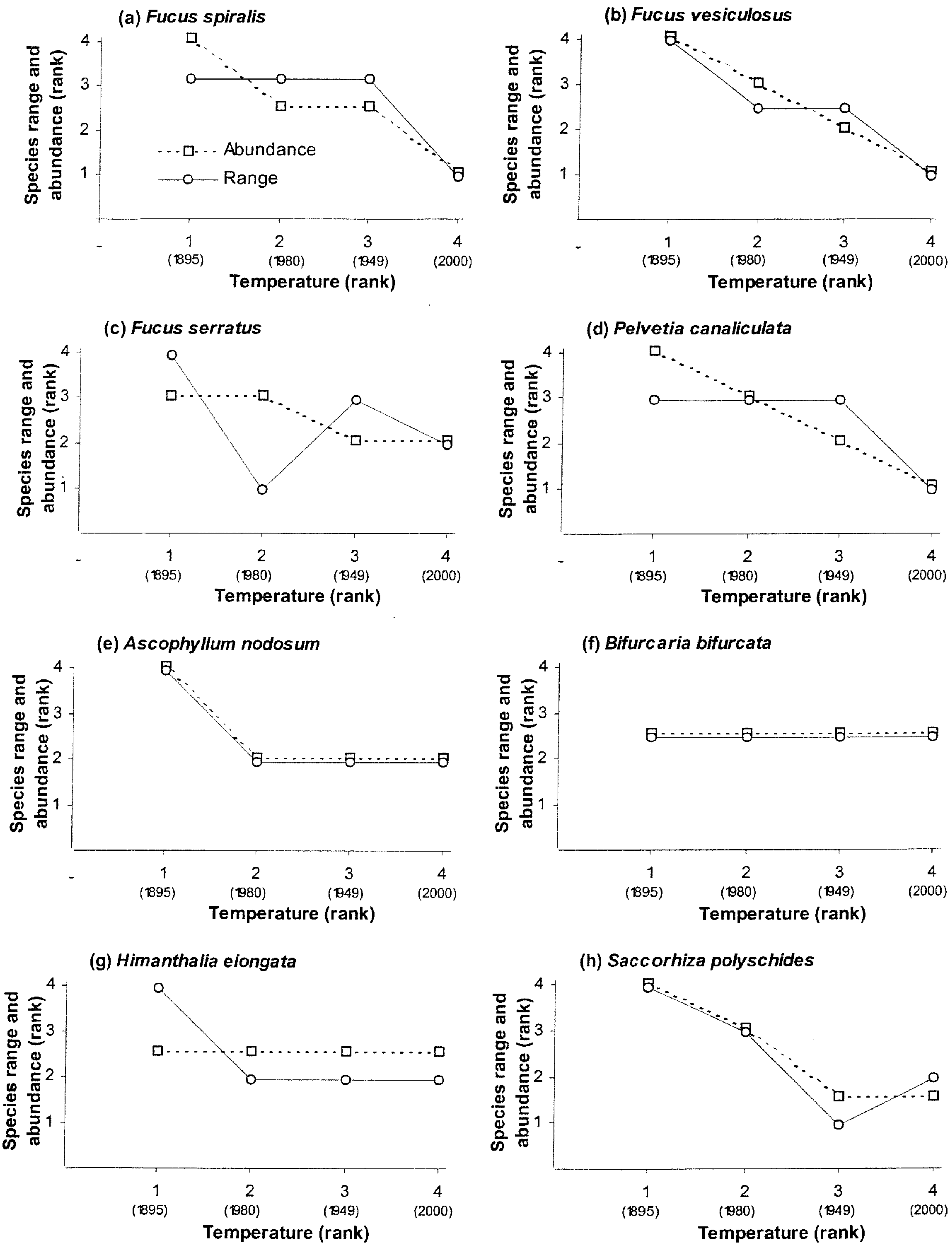


Figure 3.15. Range (circles, solid lines) and abundance (squares, dotted lines) of eight species of brown algae on the north coast of Spain against five-year mean temperature, ranked for four time periods since 1895. A rank of 4 indicates the highest temperature and the greatest range and abundance. Ranks are given in Tables 3.3 and 3.4.

Table 3.5. Summary from Table 3.4 of changes in range and overall abundance of eight species of brown algae and six species of molluscs in N Spain since 1949 (Fischer-Piette, 1955a) and in W France since 1954–55 (Crisp and Fischer-Piette, 1959). N/S: northern or southern species.
–: species has declined since 1949–55. +: species has increased. 0: no clear change.
–* indicates a decline that may be primarily due to pollution.
–? indicates an apparent decline that may be an artefact of the survey methods.

	Species	**N Spain**	**W France**
Phaeophyta	*P. canaliculata* (N)	–	–
	F. spiralis (N)	–	–
	F. vesiculosus (N)	–	–
	A. nodosum (N)	0	–
	F. serratus (N)	–	0
	B. bifurcata (S)	0	0
	H. elongata (N)	0	0
	S. polyschides (N)	+	–
Mollusca	*P. rustica* (S)	0	n/a
	P. depressa (S)	+	0
	P. vulgata (N)	–	–
	G. umbilicalis (S)	0	–?
	O. lineatus (S)	n/a	–?
	N. lapillus (N)	0	–*

3.6.3. Overall changes since 1949–55

Table 3.5 summarises the changes since mid-century in the range and overall abundance of the 14 species studied (based on the ranks in Table 3.4). Since the 1990s were warmer than the period 1945–54, northern species were predicted to decline and southern species to increase.

In Spain, seven species showed no change, six changed in the direction predicted, and one (*Saccorhiza polyschides*) changed in the opposite direction. In France, six species showed no change, six changed in the direction predicted, and two (*Gibbula umbilicalis* and *Osilinus lineatus*) changed in the opposite direction. The observed decline in *G. umbilicalis* and *O. lineatus* in France is likely to be an artefact due to the choice of study sites, while the decline of *Nucella lapillus* could have been caused by TBT pollution.

Considering the Bay of Biscay as a whole (both Spain and France), and looking at algae and limpets only, eight species (*P. canaliculata, F. spiralis, F. vesiculosus, A. nodosum, F. serratus, P. depressa* and *P. vulgata*) changed in the direction predicted, three showed no change (*H. elongata, B. bifurcaria* and *P. rustica*) and one showed inconsistent change (*S. polyschides*). A one-tailed sign test (Sokal and Rohlf, 1995) was applied, based on the null hypothesis that changes in species range and abundance were not related to temperature, so that the probability of species declining or increasing was equal. The probability of eight species moving in the direction predicted by the change in temperature and none moving in the opposite direction was $p = 0.0039$; the null hypothesis was therefore rejected ($p < 0.01$).

3.6.4. Changes since 1949 in abundance of algae in N Spain

A further comparison was made between the distribution of the eight species of brown algae studied on the north coast of Spain between 1949 (Fischer-Piette, 1955a) and 2000–01 (my survey). Because many sites in these two studies were either the same or very nearby, it was possible to make site-by-site comparisons between abundance in 1949 and 2000–01 for these species. Comparisons were made for a total of 20 sites: 13 on the open coast and 7 in sheltered estuaries/ports. *Saccorhiza polyschides* was excluded from the analysis because data on its abundance were not available at 9 of the sites studied in 1949.

One-tailed sign tests (Sokal and Rohlf, 1995) were applied to test for significance, based on the null hypothesis that species abundance is not related to temperature. Statistically significant declines in abundance were observed for three northern species: *Pelvetia canaliculata, Fucus spiralis* and *F. vesiculosus.* The other four species studied, *Ascophyllum nodosum, Fucus serratus, Bifurcaria bifurcata* and *Himanthalia elongata*, did not show significant changes in abundance. The possible reasons for these different responses are discussed in §3.7.2.

Table 3.6. Changes in local abundance of eight species of brown algae at 20 sites in northern Spain between 1949 (Fischer-Piette, 1955a) and 2000–01 (my survey). N/S: northern or southern species. p: probability resulting from a one-tailed sign test.

		No. of sites			
Species	**N / S**	**Increase**	**Decrease**	**No Change**	**p**
P. canaliculata	N	3	13	4	<5%
F. spiralis	N	3	12	5	<5%
F. vesiculosus	N	0	8	12	<5%
A. nodosum	N	0	2	18	n.s.
F. serratus	N	0	4	16	n.s.
B. bifurcata	S	3	3	14	n.s.
H. elongata	N	3	0	17	n.s.

3.7. Discussion

3.7.1. Evaluation of the design and execution of the study

The present study encountered several difficulties that limited the accuracy and generality of the results and the consequent ability to detect climate-related changes in species distribution. Some of these could be put down to the nature of the available data on past species distributions, while others were due to flaws in the design of the study and its execution. This section evaluates several aspects of its design and discusses how future investigators might learn from it.

The historical data on past species distributions used in this study were widely dispersed in time, based on studies carried out at different sites, at different times of year, with different aims, by different investigators, using different methods. Some studies included data on a wider range of species than those on which the present study is based (e.g. Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959) while others focused on a single species (Borja and Gorostiaga, 1990, on *Saccorhiza polyschides*). Some included quantitative data (e.g. Anadon *et al.*, 1979; Anadon and Niell, 1981), others were of a semiquantitative (e.g. Crisp and Fischer-Piette, 1959) or purely descriptive nature (e.g. Sauvageau, 1987; Fischer-Piette, 1955a). Some included data from a very large number of sites (e.g. Crisp and Fischer-Piette, 1959), while others were restricted to only a few sites or a single area (e.g. Borja *et al.*, 1995, 1996). Since the aim of my study was to investigate change during the whole of the

20th century, it was necessary to find some common measure by which to compare the results of such disparate studies. A simple semi-quantitative scale was chosen, whereby species were classified as either absent, present, or abundant. This enabled easy visual comparison of changes in species distributions over time, as seen in Figures 3.2 through 3.14. I think this was the simplest way of approaching an intrinsically complex task.

Another approach would have been to choose a particularly complete data set, albeit of a relatively restricted geographical area (e.g. Anadon and Niell, 1981) and resurvey the same sites using the same quantitative methods, in order to obtain a more complete and accurate picture of change between two periods with different climates, which could then provide a more detailed baseline for further studies in the future. This was not done because the main focus of the study was broad-scale change.

As noted above, the historical studies were carried out at different sets of sites. The only single studies looking at significant numbers of sites over the whole of the Bay of Biscay area, were those of Fischer-Piette (1955a) in Spain and Crisp and Fischer-Piette (1959) in France. The sites chosen for the present survey were based on these two studies. The methods of analysis used, however, were not dependent on the sites surveyed being identical to those in past studies.

A separate question is that of the power to detect change: that is, whether enough sites were surveyed in order to detect likely changes in species distribution over time. This has been examined in Appendix B, where the size of range shift D_c that can be detected at a critical level of confidence c is shown to depend largely on f, the probability of a false negative observation (Equation B.11). This critical value D_c is expressed as a number of sites, and so could be used in designing a survey in order to be confident of detecting a range shift of a given size. For example, in order to detect a range shift of 100 km with a confidence level of $c = 0.05$, the maximum distance between sites would be 14 km if $f = 0.25$, 10 km if $f = 0.5$, or just 4 km if $f = 0.75$. Values of f in the present study have varied between about 0.25 and 0.75 for different species; the sites surveyed in 2000–01 were on average about 30–40 km apart, so they were clearly not close enough together to detect a range shift of only 100 km with 95% confidence. Diligent study looking at a wider range of habitats could reduce the value of f and thus give more accurate results.

Given the wide variety of methods used in the available past studies, it was difficult to decide on the best methods for my survey. In the end I chose the methods chiefly based on criteria of speed and simplicity. The widely used SACFOR semiquantitative scale was employed, rather than more time-consuming quantitative methods, partly because the available historical data would not on the whole have repaid the effort of collecting quantitative data. Likewise, in the second phase of the survey, only species known to be abundant and likely to respond to climate change were studied, partly for reasons of speed, but mainly because these species were the ones that best served the principal aim of the study, to detect climate-related change. However, this approach did reduce the breadth of the data set, when considered as a baseline for future studies. It would also have been valuable to include a wider variety of habitats (rock pools, crevices, overhangs) which were excluded from the survey.

In the first phase of my survey (spring 2000), an equal area (10 m^2) was surveyed at each site. In the second phase, equal time (30 minutes) was spent at each site. The very heterogeneous and topographically diverse nature of rocky shores in general, and those of northern Spain in particular, mean that it is difficult to carry out a broad-scale survey based on an equal-area method, especially without considerable pre-survey preparation; this is why I switched to using an equal-time method after the first phase of the survey.

It is difficult to assess the relative search effort of my survey compared with historical studies. Early studies (e.g. Sauvageau, 1897; Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959) generally ignored the question of search effort, although it is implied that their search methods were based on spending a set time on each shore; while modern studies (e.g. Anadon and Niell, 1981) have generally used area as the basis for standardising search effort. This approach works best on shores that are reasonably smooth, flat and homogeneous, and may bias the selection of sites towards these shores. On boulder shores or very heterogeneous rocky shores, the use of area-based methods is impractical.

Neither phase of the survey included within-site replication: it was decided that surveying more sites would be more productive than surveying more areas within each site. The lack of within-site replication means that no information was gathered on within-site variability in species abundance. The abundance scale methodology used is designed to give a maximum value at a particular location for purposes of geographical comparison (Southward and Crisp, 1954b; Crisp and Southward, 1958; Crisp and Fischer-Piette, 1959).

My surveys were carried out in spring and early summer; the majority of the historical surveys also took place between early spring and early autumn. Nearly all the species studied have life spans of several years, so that making comparisons between surveys carried out in different seasons was not a major problem. Obviously, seasonal changes do occur in the abundance of populations, sometimes abruptly, as in the case of damage to macroalgae by storms, particularly in autumn. However, at the level of detail at which the comparisons were made, it is unlikely that seasonal factors have biased the results. One of the species studied, *Saccorhiza polyschides*, is a fast-growing annual, which disappears in late autumn to winter (Norton, 1970). Variation in plant size and abundance during the year is therefore great. None of the results used for this species were from the winter season. Another species, *Himanthalia elongata*, produces large reproductive structures during the growing season that disappear in winter (Stengel *et al.,* 1999). This large annual variation in plant size could lead to variations in recorded abundance between studies carried out at different times of year.

3.7.2. Variations in range and abundance of species and their relation to temperature

This study has observed large-scale, long-term changes in the distribution of selected rocky shore species in the Bay of Biscay during the course of the 20th century. Some of these results were tested and found to be statistically significant. Other changes observed could not be tested statistically because of a lack of data. Data on the distribution of algae were available, although not always very detailed and widespread, for all four time periods studied; in contrast, data on invertebrates and detailed data on algae were only available for two time periods: 1949–55 (Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959) and 2000–01 (my surveys). For this reason, the statistical analysis focussed on the changes between 1949–55 and 2000–01, and on changes in the range and abundance of algae.

In the context of 20th century climate in the Bay of Biscay, the late 1940s were an unusually warm period (see §2.3.2 and §2.5.2). The distribution of rocky shore species in northern Spain in 1949 (Fischer-Piette, 1955a) reflected this. Warm-temperate, southern species were more common, and cold-temperate, northern species less common, in 1949 than either in previous years (Fischer-Piette, 1955a) or in subsequent cool periods such as the 1980s (Ibañez, 1990). Fischer-Piette (1955a) noted in particular the decline of northern species since 1895 (Sauvageau, 1897); Figure 3.15 confirms that all seven northern species studied were at their maximum range and abundance in 1895.

The 1990s were warmer still in the Bay of Biscay, as well as globally – they were the warmest decade since formal records began in the 1860s, and probably the warmest of the past 2000 years (Pearce, 2003). The comparison between a warm period (the late 1940s) and a still warmer period (the 1990s) is important from the point of view of detecting the effects of climate change. If it can be shown that the distribution of rocky shore species in 2000–01 compared with 1949 has shifted significantly away from dominance by northern species in favour of southern species, this is good evidence that effects of climate change on rocky shore species have been detected (Southward *et al.*, 1995).

This study has, in fact, observed such a shift, both at the level of a group of 14 selected species and at the level of individual species, with three northern species (*Pelvetia canaliculata, Fucus spiralis* and *F. vesiculosus*) showing significant declines in abundance across their range in northern Spain. Both results indicate that climate-related changes in rocky shore species have taken place since 1949.

Differences were seen between the changes in the range and abundance of individual species which are likely to reflect ecological differences between the species. It is difficult to draw any clear lessons about the changes observed in invertebrates, as the records of their past distribution are much less detailed than those for algae. However, two of the species studied, *Patella vulgata* and *P. depressa,* are considered in greater detail in Chapters 4 and 5.

Of the eight species of algae studied, one, *Bifurcaria bifurcata,* showed no change in its range or overall abundance in northern Spain during the 20th century (see Figure 3.15). *Bifurcaria* was the only species of alga studied which has a relatively southern distribution, and in fact is close to the middle of its range in the Bay of Biscay, so it is not surprising that it should not show noticeable change in response to variations in temperature.

Among the seven "northern" species of brown algae studied, certain key biological characteristics seem to help explain differences in their observed responses to climate change: notably, differences in longevity, reproductive and dispersal ability, and differences in position on the vertical land-sea gradient.

3.7.2.1. Longevity, reproductive and dispersal ability

Differences in the longevity of different species and their ability to reproduce and disperse have been discussed as a source of variation in their responses to climate change. The general term "volatility" was coined to describe the difference between species that are likely to respond rapidly to climate change and those that are likely to respond mosre slowly (Hiscock *et al.,* 2001, 2004). These differences can be seen to play an important role in the variations observed in the Bay of Biscay during the 20th century.

For example, *Saccorhiza polyschides,* a fast-growing annual species, has experienced relatively large and rapid changes. From being highly abundant even in the inner Bay of Biscay in the late 19th century (a cool period), it retreated more than 150km to San Vicente by 1950 (a warm period), recolonised large areas of the Spanish Basque coast in the 1980s (a cool period), but at the end of the century (a warm period) seems to have retreated again to become rare and localised across much of northern Spain. The expansion of *S. polyschides* in the early 1980s was seen by some researchers as an indicator of cooling (Gorostiaga, 1986; Fernandez *et al.*, 1988; Borja and Gorostiaga, 1990). This expansion was not limited to the Bay of Biscay, but seems to have been regional in scale. The species was also recorded in the Canary Islands for the first time during the same period (Ballesteros et al., 1992). It has since retreated, although not as far as its 1949 range limits, leading to a net expansion between 1949 and 2000–01.

Himanthalia elongata is another species that is fast-growing and has great reproductive and dispersal ability (Creed, 1995; Stengel *et al.*, 1999). It can therefore be expected to respond rapidly to changes in climate. *H. elongata* retreated by at least 150km between the beginning and middle of the 20th century. Its abundance did not show significant changes between 1949 and 2000–01, but this is could be due to the fact that is was found at only a few sites in the far west of the area studied, so there was insufficient data to observe any significant change. It does not appear to have expanded its range during the cold period of the 1980s. Its southern limit in Portugal does seem to have retreated northwards since the mid-20th century (Fischer-Piette, 1958; Santos, 2000).

The volatile nature of *S. polyschides* and *H. elongata* may be contrasted with the long-lived, slow-growing *Ascophyllum nodosum,* which has persisted in estuarine habitats on the north coast of Spain (including the Basque coast) throughout the 20th century, without showing major alterations in its range or abundance (Fischer-Piette, 1955a). Nonetheless at least one colony of *Ascophyllum* in the inner Bay of Biscay (at Pasajes) has disappeared since the beginning of the century, possibly as a result of pollution.

3.7.2.2. Vertical position on the shore

Another contrast may be made between the variations observed in lower-shore and upper-shore species of algae. In Figure 3.15, it can be seen that the changes observed since 1949 in the range and abundance of the three upper shore species *Pelvetia canaliculata* and *Fucus spiralis* and the mid-shore species *Fucus vesiculosus* show clear linear relationships with temperature: with increasing temperature both range and abundance either remain constant or decline. By contrast, the lower-shore species *Fucus serratus* and *Saccorhiza polyschides* show range shifts that are not clearly related with temperature. *F. serratus* declined from 1949 to 1980 (a period of warming) and has expanded since then (a period of cooling). *S. polyschides* expanded markedly from 1949 to 1980 and has since declined, but not as far as its 1949 range limits. *Himanthalia elongata* has showed no substantial change since 1949 in either range or abundance.

Other differences can be seen in the response of upper and lower-shore species to spatial gradients in temperature. Lower-shore species such as *Fucus serratus* or *Himanthalia elongata* tend to have clearly defined geographical limits (Fischer-Piette, 1955a; Arrontes, 1993, 2002). As lower-shore species tend to be competitively dominant (Hawkins and Hartnoll, 1985), once established they will normally expand to fill the space available to them (Arrontes, 2002). Thus each species is abundant and widespread on one side of its "limit", and on the other side, may be present only temporarily, in isolated populations that are not reproductively viable (as observed in *H. elongata* on the French Basque coast: Crisp and Fischer-Piette, 1959). Upper-shore species such as *Pelvetia canaliculata* and *Fucus spiralis*, on the other hand, show a much more gradual change from abundance to absence: *F. spiralis* shows a marked north-south decline in abundance in France (Crisp and Fischer-Piette, 1959) and large year-to-year variations in its abundance in the inner Bay of Biscay (Fischer-Piette and Dupérier, 1960, 1961, 1963, 1965, 1966), although it has not been completely absent from significant areas of the Bay of Biscay during the 20th century. However, in my survey it was recorded as absent at nine successive sites between its observed limits of Capbreton and Mundaka, suggesting that its range limits may now have retreated. *P. canaliculata* is abundant only in the outer Bay of Biscay, but has been present throughout, albeit in isolated patches whose abundance varies, during the whole of the 20th century (Fischer-Piette, 1957c; Hawkins, pers. comm.)

The concept of a definite "geographical limit" is thus more closely applicable to some species than others. The different types of variation observed between different species, therefore, appear to require different strategies for detecting them, which have not fully been taken into account in existing studies of the effects of climate change on rocky shores (e.g. Southward *et al.*, 1995; Hiscock *et al.*, 2001, 2004).

These observed differences in the response of upper- and lower-shore species to spatial and temporal variations in climate are likely to be due to differences in the temperature regimes experienced by these species and the responses they have evolved to them. Lower shore species will tend to experience extremes of temperature relatively rarely, when low tides coincide with hot days. Therefore they are likely to have time to grow and out-compete other species and achieve dominance in a delimited area, between occasional episodes of mortality. Upper shore species, by contrast, are likely to experience extremes of temperature with considerable regularity and therefore have evolved greater resistance to desiccation, at the price of slower growth, than lower-shore species. Despite this adaptation, they are still vulnerable to extreme hot weather events, which can cause local extinction and may be responsible for setting upper limits (Schonbeck and Norton, 1978; Hartnoll and Hawkins, 1985). Extreme high summer sea temperatures on the Basque coast during the 1990s (see Figure 2.11) were around 1.0–1.5°C higher than in the preceding four decades. The range limits of upper shore species are more likely to be characterised by gradually diminishing abundance and size and increased patchiness as conditions become progressively harsher.

Lower shore species are more likely to respond to changes in the frequency and intensity of upwelling. *Fucus serratus* has extended its range in northern Spain since the 1980s (Arrontes, 1993, 2003) despite the warming climate. Increased upwelling is one possible explanation. During the 20th century there has been an upward trend in coastal upwelling off the northwest Iberian Peninsula (see §2.4) as well as in other major upwelling zones around the world (Bakun, 1973, 1990), which is likely to be related to increased wind strength due to climate change. However, it is not clear whether upwelling has, in fact, led to the expansion of *Fucus serratus*: although there is an increasing trend in upwelling on the north coast of Spain at 8°W (Figure 2.14c), this trend is not apparent at 6°W (Figure 2.14d); the limit of *F. serratus* lies between these two points, but closer to 6°W. Another possible factor is wave action: average wave height along the north coast of Spain showed a downward trend between 1972 and 1994 (Puertos del Estado, 2003) which may have allowed *F. serratus* to extend its range.

The differences between the responses of upper- and lower-shore species to variations in temperature are discussed further in Chapter 7.

3.7.3. Comparison with other studies

As discussed in §3.1.2 above, the number of studies that have looked at looked at the effects of climatic variation on rocky shore communities is relatively small. In order to obtain a full picture of change in communities, it is obviously desirable to study many species, at many different sites, and for many different years.

Existing studies, however, tend to be limited in at least one of these three important dimensions. Some studies, such as those of Southward *et al.* on limpets and barnacles in southwest Britain (Southward and Crisp, 1952, 1954; Southward, 1967, 1980, 1991; Southward *et al.*, 1995), have studied a few species at a few sites, but with replication over many years. By contrast, the work of Barry *et al.* (1995) and Sagarin *et al.* (1999) on rocky shore communities in mid-California looked at many species, but was restricted to one site, and compared only two widely separated time periods.

The present study has examined a moderate number of ecologically important species at many sites in the Bay of Biscay region, during a few different, widely separated time periods. The results support the conclusion of other authors (Southward *et al.*, 1995; Barry *et al.*, 1995) that there have been detectable effects of climate change on rocky shore communities during the course of the 20th century. In particular, cold-water species are now less abundant than they were during the warm period of the mid-20th century, which was proposed by Southward *et al.* (1995) as a test for the effects of climate change. This finding is in accordance with the pattern of climate-related change that has been observed in many ecosystems worldwide (reviewed by Parmesan and Yohe, 2003; see also review in Chapter 1 and discussion in Chapter 7).

This chapter has gone some way towards building up a broad-scale picture of climate-related change in rocky shore species in the Bay of Biscay. More extensive analysis of past data sources would be possible, particularly with reference to the unpublished field notes of past researchers. It is to be hoped that future workers will extend this investigation both backward and forward in time from the baselines that I have established.

Chapter 4: Responses of the limpets *Patella vulgata* L. and *P. depressa* Pennant to gradients in temperature in northern Spain

4.1. Introduction

This chapter investigates the responses to spatial variations in temperature of populations of the limpets *Patella vulgata* L. and *P. depressa* Pennant in northern Spain, and the mechanisms underlying these responses. In this introduction existing knowledge about the effects of climatic variation on rocky shore communities is reviewed, with a focus on its effects on limpets and the two species of interest in particular. The area of study is then described before giving the detailed objectives of the chapter.

4.1.1. Effects of climatic variation on rocky shore communities

Climatic factors, especially temperature, have profound and wide-ranging effects on rocky shore communities (see review in Chapter 1; see also, for example, Hutchins, 1947; Lewis, 1986; Breeman, 1988; Lüning, 1990; Sanford, 1999; Raffaelli and Hawkins, 1999). There are, however, many other causes of variation in these communities (Foster *et al.*, 1988), both natural (e.g. dynamic interactions between species: Hartnoll and Hawkins, 1985; Johnson *et al.*, 1998; Burrows and Hawkins, 1998; Johnson and Hawkins, 1998; Jenkins *et al.,* 1999a,b,c; variations in tidal regimes and upwelling: Helmuth *et al.,* 2002; Denny and Paine, 1998) and anthropogenic (e.g. predation: Castilla, 1999; trampling: Fletcher and Frid, 1997; Schiel and Taylor, 1999; and pollution: reviewed by Thompson *et al.,* 2002). Therefore, without a broad-scale, long-term monitoring programme, it may be hard to distinguish change in rocky shore communities due to rising temperatures from change due to other causes (Southward, 1995; Southward *et al.*, 1995; Denny and Paine, 1998; Underwood and Chapman, 2000).

One approach to detecting the effects of varying temperatures on communities is that of comparing the abundance of species with different geographical ranges but which occupy similar ecological niches. Long-term studies in Britain (Southward and Crisp 1954; Southward, 1967, 1980, 1991; Southward *et al.*, 1995) have linked variations in the abundance of warm- and cold-temperate species of barnacles with variations in sea temperature. The three species of barnacles studied were *Chthamalus stellatus* (Poli) and *C. montagui* Southward, two warm-temperate, Lusitanian species that reach their northern limits in Europe in Scotland (Lewis, 1986); and *Semibalanus balanoides* (L.), a boreal species that extends as far south as the northern Iberian Peninsula (Fischer-Piette and Prenant, 1956). The abundance of *Chthamalus* relative to that of all barnacles (mainly *Chthamalus* and *Semibalanus*) was positively correlated with inshore sea surface temperatures, with a time lag of two years, corresponding to the time between settlement and maturation (Southward, 1967, 1991). Comparing the abundance of similar species may have helped to minimize the effects of variation in other, non-climatic factors.

Southward *et al.* (1995) also found a broad relationship between sea surface temperature and the relative abundance of two species of limpets (the species considered in the present study): *Patella depressa* Pennant, a warm-temperate/subtropical species extending from Senegal to north Wales (Lewis, 1964) and the Isle of Wight (Crisp and Southward, 1958); and *P. vulgata* L., a cold-temperate/boreal species that extends from northern Norway to southwest Spain (Fischer-Piette, 1958; Guerra and Gaudencio, 1986). Correlations with temperature were not as strong for the limpets as for the barnacles, partly due to gaps in the data series; but nonetheless there was evidence that these two species do respond predictably to changes in temperature. To further explore this response it is necessary to review the existing knowledge on how the two species respond both to temperature and to other, non-climatic factors that may need to be controlled.

4.1.2. The effects of temperature on limpet populations

Extensive studies have been made of the effects of temperature on different processes affecting individual limpets, including mortality (e.g. Evans, 1948; Southward, 1958) and reproduction (e.g. Bowman and Lewis, 1986), with implications for populations and interactions with other species (e.g. Thompson *et al.*, 2000). The lethal upper temperatures of both *Patella vulgata* and *P. depressa* in air are between 40°C and 43.5°C, about 2°C higher in summer than winter (Evans, 1948). The body temperatures of rocky shore organisms are known to reach levels considerably higher than air temperatures, particularly when they are exposed to direct sunlight

(Southward, 1958; Davies, 1970; Helmuth, 1999). Heat-induced mortality of both species is therefore a possibility, particularly in southern Europe and in places where there is little shade or shelter available (Orton, 1928). However, the lethal temperatures of *P. depressa* are only about 0.6°C higher than those of *P. vulgata* (Evans, 1948). This small difference in the lethal temperatures of the two species cannot account for the large difference in their geographical range, and is unlikely to play a major part in determining their differential responses to variations in temperature. In general the lethal upper temperatures for rocky shore molluscs seem to be more closely related with their normal vertical position on the shore than with their geographical distribution (Evans, 1948; Southward, 1958).

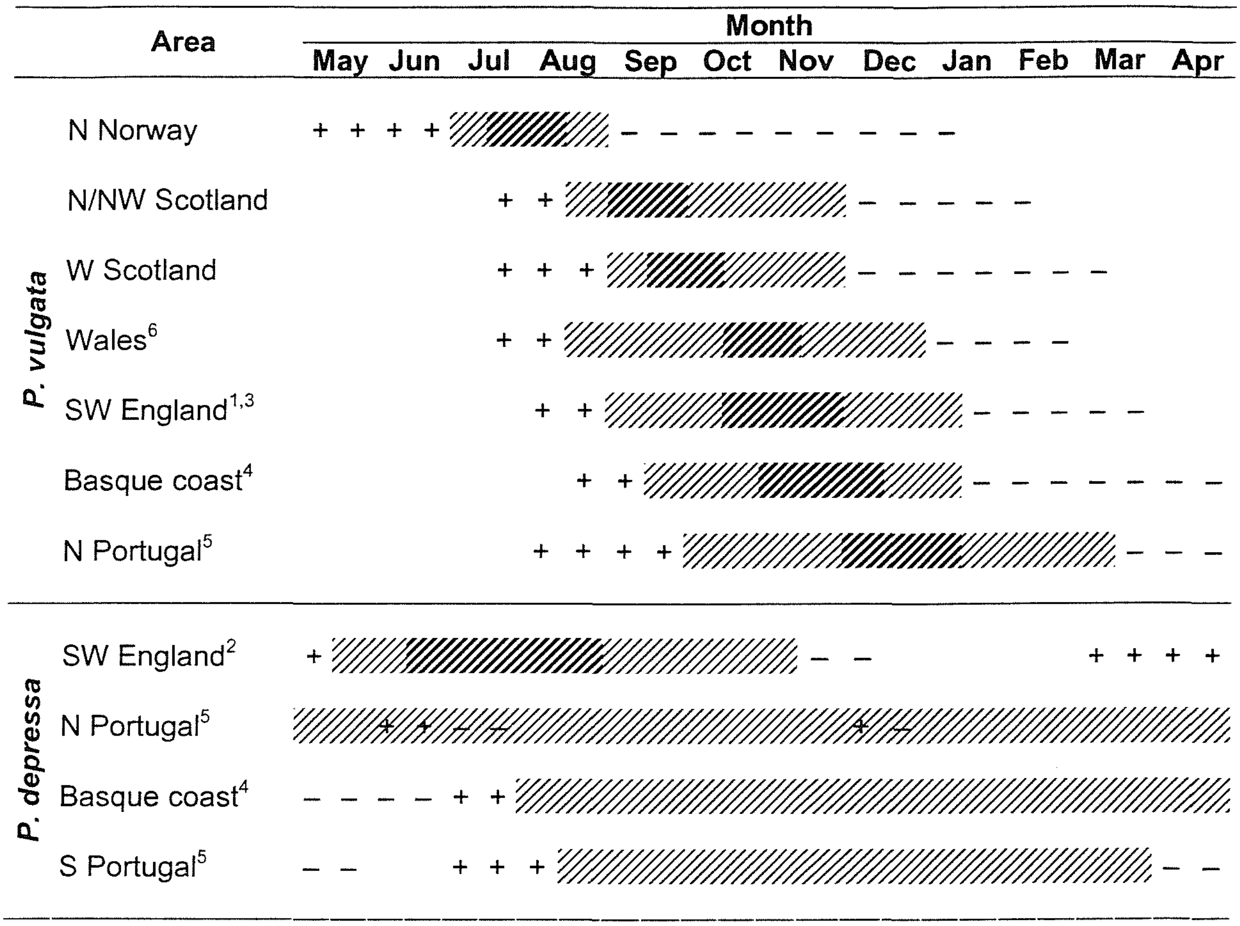
Lethal temperatures in sea water are around 35–40°C for *P. vulgata* and 40°C for *P. depressa* (Evans, 1948). Thus mortality due to high sea temperatures is unlikely to occur in either species in the northeast Atlantic; the highest sea temperature recorded since 1947 on the Basque coast, for example, was only 25.3°C (Borja *et al.*, 2000; see Chapter 2).

Extreme low temperatures are known to have caused widespread mortality of rocky shore organisms in the northeast Atlantic, for example during the very cold winter of 1962–63 (Crisp, 1964; Daguzan, 1991). Extreme low temperatures (down to –13°C) in southwest Britain in winter 1982 made *P. vulgata* unable to cling to the rock, leading to a population crash as limpets were washed away by waves (Little and Kitching, 1996). However, it is not known to what extent low temperatures affect *P. vulgata* and *P. depressa* differentially.

There have been numerous studies of the effects of temperature on limpet reproduction. External fertilization occurs in both *Patella vulgata* and *P. depressa,* with spawning thought to be triggered by storms (Orton *et al.*, 1956; Orton and Southward, 1961). In common with many other patellid gastropods (Fretter and Graham, 1962), *P. vulgata* is a protandrous hermaphrodite, with most individuals (in Britain) becoming female by their fourth year (Orton *et al.*, 1956; Bowman and Lewis, 1977), whereas *P. depressa* does not appear to change sex in Britain (Orton *et al.*, 1956; Orton and Southward, 1961). Reproductive failure can result from temperatures in the breeding season that are too low to permit successful completion of reproduction; near the northern limits of *P. depressa*, this typically leads to populations dominated by large, old individuals (Lewis, 1986).

Table 4.1. Seasonal timing of reproduction in the limpets *Patella vulgata* and *P. depressa* on rocky shores in different areas of Western Europe. Adapted from Bowman and Lewis (1986), with additional data from Orton *et al.* (1956)[1], Orton and Southward (1961)[2], Ballantine (1961a)[3], Ibañez (1984)[4], Guerra and Gaudencio (1986)[5] and Davies *et al.* (1990)[6]. Symbols give the period when spawning takes place:

+ gonads develop ▨ spawning may occur ▩ main spawning period – gonads decline



Temperature also affects the timing of reproduction (see Table 4.1.) In *P. vulgata,* spawning is possibly triggered by sea temperatures falling below 12°C (Lewis, 1986). This could explain a latitudinal trend in the onset of spawning, from July/August in northern Norway to December/January in northern Portugal (Bowman and Lewis, 1986; Ibañez, 1984; Guerra and Gaudencio, 1986). It seems likely that this temperature requirement is not often met near the southern limits of *P. vulgata* in southern Portugal, leading to reproductive failure (Lewis, 1986).

Spawning in *P. depressa* tends to be more spread out through the year, at least in southern Europe. Near its northern limits in Britain, however, there is a main spawning period in summer and early autumn (Orton and Southward, 1961;

Ballantine, 1961a). In northern and central Portugal, the species spawns throughout the year, with only some individuals displaying neuter characteristics ("resting") in midsummer and midwinter (Guerra and Gaudencio, 1986). On the Basque coast and in southern Portugal, high temperatures in summer lead to a distinct resting period (Guerra and Gaudencio, 1986; Ibañez, 1984). Thus both *P. vulgata* and *P. depressa* reproduce predominantly in summer near their northern limits and in winter near their southern limits.

The size frequency of limpet populations is also affected by the latitudinal gradient in temperature. Populations further south show faster growth, smaller maximum size and shorter lifespan (Guerra and Gaudencio, 1986). In areas where failure to repopulate limits species range, population size distribution is typically irregular, with gaps representing years of reproductive failure (Lewis, 1986). Comparison of size distributions between Northern and Southern Europe, however, needs to take an additional factor, predation, into account. Limpets are predated by a number of other species including humans. Human predation of limpets is intense throughout the Atlantic coast of Spain and Portugal (Guerra and Gaudencio, 1986) and larger limpets are no doubt taken preferentially. Discussions with fishermen in Ribadesella on the north coast of Spain (see Figure 4.1) indicate that there is also a preference for limpets with a taller shell, which suggests preferential predation of *P. vulgata* over *P. depressa.* Limpet size frequency can also be affected by local habitat variations (Lewis and Bowman, 1975) and its study requires regular and careful sampling of large numbers of limpets.

Interactions with other species may also be important. *Patella vulgata,* but not *P. depressa*, is known to shelter beneath fucoid algae canopies (Burrows and Lodge, 1950; Southward and Southward, 1978; Hartnoll and Hawkins, 1985; Johnson *et al.*, 1998; Burrows and Hawkins, 1998), so fucoid abundance may modify the effects of temperature on *P. vulgata*.

In general, it is clear that both summer and winter temperatures can affect these two species in different ways, and that their use as indicators of the effects of climate change on rocky shore communities therefore depends on being able to distinguish between the effects of changes in temperature at different times of year. Northern Spain is a particularly interesting area from this point of view because variations along the coast in summer and winter temperature show very different patterns (as discussed in §4.1.4).

4.1.3. Effects of non-climate-related factors

Like all rocky shore organisms, limpets are affected by major vertical (marine-terrestrial) and horizontal (wave exposure) environmental gradients that characterise this habitat; the effects of these gradients must therefore be controlled or sampling stratified in order to study their response to temperature. The horizontal and vertical distribution of both species varies with latitude (Ballantine, 1961a). In Britain, *P. vulgata* is the dominant species of limpet, found from the upper to lower shore and in all conditions of wave exposure from very sheltered to exposed, although it is less common on sheltered shores dominated by fucoid algae (Ballantine, 1961b). In Britain *P. depressa,* by contrast, is mainly restricted to the upper mid shore in exposed conditions (Evans, 1948, 1953; Orton and Southward, 1961). Further south, in northern Spain, *P. depressa* predominates, being common from upper to lower shore and from sheltered to exposed shores. *P. vulgata*, on the other hand, while still found at all shore levels, is progressively restricted to greater shelter towards the south (Ballantine, 1961a).

4.1.4. The area of study

The area of study extended from the Basque coast of southwest France to the Rias Bajas of Galicia, northwest Spain (a distance of about 750 kilometres; see Figure 4.1). Apart from the Basque coast (Ibañez, 1984, 1991; Ibañez *et al.*, 1986), few studies of *Patella* seem to have been carried out in northern Spain. Early studies (Fischer-Piette, 1953, 1960, 1963; Fischer-Piette and Gaillard, 1959) were mainly broad scale semi-quantitative mapping. Data extending back over long periods of time are thus not available, although some comparisons with the work of Fischer-Piette can be made.

Spatial variations in summer and winter sea surface temperatures that occur in the region make it a particularly valuable area for studying the effects of climate on rocky shore communities. Figure 4.1 demonstrates this by plotting mean winter sea surface temperatures for 1999–2001 (on the y-axis; note inverted scale) against corresponding summer temperatures on the x-axis.

Table 4.2. Sites surveyed during 2002.

		Area		
Months	**West**	**Centre**	**East**	
March-April		Ribadeo Salinas	Ribadesella San Vicente Suances	Loredo Sonabia (E-W) Hondarribia Biarritz
May		Luarca Salinas	Luanco Villaviciosa Ribadesella	
July	O Grove A Coruña	Luarca Ribadeo	Luanco Villaviciosa Ribadesella	
September	Porto do Son Muxia Malpica Prioiro	Cariño Burela Foz	San Vicente Suances	
November	Ribeira Caamaño Porto do Son Caion (E-W) Mera		Gijon Ribadesella Llanes	

Unusually, winter and summer sea temperatures do not follow the same trends along the north coast of Spain. The inner Bay of Biscay (Basque coast) is hotter in summer and colder in winter than the northwest of the peninsula (Galicia). This is due to a combination of climatic features of the region: continental influence (Ibañez, 1989, 1990), warm, stratified surface water in the Bay of Biscay in summer (Crisp, 1989), and upwelling of cold water off the northwest coast, also in summer (Molina, 1972; Bakun, 1990; Botas *et al.*, 1990; Nogueira *et al.*, 1997). These climatic patterns are discussed in greater detail in Chapter 2.

Figure 4.1 demonstrates that the relationship between summer and winter sea surface temperatures is different between two different areas of the coast. Along the north coast, mean summer sea surface temperatures decrease rapidly from Biarritz, 21.32°C, to Cariño, 19.19°C: a difference of 2.21°C. This is five times as great as the change in mean winter temperatures along the same coast (0.45°C). On the northwest coast from Prioiro to O Grove, the pattern is reversed: there is six times as much variation in mean winter temperatures (0.53°C) as in mean summer temperatures (0.08°C). Thus comparisons between sites along the north coast make it possible to study the effects of summer temperature, while minimizing variation in winter temperature between sites. Conversely, comparing sites along the northwest coast allows the effects of winter temperature to be studied while minimizing variation in summer temperature.

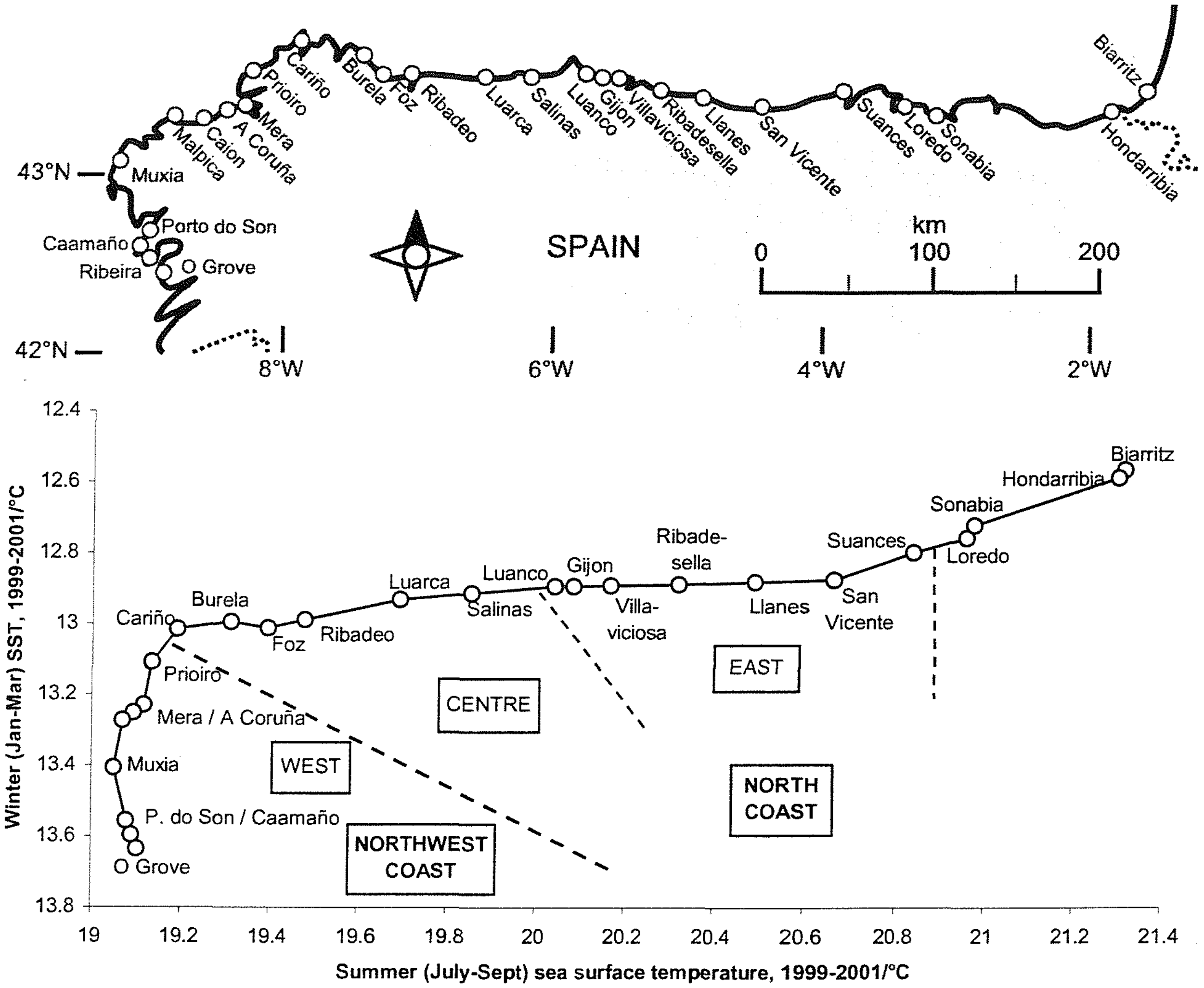


Figure 4.1. (top) Sites in northern Spain and southwest France surveyed by the author during 2002. (bottom) Mean winter (January–March) sea surface temperatures for 1999–2001 on the y-axis, plotted against corresponding summer (July–September) temperatures on the x-axis, for the same sites. Axes are equally scaled; y-axis is inverted (low temperatures at top of graph). Dashed lines and labels in boxes denote the areas that were used in the data analysis; see §4.2.2. Temperatures from the Reynolds SST data set (NOAA–CIRES Climate Diagnostics Centre, 2003).

4.1.5. Objectives

The overall aims of this chapter are to investigate the effects of gradients in temperature on the relative abundance, size frequency and reproduction of two species of limpet, *Patella vulgata* L. and *P. depressa* Pennant, in northern Spain, thereby evaluating the likely effects of climate change on these species.

The specific objectives of the chapter are as follows:

1. To survey the abundance of *Patella vulgata* and *P. depressa* in the area of study, from the French Basque coast to the Rias Bajas of Galicia.
2. To investigate variations in size, sex ratios and reproductive activity for both species within this area.
3. To relate spatial variations along the coast in these population variables with temperature and, where possible, make comparisons with other parts of the range of both species.
4. On the basis of the results of objectives 1 to 3 above, and in comparison with data from other areas, to evaluate the likely response of these two species to climate change, both in the area of study and throughout their joint range.

4.2. Methods

4.2.1. Survey, sampling and treatment of samples

Between March and November 2002, a total of 40 surveys of populations of *Patella vulgata* and *P. depressa* were made at 28 different rocky shore sites in northern Spain and one in southwest France (see Figure 4.1 and Table 4.2). All sites were moderately exposed to very exposed, with the exception of A Coruña, which was sheltered.

The sites were chosen in order to cover the area of the study as completely as possible, while maintaining a balance between different areas of the coast in each survey. Logistical considerations made it difficult to visit sites in all the areas in each survey, however. The possible implications of this are considered in §4.4.1.

All surveys were made of areas of smooth, seaward-sloping rock around mid-tide level, avoiding overhangs, rock pools and crevices of greater than 2cm in size.

In each survey the number of individuals of *Patella vulgata* and *P. depressa* were counted in 50 x 50cm quadrats. In order to obtain accurate estimates of abundance, at least 200 limpets were counted at each site. The exception was in the September surveys at San Vicente and Suances, where only 100 limpets were counted due to time limitations. At sites where less than 5 of one species were found, a wider search was made so as to make a general estimate of the abundance of that species in individuals per square metre.

As well as counting limpets *in situ,* samples were collected in all the surveys carried out between May and November 2002. At least 200 limpets were taken from each site (again, except for San Vicente and Suances, where only 100 were taken).

Samples were separated by species and preserved by freezing. On removal from the freezer the bags were immersed in warm water for a few hours. As well as thawing the limpets, this treatment weakened the bond between the body and the shell, allowing removal of the body with forceps (much easier than cutting through the foot). The gut of each animal was cut away from the mantle and turned back to reveal the gonad. Gonads were classified into stage 0 (neuter or resting) and stages I through V, male and female, using the scale described by Orton *et al.* (1956). Shell length was measured to the nearest millimetre.

4.2.2. Data analysis

4.2.2.1. Abundance

Mean abundance and standard error of the mean, in individuals per $0.25m^2$ quadrat, were calculated for each species in each survey. A Coruña, being the only sheltered site, was excluded from this analysis. Two indices of relative abundance were calculated: $Pv / (Pv + Pd)$, the proportion of *P. vulgata* out of the total abundance of both species; and $\log_{10} (Pv/Pd)$, the logarithm of the ratio in abundance between the species. Abundance of each species and both indices of relative abundance were plotted against summer temperature along the north coast (Figure 4.2) and against winter temperature along the northwest coast (Figure 4.3). The sites in each area are given in Figure 4.1. For those variables for which correlations with temperature were found, straight-line regressions were performed. The predictive power of the resulting equations was tested by comparing their predictions with existing data from 1981 for temperature (Borja *et al.*, 1997) and the abundance of *P. vulgata* and *P. depressa* at Zumaya on the Basque coast (Ibañez, 1991).

To test for seasonal differences, the results from surveys carried out in the months of March–April, May–July, and Sept–Nov were individually regressed against temperature. The resulting regression lines were tested for homogeneity of slope using ANCOVA.

4.2.2.2. Size frequency

The samples collected during the May, July and September surveys were analysed to determine whether there was a difference in size frequency between different areas of the coast. The November surveys were excluded from this analysis, because in these surveys individuals were collected from outside the quadrats to augment the number of samples, so the resulting size frequency distributions were not considered to be an unbiased representation of the population as a whole. The data were grouped into three areas (shown on Figure 4.1): east (summer SST of 20.04–20.84°C), central (summer SST of 19.19–19.85°C), and west (summer SST of 19.05–19.13°C). Histograms based on 2mm size classes were plotted for each species and each area (Figures 4.4 and 4.5).

G-tests (Fowler *et al.*, 1998) were used to test whether there was a difference in the size frequency of each species between the three areas.

Because the size frequency distributions were approximately log-normal, a nested ANOVA was performed on log length data, to test for differences in mean length among shores within each area, and among the three areas. Both shore and area were treated as random variables.

In order to detect seasonal variations in mean length, a comparison was made, again using ANOVA on log-length data, between May and July, in the East and Central areas only. These were the only months for which an unbiased comparison was possible because the sites surveyed were very similar (see Table 4.2).

4.2.2.3. Sex ratios

Sex ratios (proportion of males out of males plus females) were calculated in 5 mm size classes for each species and plotted on histograms (Figure 4.6) together with corresponding sex ratios observed in studies carried out in Britain (Orton *et al.*, 1956;

Orton and Southward, 1961). Binomial standard errors for the sex ratios from the present study were estimated using the formula $\sqrt{[p(1-p)/(n-1)]}$, where p is the sex ratio and n is the number of individuals (Fowler *et al.*, 1998).

For *P. vulgata*, because the species is protandrous, the ratio of males to females is known to vary with size in Britain (Orton *et al.*, 1956). A G-test was used to test the hypothesis that the number of males and females in each size class did not differ as a whole from the ratios observed in Britain.

The sex ratios for *P. vulgata* were also plotted separately for samples from the north coast and the northwest coast (Figure 4.7) to observe whether the ratios differed systematically between the two areas.

In the case of *P. depressa,* the sex ratio is approximately the same in all size classes (Orton and Southward, 1961) although the raw data have not been published. A G-test was performed to test the hypothesis that the sex ratio for *P. depressa* in Spain was the same in all size classes. A comparison between sex ratios for the north and northwest coasts was also performed, again using a G-test.

4.2.2.4. Reproductive activity

Two indices of reproductive activity were used: (a) the modal reproductive stage, 0–V; (b) the percentage of individuals classified as stage IV or V (Orton *et al.*, 1956). Both indices were based on individuals of shell length 21mm or greater. These indices were calculated for each species, month (May, July, September and November) and area of coast (north versus northwest coast: see Figure 4.1). The May survey only covered the north coast, so no samples were available from the northwest coast in that month. For months when there was a notable difference (approximately one standard error or more) in the percentage of individuals classified as stage IV or V between the two areas, a G-test was performed to test whether this difference was significant. The results were compared qualitatively with reproductive patterns from other areas of Europe (Table 4.1) to see whether they conformed to the observed latitudinal patterns.

The "Prestige" oil spill, which began on 13 November 2002 (Bohannon *et al.*, 2002), one week prior to the November 2002 surveys, affected four of the sites surveyed in this month: Caion (East and West), Porto do Son and Caamaño. These four sites were excluded from the analysis of reproductive activity because of the possibility that the oil might have had short-term effects on the reproductive biology of the limpets.

4.3. Results

4.3.1. Abundance

There was no correlation between the abundance of either species, or the two indices of relative abundance, and winter temperature for the sites along the northwest coast (Figure 4.3: 9 d.f., $p>0.05$). However, correlations between all four variables and summer temperature were found for sites along the north coast (Figure 4.2: 26 d.f., $p<<0.001$). The abundance of *Patella vulgata* was negatively correlated with summer temperature while the abundance of *Patella depressa* was positively correlated. The correlation was better when the two indices of relative abundance were considered than for each species on its own.

The best correlation with summer temperature was for $\log_{10}(Pv/Pd)$, the index of log relative abundance. The equation of the best-fit straight line was:

$$\log_{10}(Pv/Pd) = (19.66°\text{C} - T) / 0.71°\text{C} \qquad (R^2 = 0.6573^{***}) \qquad [4.1]$$

This equation predicts that, on the north coast of Spain, a 0.71 °C increase in summer sea temperature will lead to a tenfold reduction in the abundance of *Patella vulgata* relative to *P. depressa*. The intercept, 19.66°C, represents the temperature at which the abundance of the two species is predicted to be equal.

For $Pv/(Pv+Pd)$, the proportion of *Patella vulgata* relative to the total of both species, the correlation was almost as good. The equation of the best-fit straight line was:

$$Pv/(Pv+Pd) = (20.98°\text{C} - T) / 2.648°\text{C} \qquad (R^2 = 0.6495^{***}) \qquad [4.2]$$

This equation predicts that the proportion of *Patella vulgata* relative to both species will be zero at a summer sea temperature of 20.98°C and 100 per cent at 18.33°C. Equation 4.2 is clearly only applicable between these extremes; it does not work, for example, where summer temperatures exceed 21 °C: according to the equation, the abundance of *Patella vulgata* ought then to be negative. By contrast, equation 4.1 is, in theory, applicable at any temperature within the joint range of the two species.

To test the predictive power of these two equations, predictions were made of the relative abundance of the two species at Zumaya on the Basque coast in 1981. Data on the abundance of the two species are available for this location (Ibañez, 1991), while temperature data are available from San Sebastian Aquarium (Borja *et al.*, 2000).

Mean July–September sea temperatures for 1978–1980 at San Sebastian were 20.38°C. Correcting for the position of Zumaya 30km west of San Sebastian, based on the typical change in sea temperature with distance along the Basque coast (see Chapter 2), gives a summer temperature of approximately 20.3°C. For this temperature, Equation 4.1 predicts a value for $\log_{10}$ (*Pv/Pd*) of –0.901, meaning that *P. vulgata* would comprise 11.1% of total abundance of both species. Equation 4.2, by contrast, predicts that *P. vulgata* would comprise 25.7% of total abundance. The observed abundances of each species at Zumaya in 1981 (Ibañez, 1991) were 26.5 ±2.9 *P. depressa* per square metre and 3.76 ±0.38 *P. vulgata* per square metre. Thus *P. vulgata* in fact constituted 12.4% ±2% of the total abundance of both species. Equation 4.1 thus successfully predicts relative abundance at Zumaya in 1981 while Equation 4.2 overestimates the abundance of *P. vulgata* by a factor of two.

The results from surveys carried out in the months of March–April, May–July, and Sept–Nov were each, individually, correlated with temperature ($p<0.00001$). The resulting regression lines were tested for homogeneity of slope using ANCOVA; no differences between months were found (Pv/(Pv+Pd): $F_{(2,22)}=0.29$, $p=0.75$; $\log_{10}$ (Pv/Pd): $F_{(2,22)}=0.11$, $p=0.90$).

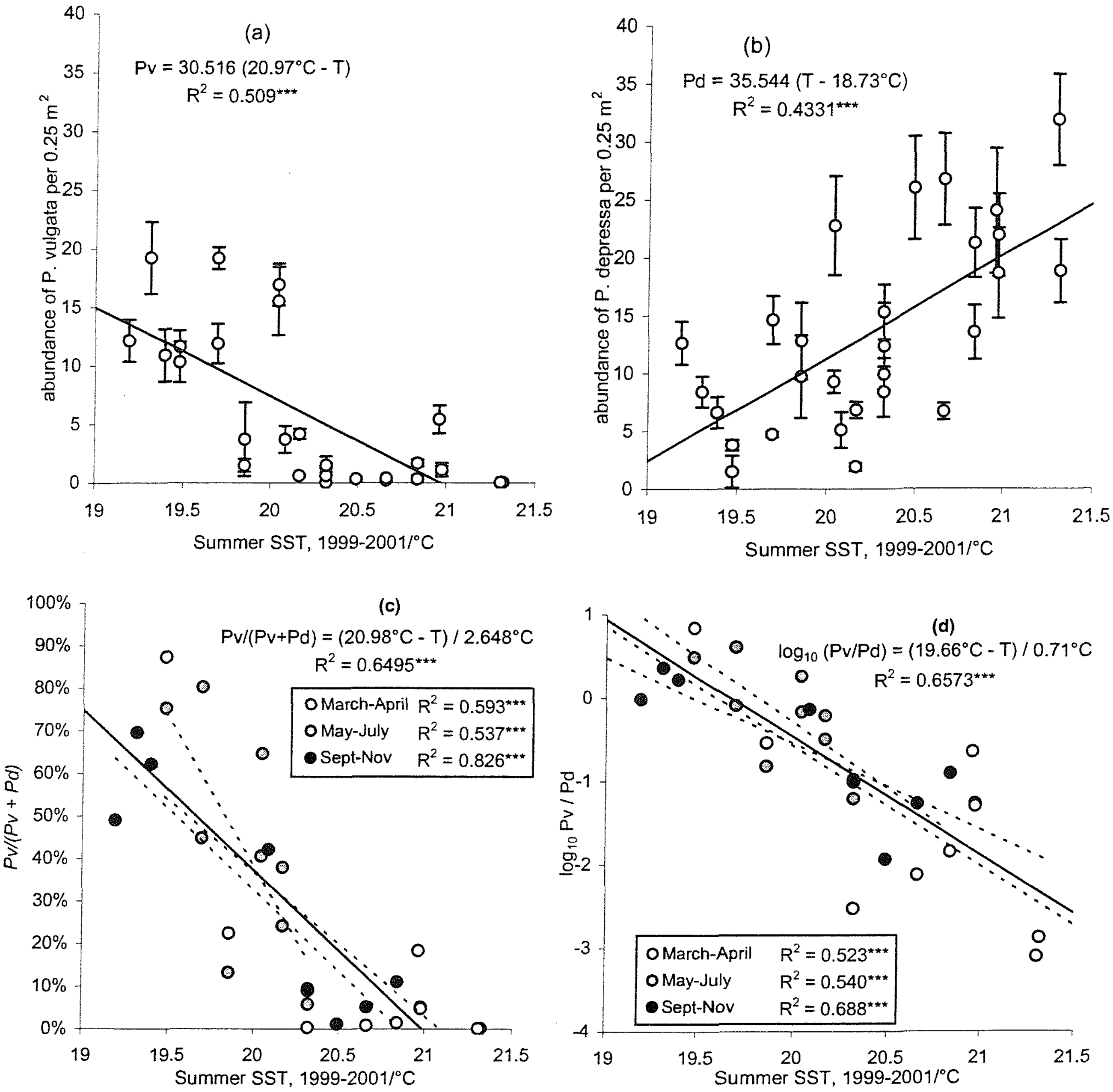


Figure 4.2. Plots against summer (July–Sept) sea surface temperature for 1999–2001, of four measures of limpet abundance based on 28 surveys carried out in March–Nov 2002 at sites along the coast from Biarritz (Pays Basque) to Cariño (Galicia). See Figure 4.1 for sites. Temperatures from the Reynolds SST data set (NOAA–CIRES Climate Diagnostics Centre, 2003).
(a–b): Abundance in individuals per 0.25 square metres of *Patella vulgata* (a) and *P. depressa* (b).
(c): Index of relative abundance of *P. vulgata* as a percentage of total abundance of both species.
(d): Log_{10} of abundance of *P. vulgata* divided by abundance of *P. depressa.*
The correlation with temperature in each case was significant (a: $F_{(1,26)}=27.0$, $p=0.00002$; b: $F_{(1,26)}=19.9$, $p=0.00014$; c: $F_{(1,26)}=48.2$, $p<0.00001$; d: $F_{(1,26)}=49.9$, $p<0.00001$). Statistics were performed on mean abundance at each site.
In (c–d), the results from surveys carried out in the months of March–April, May–July, and Sept–Nov were each, individually, significantly correlated with temperature ($p<0.00001$). The resulting regression lines (dotted lines) were tested for homogeneity of slope using ANCOVA; no significant differences between months were found (c: $F_{(2,22)}=0.29$, $p=0.75$; d: $F_{(2,22)}=0.11$, $p=0.90$).

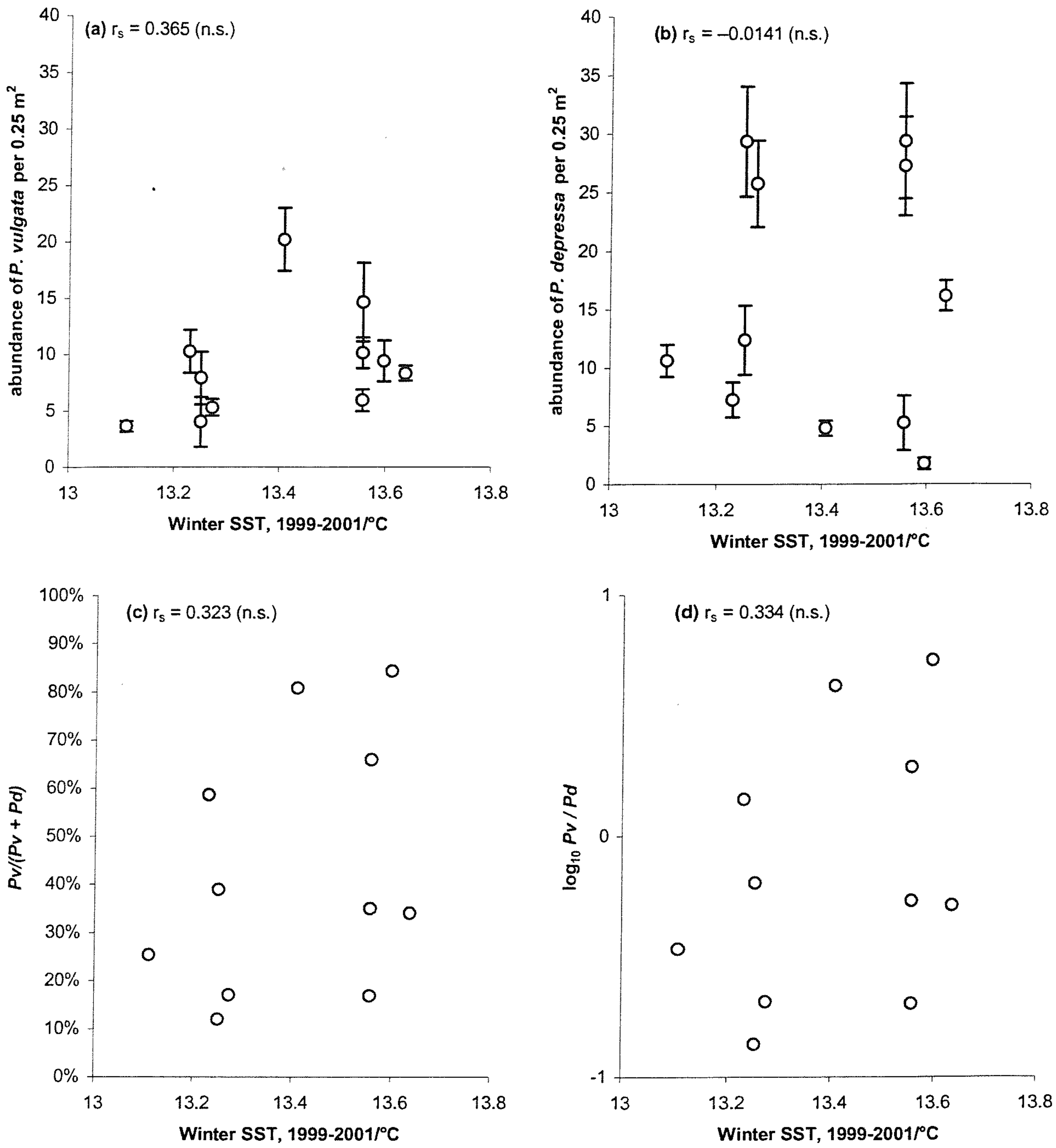


Figure 4.3. Plots against winter (Jan–March) sea surface temperature for 1999–2001, of four measures of limpet abundance based on 12 surveys carried out in Sept–Nov 2002 at sites along the coast of Galicia (NW Spain) from Prioiro to O Grove. See Figure 4.1 for sites. Temperatures from the Reynolds SST data set (NOAA–CIRES Climate Diagnostics Centre, 2003).

(a–b): Abundance in individuals per 0.25 square metres of *Patella vulgata* (a) and *P. depressa* (b). (c): Index of relative abundance of *P. vulgata* as a percentage of total abundance of both species. (d): Log_{10} of abundance of *P. vulgata* divided by abundance of *P. depressa*. No significant correlation with temperature was found for any of the four variables (a: $F_{(1,9)}=1.38$, p=0.27; b: $F_{(1,9)}=0.02$, p=0.97; c: $F_{(1,9)}=1.04$, p=0.33; d: $F_{(1,9)}=1.13$, p=0.32). Statistics were performed on mean abundance at each site.

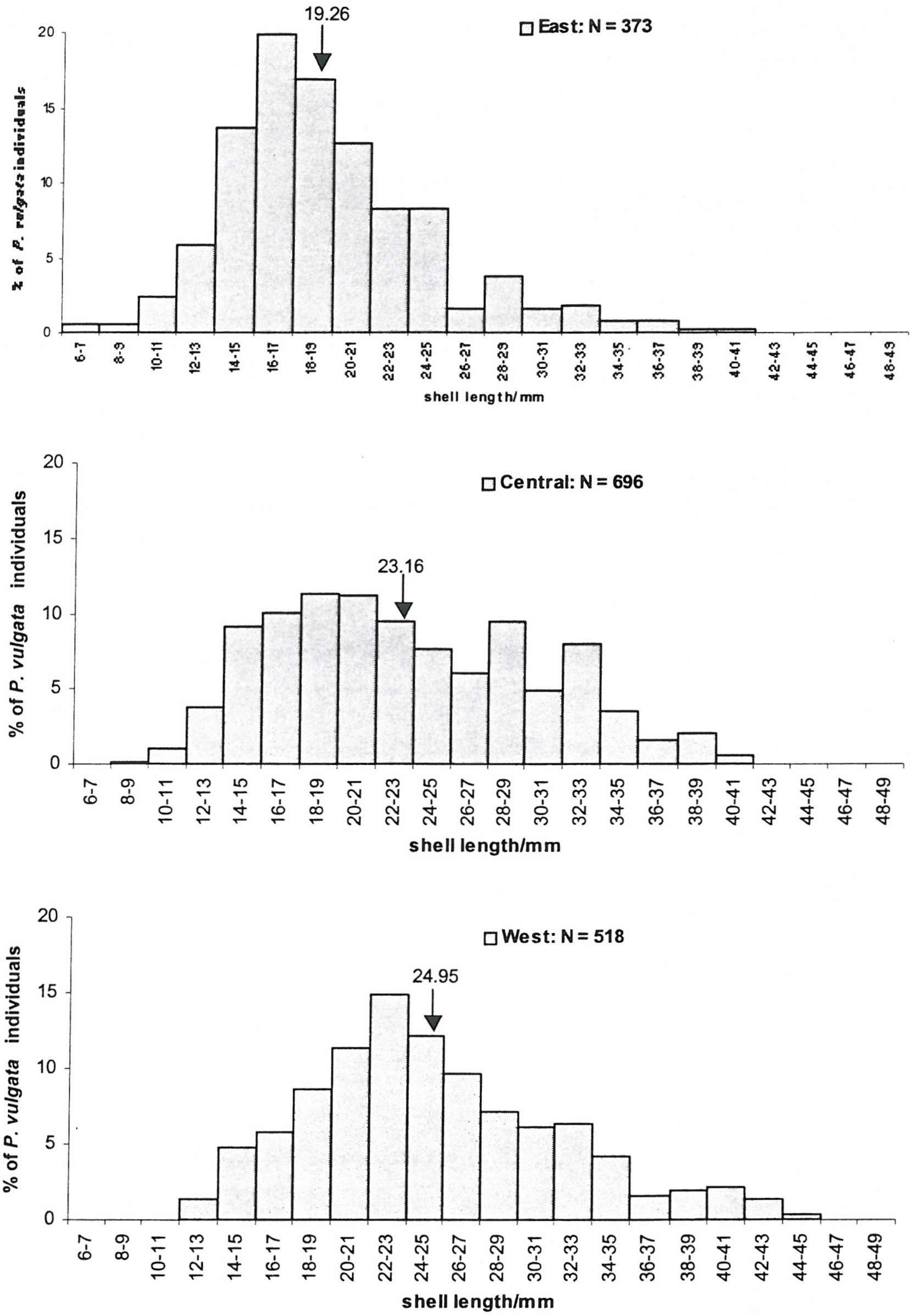


Figure 4.4. Size frequency by 2mm length classes, for samples of *Patella vulgata* collected in 2002, pooled from different shores in three areas of northern Spain. The mean size in each area is indicated with an arrow.

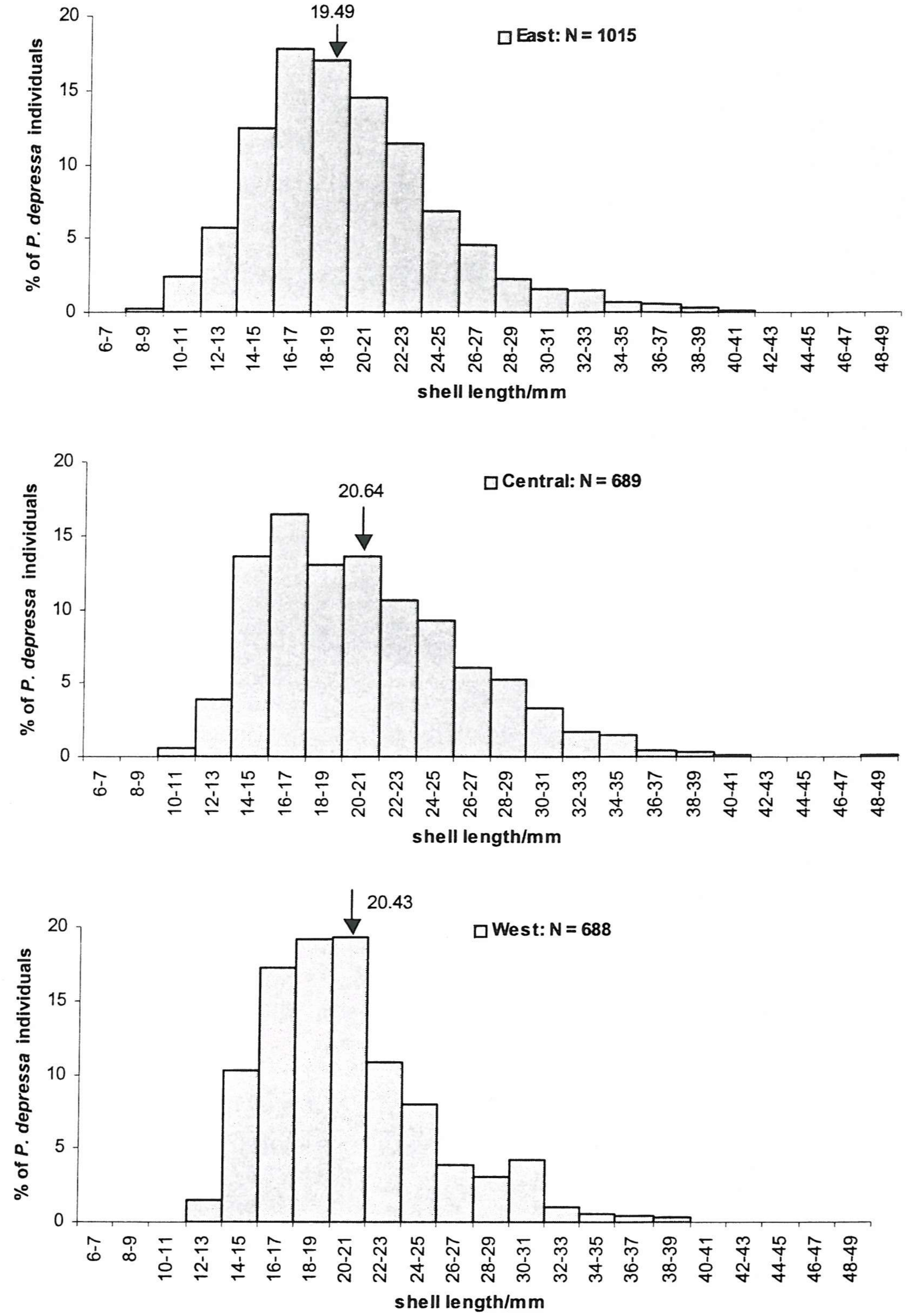


Figure 4.5. Size frequency by 2mm length classes, for samples of *Patella depressa* collected in 2002, pooled from different shores in three areas of northern Spain. The mean size in each area is indicated with an arrow.

4.3.2. Size frequency

For both species, differences were found in mean length among shores within each area (East, Central and West) ($p<<0.001$), while no differences were found among areas ($p>0.05$); see Table 4.3.

Differences (G-test: $p<<0.001$) were found in limpet size frequencies between areas of the coast (East, Central and West) for both *P. vulgata* and *P. depressa*. However, because of the nature of the test, this did not give an indication of which areas were different or in what way.

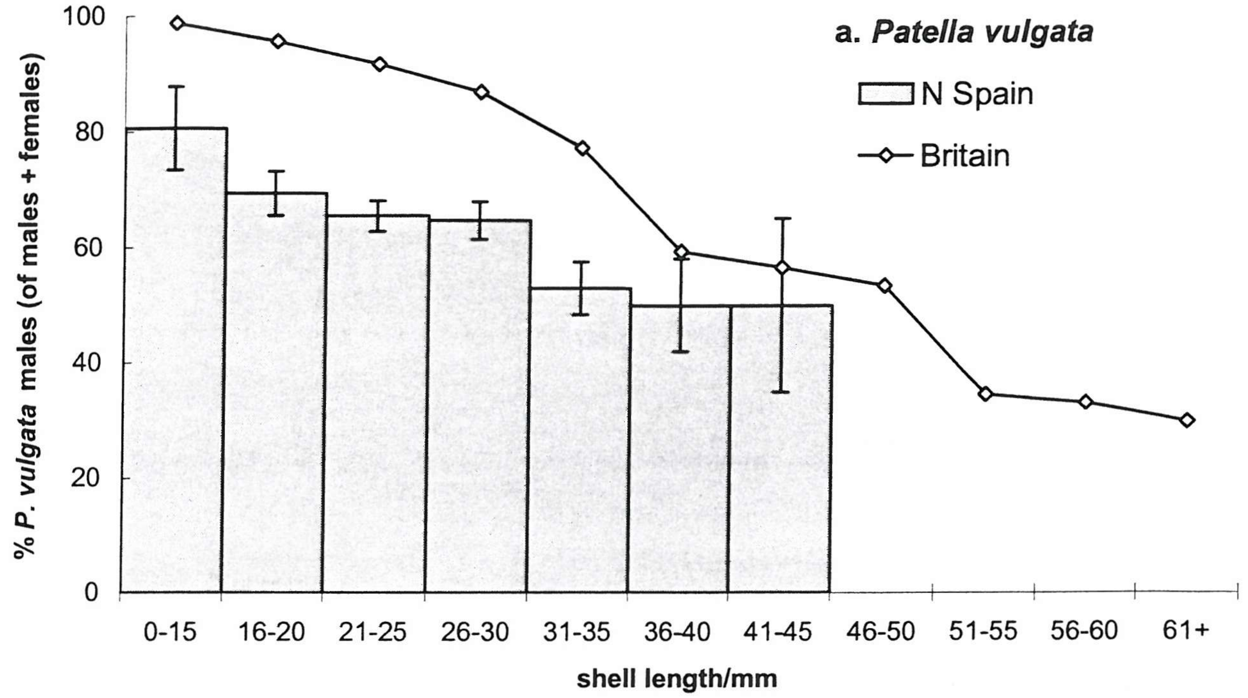
In qualitative terms, for *P. vulgata* there was a notable dearth of larger individuals (longer than 25mm) in the eastern area. This is suggestive of elevated mortality that could be linked to high summer temperatures or to human predation.

The peaks in the frequency of *P. vulgata* in the east and central areas at 28–29 mm and 32–33 mm could be due to variation between the sizes of successive cohorts, indicative of intermittent reproductive failure (Lewis, 1986). In general, the differences between areas were much more marked for *P. vulgata* than for *P. depressa,* suggesting that *P. vulgata* responds more to variations in temperature. However, it should be noted that variation among shores could account for the differences in size frequency between areas, as it did for the differences in mean size.

Comparison between months for samples taken in the East and Central areas found no difference between the mean length of *P. depressa* in May (19.6mm) and in July (19.7mm) ($F_{(1,1272)}=0.58$, $p=0.45$). For *P. vulgata,* mean length in May (21.9mm) was less than in July (22.8mm) ($F_{(1,735)}=4.0$, $p=0.045$).

Table 4.3. Nested ANOVA of mean log length, among areas and shores within areas.

Sp.	Source of variation	d.f.	SS	MS	F
P. depressa	Among areas	2	0.413	0.207	0.429 *n.s.*
	Among shores, within areas	14	6.749	0.482	61.320 ***
	Within shores	2424	19.058	0.008	
	Total	2440			
P. vulgata	Among areas	2	1.789	0.895	3.132 *n.s.*
	Among shores, within areas	14	3.998	0.286	22.344 ***
	Within shores	1392	17.792	0.013	
	Total	1408			



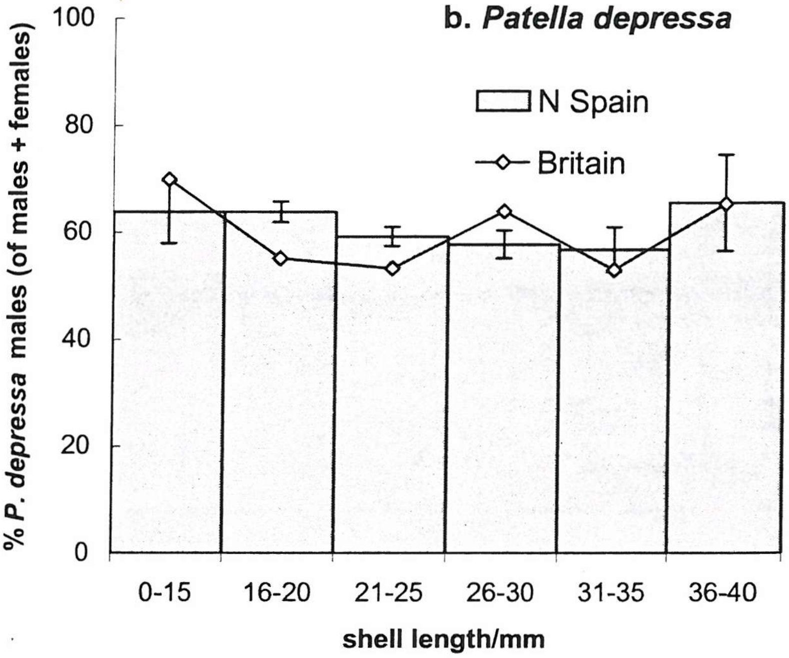


Figure 4.6. Sex ratios in Spain and Britain of two species of limpets: *Patella vulgata* (a) and *P. depressa* (b). Y-axes give number of males (as a percentage of males plus females), by 5mm length classes, among samples of two species of limpets collected in northern Spain in May–November 2002 (bars), compared with the corresponding percentage for Britain (lines). Error bars give standard errors for the sex ratios calculated using the formula given in §4.2.2.3 above (Fowler *et al.*, 1998). (a) *Patella vulgata,* based on 894 individuals collected in northern Spain in May–Nov. 2002, compared with 5 278 individuals collected in Britain in 1946–52 (Orton *et al.*, 1956). (b) *Patella depressa,* based on 1 952 individuals collected in northern Spain in May–Nov. 2002, compared with estimated sex ratios based on an unspecified number (about 1000) of individuals collected in Britain in 1946–48 (Orton and Southward, 1961).

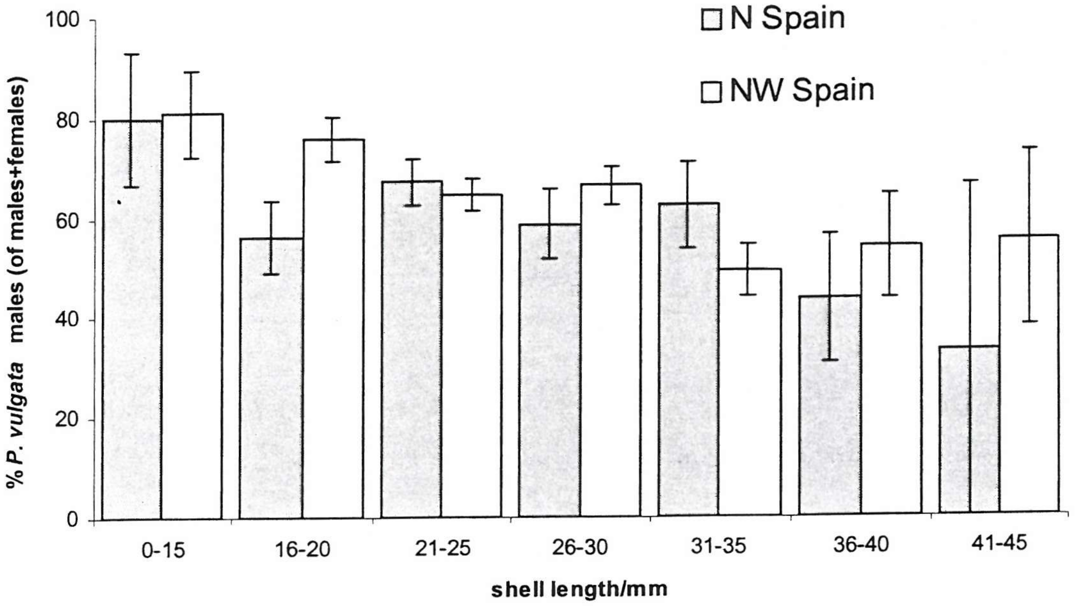


Figure 4.7. Males (as a percentage of males and females), by 5mm length classes, among 258 individuals of *Patella vulgata* collected on the N coast of Spain, and 624 individuals collected on the NW coast of Spain, in May–November 2002. See Figure 4.1 for location of sites. Error bars give standard errors for the sex ratios.

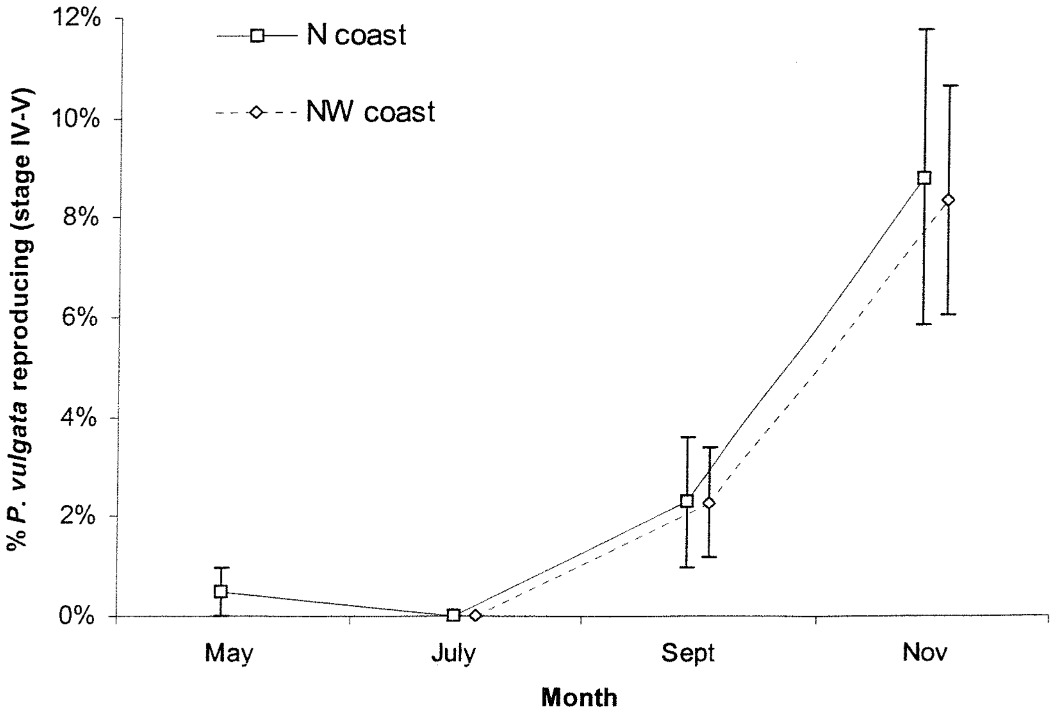
4.3.3. Sex ratios

Testing to see whether the numbers of males and females of *P. vulgata* in each 5mm size class in Spain (Figure 4.6a) differed from the sex ratios previously found in the same size classes in Britain (Orton *et al.*, 1956), gave a difference ($G_{(6)}=391$, $p<0.00001$): more females were found in all size classes in Spain than in Britain. The difference between sex ratios in Spain and Britain was smaller with increasing shell length. Visual comparisons of sex ratios for the north and northwest coasts of Spain (Figure 4.7) showed no systematic difference between the two areas.

Sex ratios in *P. depressa* (Figure 4.6b) showed no difference between 5mm size classes ($G_{(5)}=6.0$, $p=0.43$). The overall sex ratio for all individuals of *P. depressa* combined was 60.5%, with 95% confidence limits of 58.3–62.7% (using the formula for standard error of a proportion from Fowler *et al.,* 1998, cited above in §4.2.2.3). Comparing sex ratios for *P. depressa* from the north and northwest coasts (for all size classes combined) gave no difference between the two areas. ($G_{(1)}=1.65$, $p=0.20$)

4.3.4. Reproductive activity

The pattern of reproduction in both species conformed to the general latitudinal trends shown in Table 4.1. For *P. vulgata* (Figure 4.8) there were no differences between reproduction on the north and northwest coasts. Both areas showed a clear pattern of autumn/winter reproduction similar to that seen in southwest Britain, the Basque coast and northern Portugal (Table 4.1). *P. depressa,* in contrast, did show differences in reproduction between the north and northwest coasts in November ($G_{(1)}=12.6$, $p=0.0005$) but not in September ($G_{(1)}=3.46$, $p=0.06$) (Figure 4.9). On the northwest coast, indices of reproduction were more-or-less constant throughout the period of study, with little indication of a summer resting period as observed in northern Portugal (Guerra and Gaudencio, 1986). On the north coast, however, reproduction came to a peak in September and declined rapidly thereafter, indicating a main spawning period similar to that occurring in southwest Britain (Bowman and Lewis, 1986).



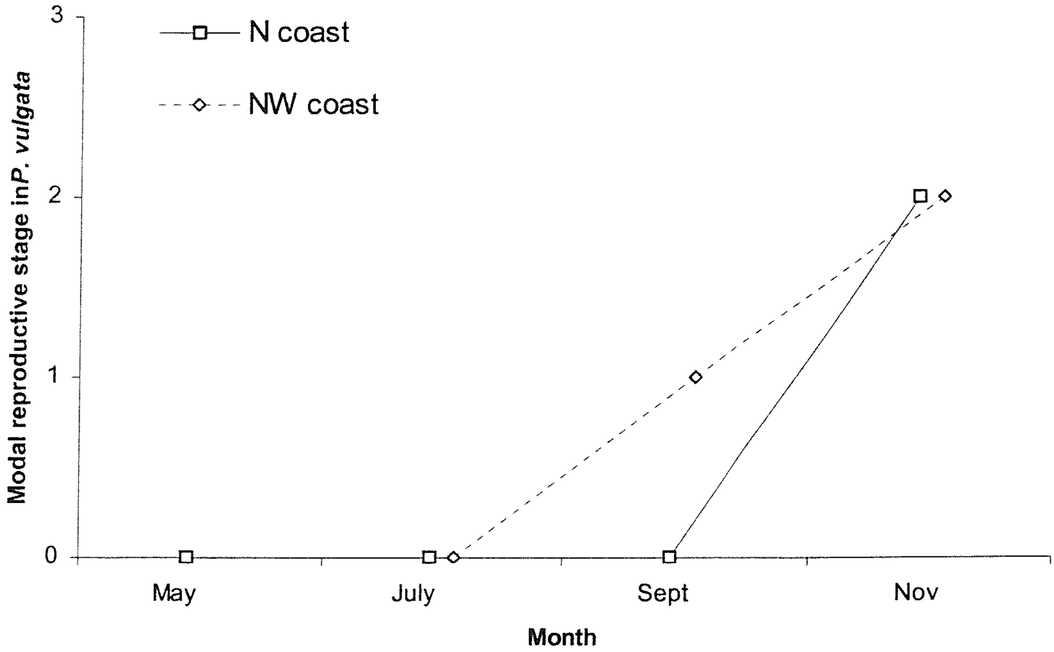
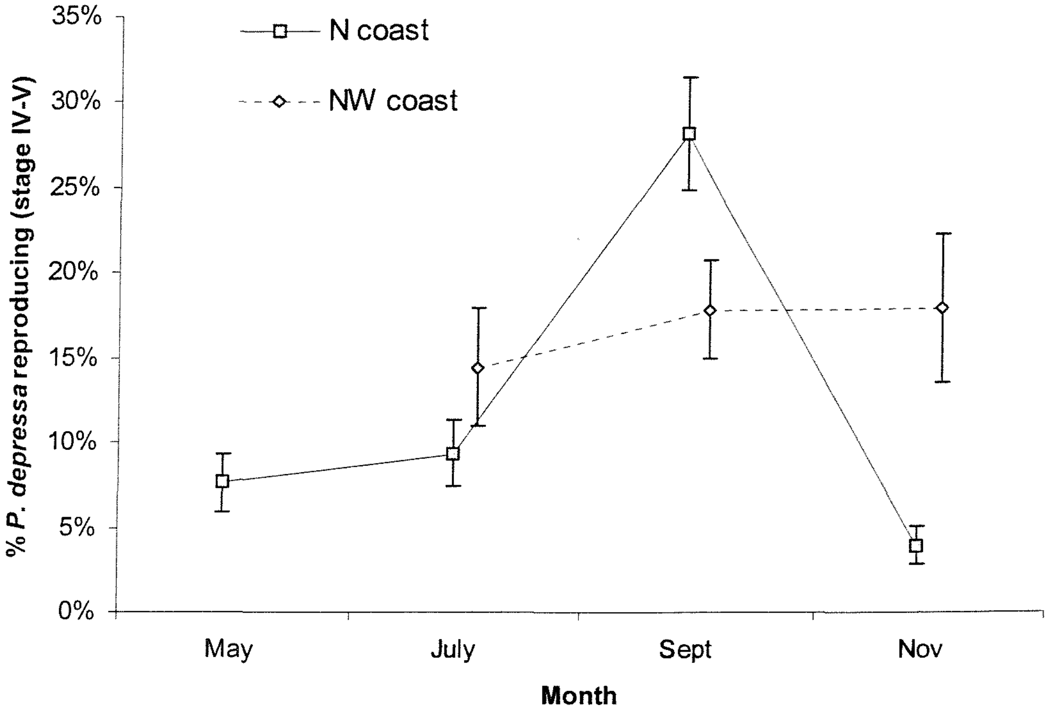


Figure 4.8. Reproductive activity of *Patella vulgata* in northern Spain, May–November 2002. Top graph gives percentage of individuals classified as reproductive stage IV or V, with error bars giving the standard error based on the formula cited in §4.2.2.3. Bottom graph gives modal reproductive stage. Both are based on individuals of length 21mm or more. Results are grouped by area (see Figure 4.1).



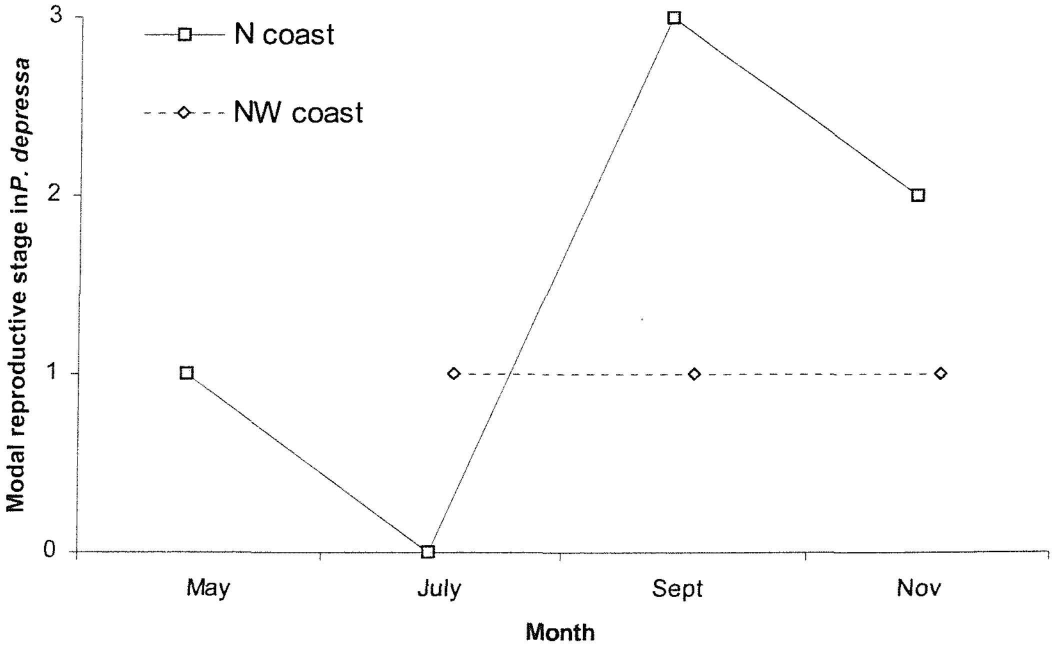


Figure 4.9. Reproductive activity of *Patella depressa* in northern Spain, May–November 2002. Top graph gives percentage of individuals classified as reproductive stage IV or V, with error bars giving the standard error based on the formula cited in §4.2.2.3. Bottom graph gives modal reproductive stage. Both are based on individuals of length 21mm or more. Results are grouped by area (see Figure 4.1).

4.4. Discussion

4.4.1. Limitations of the study

This study has analysed the relationship between selected biological variables – namely, the abundance, size frequency and reproduction of the two species of limpets studied – and physical variables, namely mean winter and summer sea surface temperature for the same sites, estimated from satellite data (see Figure 4.1 and Table 4.2). This mode of analysis assumes that other factors that may vary between surveys, whether in space, time or both, do not affect the variables to the extent that they significantly bias the results of the study.

Table 4.3 lists variables other than sea surface temperature. Air temperature, cloud cover, wave height, and the time of low tide are all factors that vary in space, and which could potentially influence the results of the study. Patterns of spatial variation of these factors in the area of study are described in §2.2. Air temperature (Figure 2.2) shows a strong spatial relationship with sea surface temperature (Figure 2.1) in the region, and is thus likely to contribute to the relationships observed in this study. It would be difficult to distinguish between the effects of air and sea temperature based on the analysis of spatial patterns as in this study.

Summer cloud cover is higher in the central area than in the other two areas studied (Figure 2.4). Higher cloud cover, which is related with rainfall and humidity, is likely to modify the effects of temperature by reducing desiccation stress and therefore favouring *P. vulgata* over *P. depressa.* Cloud cover may have contributed to the patterns in limpet abundance and size observed along the north coast.

As regards wave action, all the sites were moderately exposed or exposed; exposure to wave action is therefore unlikely to be a contributing factor to the patterns observed, although it is likely to add noise. Mean wave height is larger in the west than the other two areas (Figure 2.6), which would tend to give *P. depressa* a relative advantage over *P. vulgata* in the west compared to the other two areas. Thus the effect of spatial variations in wave height, if any, is likely to act in the opposite direction to the patterns of abundance of the two species observed in this study.

Variations in the time of low tide within the region studied are no more than about 60 minutes between the earliest and latest points (Figure 2.5). This indicates that the time of low tide is unlikely to have a significant effect on the conditions experienced by rocky shore organisms in this region.

Due to logistical difficulties, the sites surveyed were not evenly distributed between the different areas of the coast in each month (see Table 4.2). More sites in the east were surveyed during March–May and more in the west during September–November. Therefore, seasonal variations are a possible source of bias in the results.

Regression of the relative abundance of *P. vulgata* and *P. depressa* samples taken in March–April, May–July and September–November against summer sea temperature (Figure 4.2) found the slopes of individual regression lines for the three time periods to be homogeneous. Seasonal variations do not, therefore, appear to have a significant effect on the relationship between relative abundance and summer temperature observed in this study.

A difference was found in mean length between samples of *P. vulgata* taken in different months (May and July); however, the level of significance was marginal (p=0.045). Therefore, seasonal variation in mean size may have contributed to the spatial variation in mean sizes in *P. vulgata.* No difference in mean length between months was found for *P. depressa*.

Table 4.3. Variables other than sea surface temperature that may in the present study. Each factor is listed together with the direction , if any, in which it is likely to bias the results of the study, relative to the observed effects of spatial variations in sea surface temperature.

Factor	**Direction relative to SST**
Air temperature	+ (contributes)
Wave exposure / Wave height	0 (noise) / – (counteracts)
Cloud cover	+ (contributes)
Time of low tide	0 (no effect)
Seasonal variation	+ (contributes) / 0 (no effect)

4.4.2. Inter-regional comparison of abundance in Northern Spain with the English Channel region

The present study has looked at spatial variations in populations of *Patella vulgata* and *P. depressa* in northern Spain. The area of coast studied corresponds to roughly one-fifth of the joint range of the two species, which extends from southwest Spain (Fischer-Piette, 1958; Guerra and Gaudencio, 1986) to Barfleur (Crisp and Southward, 1958), the Isle of Wight (Crisp and Southward, 1958) and north Wales (Lewis, 1964). In order to understand how these species respond to spatial variations in temperature over the whole of their joint range, it is valuable to compare the results of the present study with data on the abundance of *P. depressa* and *P. vulgata* in the English Channel in the 1950s, to test the predictive power of the observed relationships.

Crisp and Southward (1958) recorded the abundance of common rocky shore species on both sides of the English Channel in 1947–57. Most of the surveys were carried out between 1954 and 1957. The abundance of *P. depressa*, as a percentage of all limpets at mid-tide level, was recorded at 31 sites along the south coast of Britain from near Land's End to the Isle of Wight, the eastern limit of *P. depressa* in Britain; 32 sites in France, from Le Conquet to Barfleur, its eastern limit in France; and 5 sites in the Channel Isles. Note that more than these 68 sites were surveyed, but these are the sites at which percentages of *P. depressa* were recorded.

The two indices of relative abundance described in §4.2.2.1 above, i.e. *Pv/(Pv+Pd)* and $\log_{10}$ (*Pv/Pd*), were calculated based on Crisp and Southward's data for these 68 sites. Note that both indices are expressed in terms of the abundance of *P. vulgata* relative to *P. depressa*, whereas Crisp and Southward (1958) recorded their results in terms of the abundance of *P. depressa* relative to all species of limpets at mid-tide level. Although *P. depressa* and *P. vulgata* were not the only species recorded by Crisp and Southward – *P. ulyssiponensis* was also present at mid-tide level at some sites, particularly in the western Channel – it is safe to assume that the percentages recorded accurately represent the true proportion of *P. depressa* out of the total abundance of both *P. depressa* and *P. vulgata* (Hawkins, pers. comm., from discussions with Crisp and Southward). The results of Crisp and Southward can therefore be converted into the same form as my results from northern Spain.

In order to see whether the indices of relative abundance of *P. vulgata* and *P. depressa* in the English Channel show a similar relationship with temperature to that found in northern Spain, sea surface temperature charts for the English Channel for 1952–56, the five-year period preceding most of Crisp and Southward's surveys, were generated based on the Comprehensive Ocean-Atmosphere Data Set, COADS (NOAA-CIRES Climate Diagnostics Centre, 2003). Mean summer (July–September) and winter (January–March) temperatures at each of the 68 sites were estimated based on these charts (Figure 4.10). It can be seen that summer and winter temperatures both vary across the region, with winter temperatures varying about twice as much as summer temperatures.

The two indices of relative abundance were plotted against both summer and winter temperatures to see whether correlations existed (Figure 5.11). A correlation of both indices with both summer and winter temperatures was found. The Pearson's correlation coefficient for $\log_{10}$ (*Pv/Pd*) with summer temperature was $r_s = 0.459$ ($F_{(1,65)}=23.0$, $p<0.00001$), while for *Pv/(Pv+Pd)* with summer temperature it was $r_s = 0.495$ ($F_{(1,65)}=28.3$, $p<0.00001$). For $\log_{10}$ (*Pv/Pd*) with winter temperature the correlation coefficient was $r_s = 0.289$ ($F_{(1,65)}=5.96$, $p=0.01$) while for *Pv/(Pv+Pd)* with winter temperature it was $r_s = 0.283$ ($F_{(1,65)}=5.66$, $p=0.01$).

Although the data were very scattered, regression lines were fitted to the plots of both indices of relative abundance against summer temperature. The regression showed that variations in summer temperature accounted for approximately 21% of variance in $\log_{10}$ (*Pv/Pd*) and 25% of variance in *Pv/(Pv+Pd)* across the English Channel region. There was therefore far more variance in relative abundance that could not be explained by summer temperature in this region than in northern Spain, where summer temperature accounted for approximately 65% of variance in both indices. Nonetheless, it could be concluded that summer temperature has an effect on the relative abundance of *P. vulgata* and *P. depressa* in the English Channel, as it does in northern Spain. The regression equations of the two indices of relative abundance against summer temperature were as follows:

$$\log_{10}(Pv/Pd) = (16.30°\mathrm{C} - T) / 1.12°\mathrm{C} \qquad (R^2=0.211^{***}) \qquad [4.3]$$

$$Pv/(Pv+Pd) = (17.47°\mathrm{C} - T) / 2.39°\mathrm{C} \qquad (R^2=0.245^{***}) \qquad [4.4]$$

Because there was a correlation between summer and winter temperatures across the region (see Figure 4.10), it was necessary to test whether variations in winter temperature, independently of summer temperature, were also correlated with the relative abundance of the two species. To do this, the deviations of the two indices of relative abundance from the values predicted by summer temperature based on Equations 4.3 and 4.4 were calculated, and plotted against winter temperature for each site (Figure 4.12). For $\log_{10}$ (*Pv/Pd*) the resulting Pearson's correlation coefficient was $r_s = 0.0427$ ($F_{(1,65)}=0.269$, $p=0.30$) while for *Pv/(Pv+Pd)* it was $r_s = 0.0642$ ($F_{(1,65)}=0.119$, $p=0.37$). Thus, although the range of spatial variation in winter temperatures in the western English Channel is roughly twice the variation in summer temperatures, no relationship between winter temperature and relative abundance of *P. vulgata* and *P. depressa* can be demonstrated. This agrees with the observation of Crisp and Southward (1958) that there is little reduction in the abundance of *P. depressa* from west to east, despite a sharp gradient in winter temperatures.

This implies that the eastern limits of *P. depressa* in the English Channel are likely to be set mainly by non-climatic factors. Crisp and Southward (1958) speculate that these factors may include aspect (the direction in which the shore faces), larval dispersal, and the availability of suitable substrata, all of which could help to stop the eastward spread of *P. depressa*.

There is, however, a relationship between spatial variations in summer temperature and the relative abundance of *P. vulgata* compared with *P. depressa* in the English Channel, as in northern Spain. It is interesting to compare the relationship found in the two regions: this can be done by plotting the indices of relative abundance against summer temperature on the same axes for both regions (Figure 4.13). It can be seen that although the absolute values of these indices for each region are very different, the slopes of the best-fit regression lines are similar.

In particular, the regression line of $\log_{10}$ (*Pv/Pd*) against summer temperature (Figure 4.13a) predicts that an increase of approximately 1°C in summer temperature will result in a tenfold increase in the relative abundance of *P. vulgata* compared to *P. depressa* in both regions. Nonetheless, at any given temperature, the relative abundance of *P. depressa* compared to *P. vulgata* in Crisp and Southward's surveys is about 3 orders of magnitude greater than would be predicted by extrapolating the regression line based on the data from my 2002 surveys. The most obvious explanations for this large discrepancy are differences in surveying methods and/or the characteristics of the sites between the two surveys. Mean wind speed in the English Channel area is considerable higher than in the Bay of Biscay region (see Chapter 2, Figure 2.3) and this is likely to result in higher wave exposure. Crisp and Southward's choice of sites may also have tended more towards exposed sites than mine.

Despite these discrepancies, within each region a similar relationship was found between summer temperature and the relative abundance of *P. vulgata* and *P. depressa*. This suggests that such a relationship is likely to be widespread throughout joint range of the two species. No relationship with winter temperature has been found. Therefore, in order to explain the mechanisms governing the response of these two species to variations in temperature, it is necessary to look principally at processes that are likely to be affected by summer, not winter, temperatures. The next section discusses possible mechanisms.

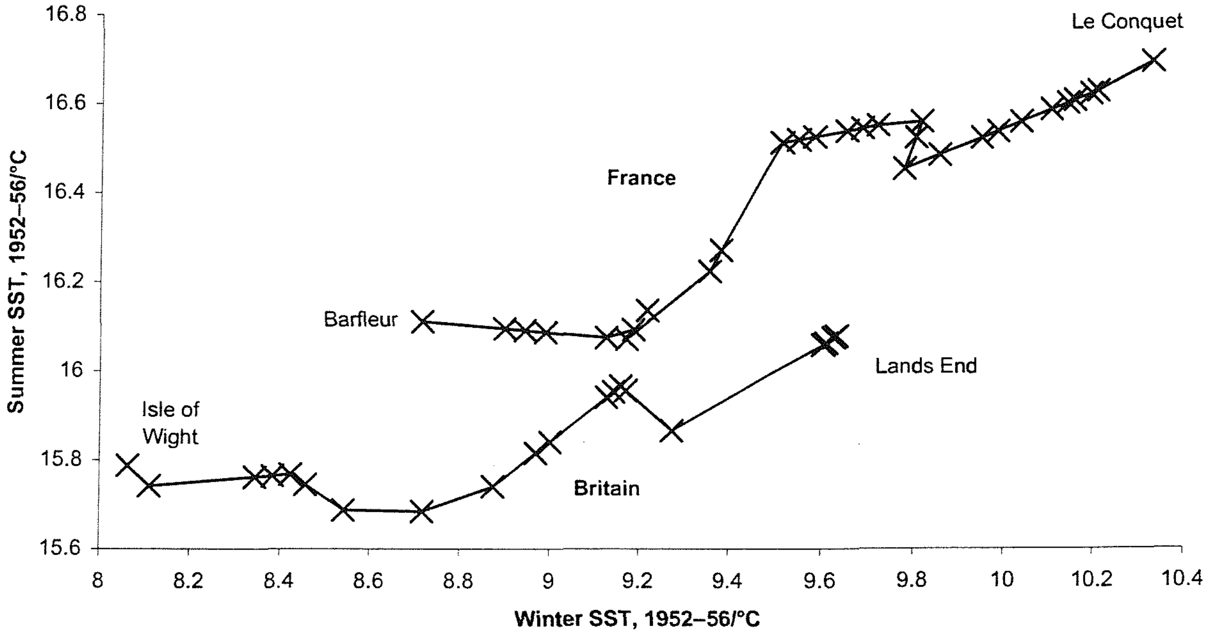


Figure 4.10. Mean summer (July–September) sea surface temperatures for 1952–56 on the y-axis, plotted against corresponding winter (January–March) temperatures on the x-axis, for 68 sites along both sides of the western English Channel surveyed by Crisp and Southward (1958). Axes are equally scaled. Temperatures from the Comprehensive Ocean-Atmosphere Data Set, COADS (NOAA-CIRES Climate Diagnostics Centre, 2003).

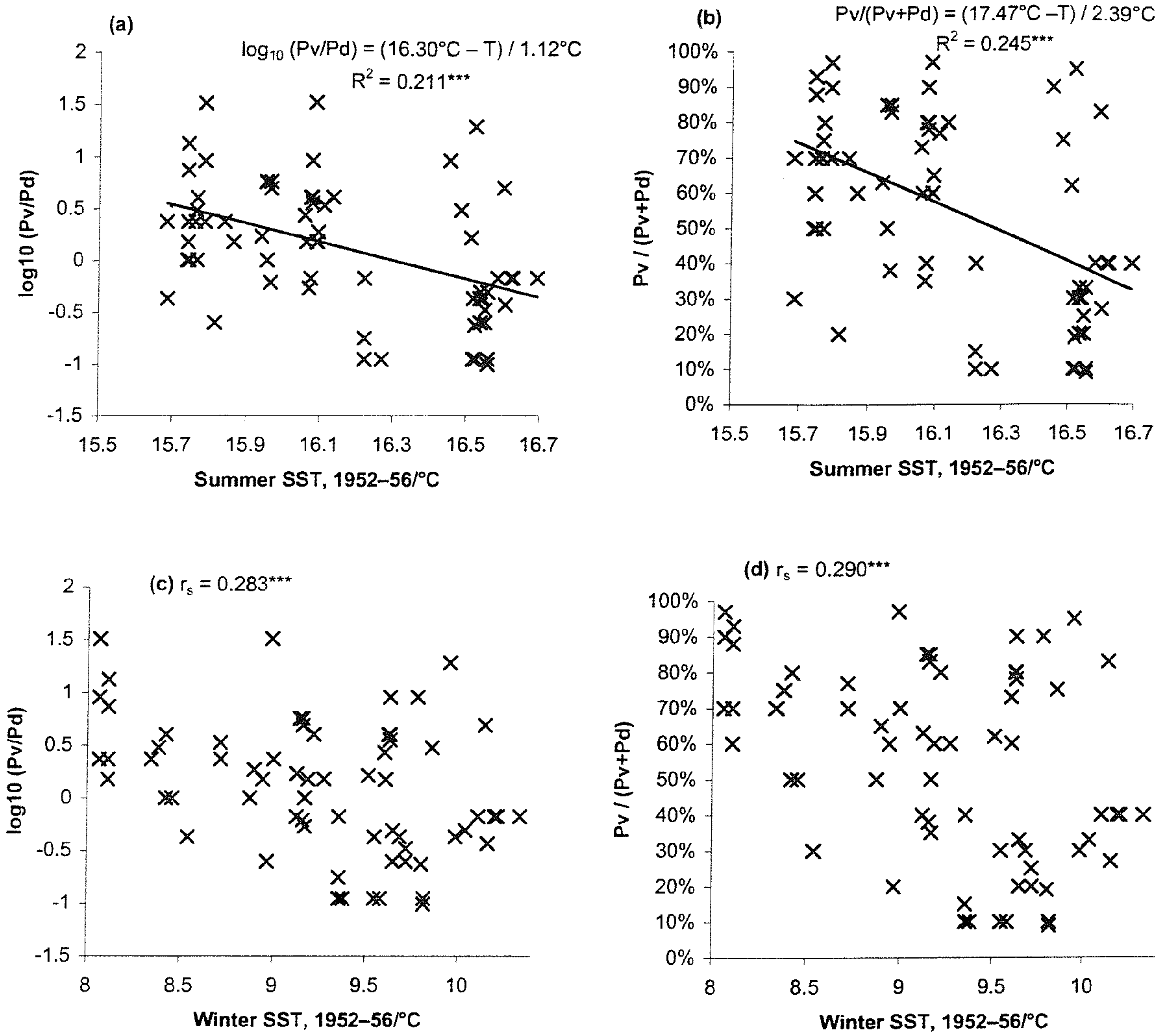
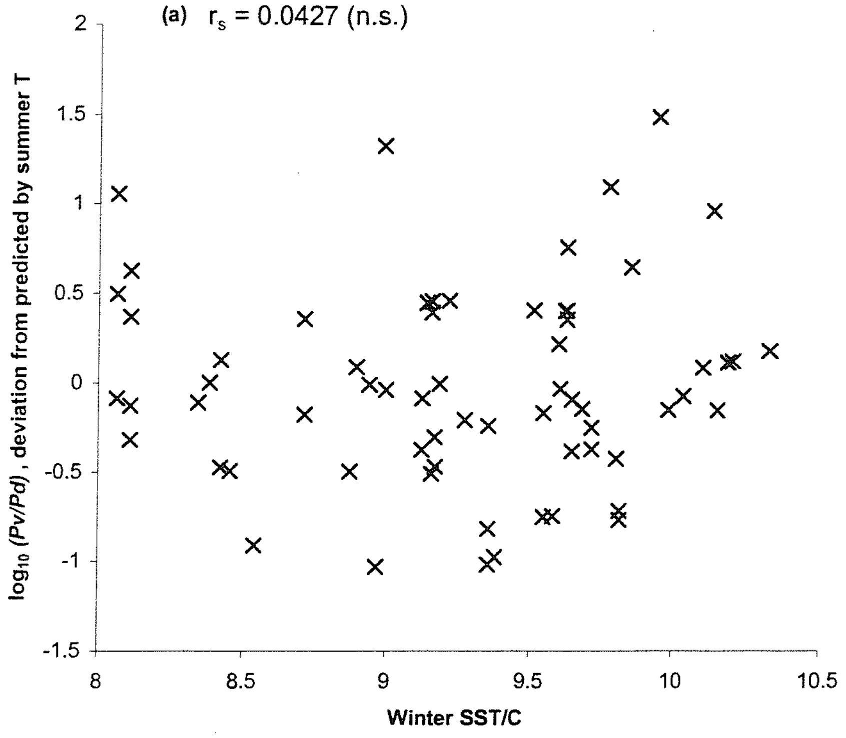


Figure 4.11. Two indices of relative limpet abundance at 68 sites in the western English Channel, based on the surveys of Crisp and Southward (1958), plotted against 1952–56 mean summer (a–b) and winter (c–d) temperatures at the same sites. (a) and (c) plot log relative abundance, $\log_{10}$ (*Pv/Pd*), against temperature. (b) and (d) plot *Pv/(Pv+Pd)*, the proportion of *P. vulgata* out of total of *P. vulgata* plus *P. depressa.* Temperatures from the Comprehensive Ocean-Atmosphere Data Set, COADS (NOAA-CIRES Climate Diagnostics Centre, 2003). There is a significant correlation in each case. (a: $F_{(1,65)}=28.3$, $p<0.00001$; b: $F_{(1,65)}=23.0$, $p<0.00001$; c: $F_{(1,65)}=5.96$, $p=0.01$; d: $F_{(1,65)}=5.66$, $p=0.01$)



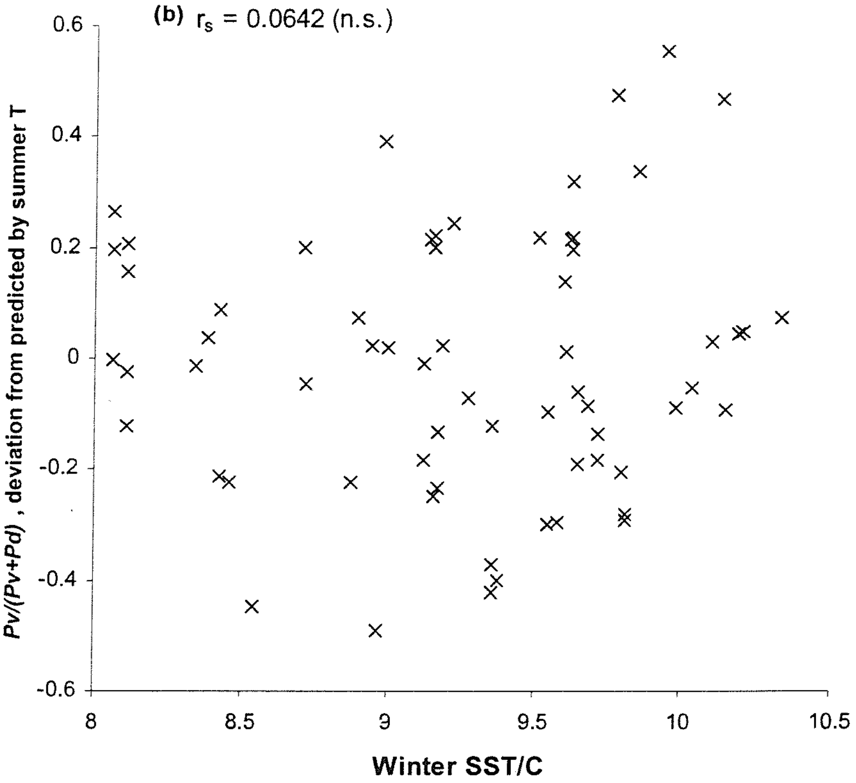


Figure 4.12. Deviations from the values predicted by summer temperature, according to Equations 4.3 and 4.4, of two indices of relative limpet abundance at 68 sites in the English Channel (Crisp and Southward, 1958), plotted against mean winter temperatures for 1952–56. No significant correlation was found in either case. (a: $F_{(1,65)}$=0.269, p=0.30; b: $F_{(1.65)}$= 0.119, p=0.37)

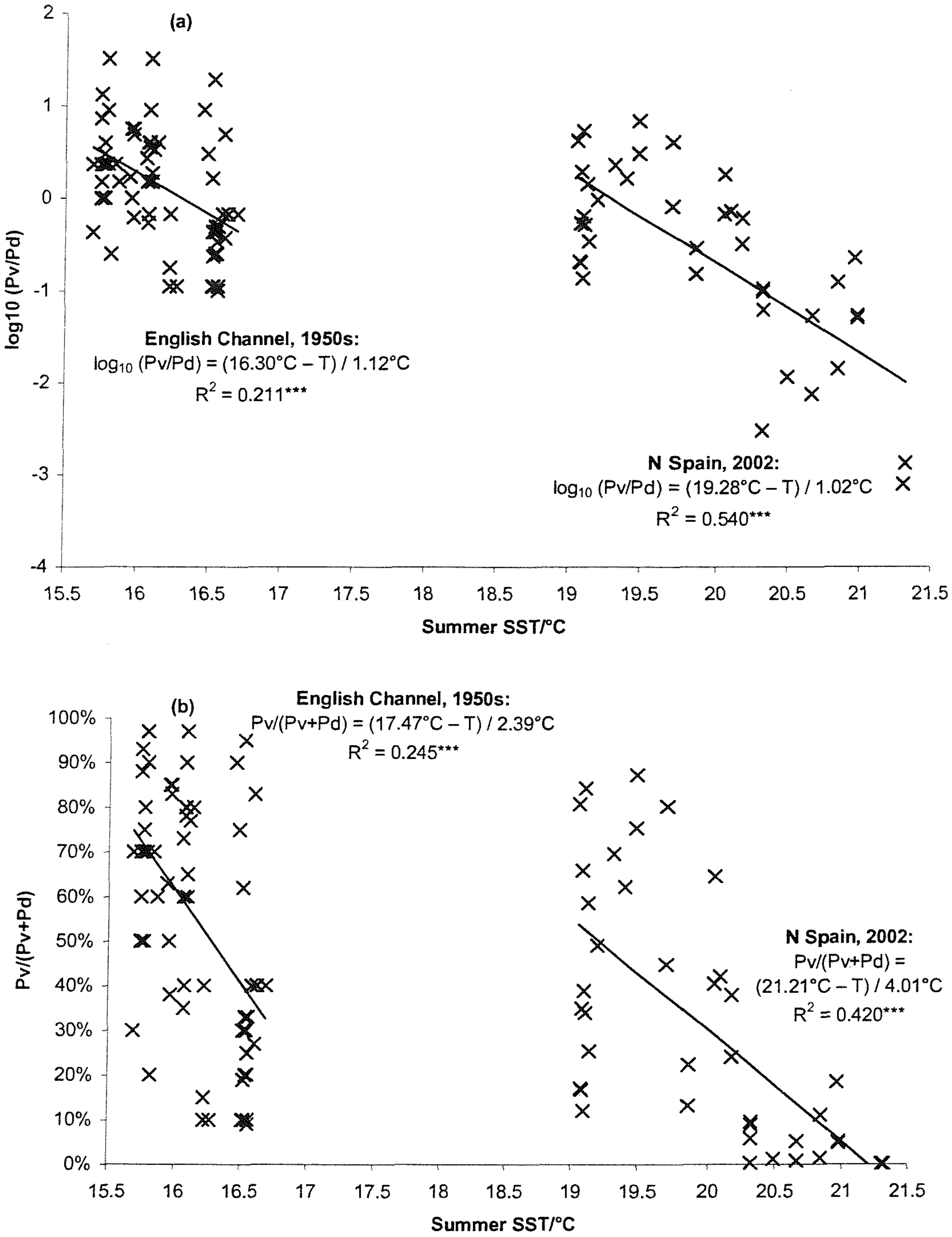


Figure 4.13. The data from Figure 4.11(a–b) plotted on the same axes as the data from my 2002 surveys in northern Spain (Figures 4.2 and 4.3). Note that here the data from the north and northwest coasts of Spain are combined, not separated as in Figures 4.2 and 4.3.

4.4.3. Possible mechanisms governing the relationship of relative limpet abundance with summer temperature

The relationship between summer temperature and the relative abundance of *P. vulgata* and *P. depressa,* observed in this chapter, is unlikely to have any single definite cause. It is more likely that this relationship results from the interaction of many temperature-dependent effects acting on different processes such as reproduction (Bowman and Lewis, 1977, 1986; Lewis *et al.*, 1982; Lewis, 1986), larval dispersal and settlement and early survival (Orton *et al.*, 1956; Orton and Southward, 1961; Ballantine, 1961b), growth (Fischer-Piette, 1948; Ballantine, 1961), competition (Ballantine, 1961b; Branch, 1976; Thompson *et al.*, 2000; Jenkins *et al.*, 2001; Roberts, 2002; Boaventura *et al.*, 2002a,b, 2003) and mortality (Evans, 1948; Southward, 1958). In any case, the mechanisms governing this relationship must be chiefly influenced by summer temperatures, because no relationship of relative abundance with winter temperatures has been found. This fact helps to narrow down the possible candidate mechanisms.

The timing of reproduction in both species is known to vary geographically and to be broadly related to temperature (Bowman and Lewis, 1977, 1986; Lewis *et al.*, 1982; Lewis, 1986). The populations examined in the present study fit into the overall latitudinal pattern given in Table 4.1. Within the joint range of the two species (from north Wales to the southwest Iberian Peninsula), *P. vulgata* reproduces mainly in autumn and winter, so summer temperature is less likely to affect this stage of its life cycle. *P. depressa*, however, reproduces principally in summer in Britain, so it is likely this stage of its life cycle could be critically affected by low summer temperature. In southern Europe, *P. depressa* can reproduce throughout the year and low summer temperatures are unlikely to present a problem. The stages of dispersal and larval settlement take place in the months following spawning (Orton *et al.*, 1956; Orton and Southward, 1961; Ballantine, 1961b). Again, only in *P. depressa* near its northern limits are these processes likely to take place in summer, and therefore to be candidates for mechanisms governing the response of relative limpet abundance to variations in temperature.

There is a small difference (about 0.6°C) in the lethal temperatures of *P. depressa* and *P. vulgata* in air (Evans, 1948). Temperature-related mortality is therefore a possible, but not very likely, mechanism accounting for the observed relationship of relative abundance of the two species with summer temperatures. The size frequency of *P. vulgata* showed a marked reduction in the proportion of larger (25 mm+) limpets in the eastern area (where summer sea surface temperatures are highest). Both species showed increasing modal size from east to west; thus, populations in areas with higher summer temperatures tended to have smaller modal sizes. However, this difference in size frequency could also be accounted for by differences in growth: in general limpets in warmer conditions grow faster but live less long, reaching smaller sizes (Fischer-Piette, 1948; Ballantine, 1961b). The observed differences in size frequency need not necessarily be related to temperature. Random differences between shores within areas account for the observed variation in mean length. In other words, length varied at the scale of shores and not the coarser scale of areas. It is also possible that human predation of limpets is particularly intense in the eastern area, with large individuals of *P. vulgata* taken preferentially (personal communication from fishermen in Ribadesella, in the eastern area).

Competition is a more likely candidate mechanism than mortality to account for variations in abundance. Inter- and intraspecific competition for space and food resources are widespread among *Patella* spp. (Ballantine, 1961b; Branch, 1976; Roberts, 2002; Boaventura *et al.*, 2002a,b, 2003). Competition can lead to reduced growth rate and death by starvation (Ballantine, 1961b; Thompson *et al.*, 2000; Boaventura *et al.*, 2002a). The availability of food resources (biofilms) and the intensity of limpet grazing vary seasonally (Jenkins *et al.*, 2001; Thompson *et al.*, 2000) and geographically (Jenkins *et al.*, 2001): high temperatures lead to a reduction in available food resources and an increase in the intensity of grazing (Jenkins *et al.*, 2001; Thompson *et al.*, 2000). Thus competition among limpets for food resources is in general likely to be much more intense in summer than in winter, and this may be a key process affected by summer temperature. However, studies in Portugal where *P. vulgata* is near its southern limit found that *P. vulgata* had a higher rate of growth and survival than *P. depressa*, and that intraspecific competition in both species was stronger than interspecific competition, and that both types of competition were symmetrical as to species (Boaventura *et al.*, 2002a). These results are not consistent with the hypothesis that the competitive dominance of *P. depressa* over *P. vulgata* in areas with high summer temperature is responsible for maintaining the pattern of relative abundance observed in this study. More investigation is needed to understand the role of competition in the co-existence of these species.

Sex ratios are another aspect of the populations studied where differences were observed (this time between the present study in Spain and existing data for Britain) that could be related to temperature. However, sex ratios and sex switching do not play a clearly understood role in the response of these species to temperature. *Patella vulgata* individuals appear to change sex from male to female at a smaller size in Spain than do individuals of the same species in Britain (Orton *et al.*, 1956: see Figure 4.7), despite the fact that they are grow faster and live for fewer years in southern than in northern Europe (Fischer-Piette, 1948). This could be a direct response to temperature or, perhaps more likely, an indirect response to the population structure: with fewer large females in the population as a whole, an individual would be likely to gain more offspring by "switching" to producing costly eggs rather than cheap sperm at a smaller size, although the possible trigger for this switching is not known. This would be an interesting problem for evolutionary modelling. *P. depressa* in contrast seems to have a fixed sex ratio. The present study has established that this sex ratio is indeed independent of size. The 95% confidence intervals for the percentage of males in *P. depressa* in northern Spain are 58.3% to 62.7%.

In general, then, the mechanisms underlying the response of these two species to spatial variations in temperature have not been ascertained. However, the evidence suggests that interspecific competition is likely to play an important role. Reduction in growth and heat-induced mortality in *P. vulgata* and lack of reproductive success of *P. depressa* near its northern limits in Britain are other processes likely to be implicated.

4.4.4. Comparison of the two indices of relative abundance

As this chapter has shown, on the north coast of Spain the relative abundance of *P. vulgata* and *P. depressa* can be predicted accurately by summer sea temperature. Two indices of relative abundance were used as measures of the response to temperature of these species: log relative abundance, $\log_{10}(Pv/Pd)$, and proportional abundance, $Pv/(Pv+Pd)$. The use of log relative abundance as a measure of the response of these two species to variations in temperature, whether over part or all of their joint range, has three advantages over the use of proportional abundance. First, meaningful predictions of log relative abundance from temperature, based on an equation such as

Equation 4.1, can in theory be made across the entire joint range of the two species. Predictions of relative abundance, on the other hand, based on an equation such as Equation 4.2, only work across a limited range of temperatures, beyond which the equation gives meaningless predictions of negative abundance for one or other species. Second, predictions based on log relative abundance are more sensitive to small changes in abundance near the limits of the species. Relative abundance, on the other hand, cannot easily distinguish between a species that comprises 99% of the total abundance, and one that comprises 99.99%. Finally, log relative abundance can potentially be derived from semi-logarithmic abundance scales such as the (S)ACFOR scale (Crisp and Southward, 1958; Southward and Crisp, 1954a; Crisp and Fischer-Piette, 1959; Hawkins and Jones, 1992). Log relative abundance is therefore to be recommended as a potentially useful index of the relative abundance of these and other species.

The relative abundance of *Patella vulgata* and *P. depressa* shows a response to spatial variations in summer sea temperature, both in northern Spain and in the English Channel region. Along the north coast of Spain, where there is a sharp east–west gradient in summer temperatures, relative abundance of the two species, can be predicted accurately by summer temperature using Equation 4.1, as was done in §4.3.1 for the relative abundance of the two species at Zumaya in 1981. It can therefore be predicted that the response of the relative abundance of the two species to climate change in this area will follow the same equation. To find out whether this prediction holds true in northern Spain, and whether it can be extended to other parts of the joint range of these two species (as is suggested by the observed relationship in the English Channel), it would be necessary to carry out a broader study in time and/or space, with comparable methods.

The ecological repercussions of a shift in the dominant limpet species from *P. vulgata* to *P. depressa* under a scenario of climate change would probably be limited in extent, since the two species are ecologically similar. Therefore, although the relative abundance of these two species may be a good "indicator" of changes in temperature, which is an interesting and valuable piece of knowledge in itself, it is not clear that they will necessarily act as "indicators" of the effects of changes in temperature on rocky shore communities as a whole. This topic is discussed further in Chapter 7.

Chapter 5: Distribution, growth and survival of the limpets *Patella vulgata* L. and *P. depressa* Pennant in estuaries on the Basque coast, northern Spain

5.1. Introduction

The rocky shores of the inner Bay of Biscay are characterised by "southern" warm-temperate algae and invertebrates, with red algae predominating on the lower shore, and few species of brown algae (Fischer-Piette, 1955a; Ibañez, 1985; see review in Chapters 1 and 3). These communities are similar to those found in southern Portugal and southwest Spain, but very different from the "northern" cold-temperate communities found in northwest Spain and further north in Brittany, where canopy-forming brown algae are more prevalent. These anomalous patterns of distribution have been attributed to regional summer sea temperatures (see Chapter 2), with high temperatures in the inner Bay due to thermal stratification and the continental effect (Ibañez, 1989), and low temperatures off northwest Spain due to wind-induced upwelling (Molina, 1972; Botas *et al.*, 1990).

The north coast of Spain is backed by a range of mountains, the Cantabrian Cordillera, giving rise to many small rivers that enter drowned valleys (*rías*) along the coast. Within these estuaries, certain cold-temperate rocky shore species, notably fucoids, the limpet *Patella vulgata*, the winkle *Littorina littorea* and the common shore crab *Carcinus maenas,* are more abundant, and in some cases extend their range further east (into warmer waters), than on the open coast (Fischer-Piette, 1955a; see also Chapter 3). The same phenomenon has been observed in Portugal near the southern limits of northern species (Ardre, 1971; Santos, 2000; Ladah *et al.,* 2003).

On the north coast of Spain, changes in community composition that take place over hundreds of kilometres on the open coast, can be observed in estuaries over distances of a few hundred metres. These estuaries, therefore, have the potential to serve as tractable experimental systems for studies of transitions between cold- and warm-temperate biotas, including patterns of distribution, the mechanisms involved in creating and maintaining them, and the possible effects of climate change on these communities.

These estuaries may provide reservoirs of northern species that can re-colonise the open coast in cold periods, and which retreat into the estuaries in warm periods such as the present day. This could mean that the estuarine populations are isolated relicts of connected communities that were once widespread along the open coast. The factors that account for this pattern of distribution have not been investigated in detail, but variations in physical factors such as wave exposure, siltation, temperature and salinity between estuaries and the open coast are probably the underlying physical causes, although biological interactions may be the proximate cause.

Wave exposure is likely to have a major influence. Many species characterising cold-temperate rocky shore communities in the northeast Atlantic tend to be more common in sheltered conditions than their warm-temperate counterparts (Ballantine, 1961a). Fucoid algae, for example, predominate on sheltered, cold-temperate rocky shores. Their abundance decreases towards the south as well as with increasing wave exposure, where they are progressively replaced by grazers, barnacles, and (on the lower shore) red algae. This pattern is believed to be partly the result of differences in the effectiveness of grazers mediated by both wave exposure and climate (Ballantine, 1961a; Hawkins *et al.*, 1992).

The same pattern holds true for cold- and warm-temperate species of limpets and barnacles. *Patella vulgata* (a cold-temperate limpet species) prefers sheltered conditions towards the southern end of its range, while *P. depressa* (warm-temperate) prefers more exposed conditions near its northern limits in Britain (Ballantine, 1961a, 1961b). *Semibalanus balanoides* L. (a cold-temperate barnacle species) predominates in more sheltered conditions and penetrates further into estuaries than *Chthamalus* spp. (warm-temperate) which predominate in more exposed conditions (Ballantine, 1961a; Connell, 1961b; Southward, 1964; Crisp *et al.*, 1981). Thus the species composition of communities on sheltered shores in northern Spain resembles that of communities on exposed shores in south-west Norway, some 3000 km further north (Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959; Ballantine, 1961a). In southern Europe generally, many cold-temperate species are largely restricted to sheltered or estuarine conditions (Fischer-Piette, 1955a; Ballantine, 1961a).

At present, however, it is unclear to what extent wave exposure and other physical factors combine to maintain the observed distribution of species in estuaries. Nor is it known by what mechanism they may do so. Differences is growth rate, survival or reproduction could be responsible. Biological interactions may also play a part, with estuaries providing refuges for northern species from more competitive southern species or predators that cannot tolerate conditions of low salinity or shelter and associated turbidity and siltation (e.g. *P. depressa*: Hawkins, pers. comm.)

The species chosen for the present study, *Patella vulgata* and *P. depressa,* are abundant and ecologically important grazing gastropods on rocky shores throughout the northeast Atlantic. Their responses to temperature and potential as biological indicators of climate change have been discussed (Southward *et al.*, 1995; see also Chapter 4). In the Basque region, *P. depressa* predominates on the open coast, while *P. vulgata* is rare on the open coast, but fairly common in estuaries and other sheltered habitats (Fischer-Piette, 1955a; Ibañez, 1984). The preference of *P. depressa* for more exposed shores is well known (Evans, 1948; Orton and Southward, 1961; Ballantine, 1961a). Experiments have shown that for *P. vulgata* at least, growth rate is higher in moderately wave-exposed areas, but this may be the result of overcrowding in sheltered areas (Jenkins and Hartnoll, 2001). Other physical variables associated with wave action, notably turbidity, may also affect the relative success of the two species.

The general biology and ecology of *P. vulgata* have been extensively studied. At the individual and population levels this includes work on physiological tolerances (Evans, 1948; Southward, 1958), reproductive cycles (Orton, 1928; Orton *et al.*, 1956; Blackmore, 1969), growth and mortality (Orton, 1928; Blackmore, 1969), behaviour (Cassidy and Evans, 1980) and recruitment and population dynamics (Bowman and Lewis, 1977; Baxter, 1982; Delany *et al.*, 1998). Much work has been done using manipulative experiments to examine the role of *P. vulgata* in structuring communities (Jones, 1948; Ballantine, 1961b; Southward, 1964a; Lewis and Bowman, 1975; Hawkins, 1981a, 1981b; Smith, 1992; Dellasantina *et al.*, 1994; Gray and Naylor, 1996; Thompson *et al.*, 1997; Johnson *et al.*, 1997; Williams *et al.*, 1999; Jenkins *et al.*, 1999a, 2001; Jenkins and Hartnoll, 2001). Far fewer studies dedicated to *P. depressa* have been carried out. Orton and Southward (1961) studied the reproductive biology of this species; recent studies have looked at intraspecific interactions in *P. depressa* (Boaventura *et al.*, 2003) as well as at the interactions of the two species in Portugal (Boaventura *et al.*, 2002b) and southern England (Roberts, 2002). The two species have not been studied comparatively and experimentally across environmental gradients.

5.1.1. Objectives

This chapter describes studies carried out on intertidal rocks in two estuaries on the Basque coast (northern Spain) with the aim of investigating the spatial distribution of the limpets *Patella vulgata* L. and *P. depressa* Pennant, and carrying out preliminary experiments on the causes of the observed distribution patterns. The specific objectives were as follows:

1. To map the spatial distribution of *Patella vulgata* and *P. depressa* in estuaries on the Basque coast of northern Spain.
2. To study the relationship between spatial distribution of the two species in estuaries and variation in physical factors (temperature, salinity, and wave exposure).
3. To investigate experimentally, using translocation experiments, the hypotheses that differences in (a) mortality or (b) shell growth rates of the two species at different locations within estuaries might explain the observed patterns of spatial distribution.
4. To discuss the probable causes of the observed distribution patterns of the two species in estuaries in the area of study, and the possible implications of the study's findings for the responses of these species to climate change.

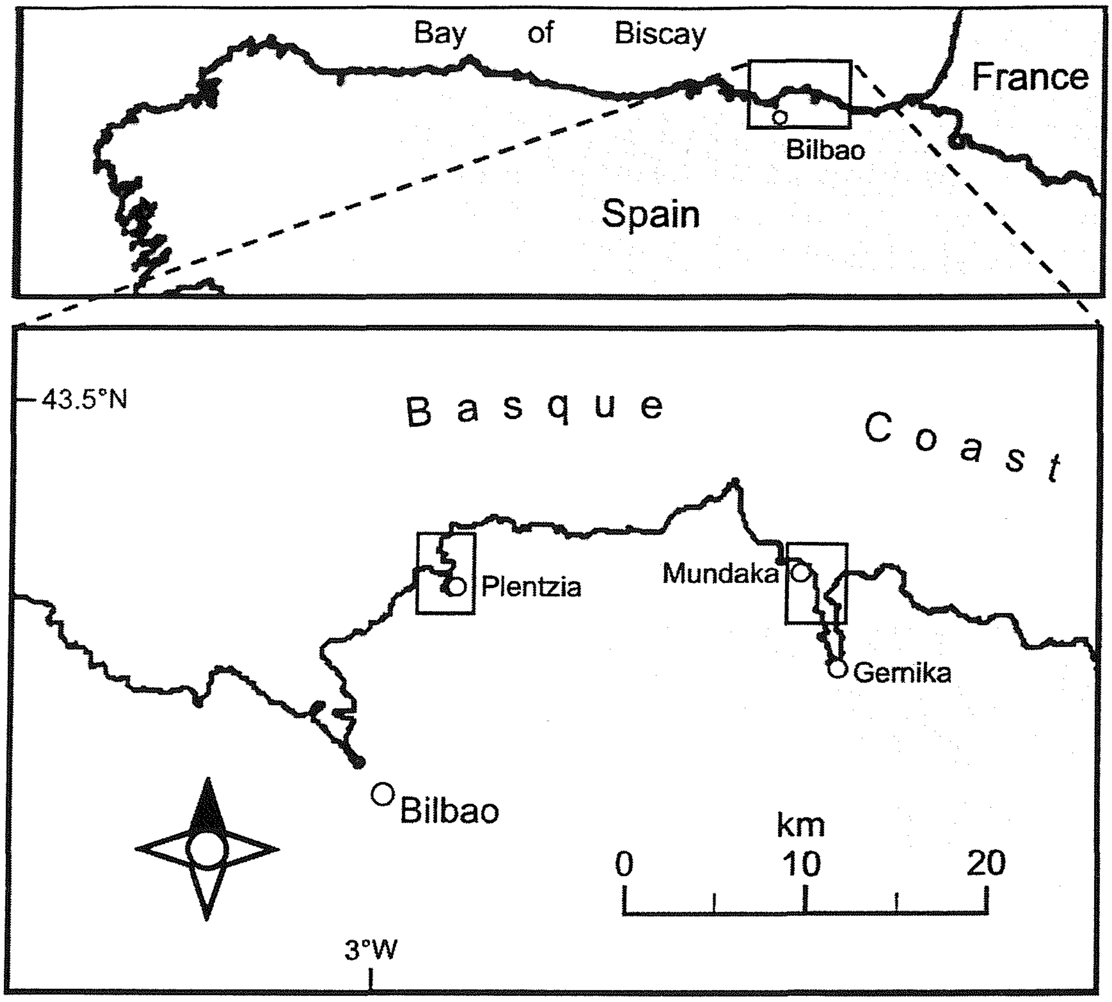


Figure 5.1. Location of the Plentzia and Mundaka Estuaries (Basque coast, northern Spain). Boxes (lower map) indicate the areas shown in Figure 5.2.

5.2. Methods

5.2.1. Area of the study

The Plentzia and Mundaka Estuaries were chosen for the study, both located on the Basque coast of northern Spain, in the inner Bay of Biscay (see Figure 5.1). The two estuaries are unpolluted and similar in size, the Mundaka Estuary being somewhat larger (see Figure 5.2). The mouth of the Plentzia Estuary is protected by a breakwater, and the river empties into a semi-exposed bay. Thus the Plentzia Estuary is less subject to wave action than is the Mundaka Estuary, which empties into a much more open bay next to a beach that is subject to strong surf. The west side of the lower Mundaka Estuary is a boulder/bedrock shore with patches of sand and mud; the east side is a sandy beach with no hard substrates. Both sides of the Plentzia Estuary are mud/boulder shores, with a sea wall on the east side (upper shore).

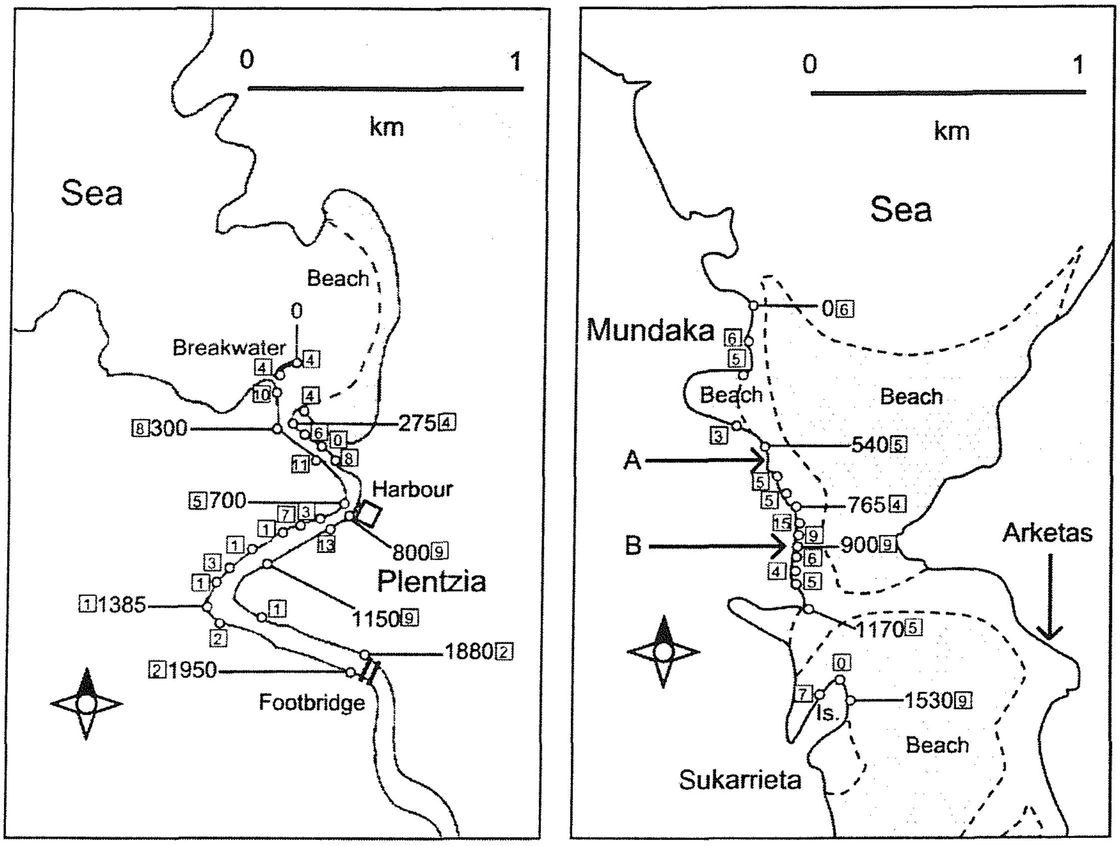


Figure 5.2. Maps of the Plentzia (left) and Mundaka (right) Estuaries (Basque coast, northern Spain). Open circles indicate the locations surveyed in the distribution study. Numbers in squares indicate the number of 50x50cm quadrats sampled at each location; "0" indicates a location where no limpets were present. Numbers not in squares indicate approximate distances, in metres, from the first site at the mouth of the estuary. "A" and "B" are the sites used in the translocation experiment. "Arketas" indicates the location of the lowest station where temperature and salinity measurements were made by AZTI Foundation (J. Franco, pers. comm.)

5.2.2. Study of distribution

The first part of the study mapped the distribution of *Patella vulgata* and *P. depressa* in both estuaries. The number of each species was counted using replicated 50 x 50 cm quadrats at roughly 50m intervals up each estuary. The distance between sampling locations varied, and the number of quadrats counted at each location (given in Figure 5.2) ranged from 1 to 15, due to variations in the area of hard substrate. Both sides of the Plentzia Estuary were surveyed, but only the west side of the Mundaka Estuary (the east side having no hard substrates in the lower reaches). In both estuaries, the lower limit of the survey was the mouth of the estuary, while the upper limit was determined by a gap in hard substrates. Areas of reasonably smooth rock were surveyed wherever possible. Crevices, overhangs, undersides of boulders, and pools were ignored.

5.2.3. Experimental study of mortality and growth

The experimental study was carried out in the Mundaka Estuary only, because it has a greater area of hard substrate and hence greater total abundance of limpets than in the Plentzia Estuary. Also, data on temperature and salinity in the Mundaka Estuary have been collected at irregular intervals since 1990 by AZTI Foundation (J. Franco, pers. comm.), while no data for the Plentzia Estuary were available.

Survival and growth of both species were studied during the course of a month (22 April to 23 May 2002) at two sites on the west side of the Mundaka Estuary (A and B in Figure 5.2). At the downstream site, about 550m above the river mouth, *P. depressa* was predominant (about 95% of total abundance); at the upstream site, some 350m further up the estuary (south), *P. vulgata* was predominant (about 80% of total abundance). Both sites were mixed boulder/rock substrates with patches of sand and mud. The average size of boulders in at the lower site was about 60cm; at the upper site boulders were smaller, about 30cm on average. Both sites were defined as areas of about 10m^2 at mid-tide level.

Because there were insufficient numbers of the less common species at each site to follow their growth and survival *in situ*, a translocation design was chosen (see Figure 5.3). On 22 April 2002 (day 0 of the experiment), 100 individuals of the predominant species were collected from each site. This was done on an evening low tide, while the limpets were feeding, to minimize the shock of removal. Limpets of medium size (about 20–35mm) were selected. The limpets were labelled with a coloured paper tag attached with superglue, but not measured or numbered at this stage. Fifty individuals of each species were then placed at each site, during the same low tide. Thus for each species there was an experimental group (which was moved to the other site) and a control group (which was returned to its original site), both of 50 individuals.

On 24 April (day 2), a thorough search of each site was made and all surviving tagged limpets were measured (shell length) and labelled again with a numbered tag, also attached with superglue, to allow the growth of individuals to be followed.

On 22–23 May (days 30–31) a thorough search was again carried out of both sites and surviving limpets with numbered tags were measured again. The original intention was to continue repeated sampling at monthly intervals during the summer, in order to compare survival and growth between species and sites during the whole season. In the event the experiment was terminated after one month because of low survival rates in three of the four groups. The results, therefore, are less representative that they would otherwise have been of the response of these species to the varying conditions experienced during a more extended period of time.

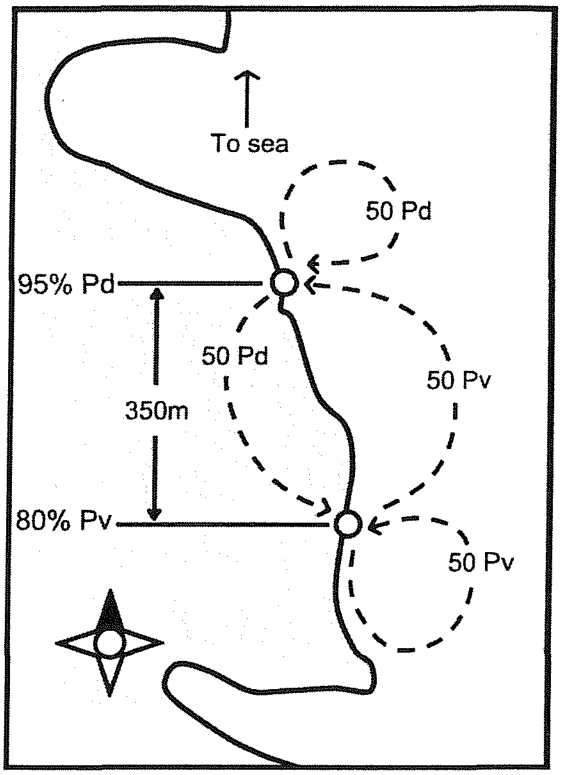


Figure 5.3. Diagram showing the design of the limpet translocation experiment carried out in the Mundaka Estuary, April–May 2002. 100 individuals of *Patella depressa* from the downstream site and 100 of *P. vulgata* from the upstream site (350m further upstream) were collected and labelled; 50 of each species were then replaced at each of the two sites.

5.2.4. Data analysis

5.2.4.1. Physical factors

Temperature and salinity data collected by the AZTI Foundation at three sites in the Mundaka Estuary (J. Franco, pers. comm.) were analysed to see whether variations in physical conditions could account for the observed distribution patterns. The lowest of the AZTI sites, Arketas, was some 2500m from the river mouth (see Figure 5.2), higher up than the top site in the limpet study. The other two sites were at Kanala (5km above the river mouth) and Murueta (7.5km).

Monthly mean sea surface temperature data were available for 1990–2000, giving an indication of the long-term variability in temperature in the estuary (although the number of data points at each site was small, approximately 50). As summer sea surface temperature was found in Chapter 4 to have an influence on the relative abundance of *P.*

vulgata and *P. depressa,* it was decided to focus on summer (July–Sept) temperatures. These were compared with mean temperatures for the same period from a fully marine sampling location at San Sebastian, 60km east of Mundaka (Borja *et al.*, 2000), with a correction for the known east-west gradient in summer temperature along the north coast.

Salinity data collected by the AZTI Institute in 1990–2000 at Arketas, Kanala and Murueta were also examined to see whether low salinity might have an effect on the limpet populations. Data collected within 1.5 hours before and after high tide, when limpets are likely to be immersed, were analysed. Mean salinity values were calculated for the three sites. Estimates were also made of the frequency of occurrence of extreme low salinity values at each of the three sites. As relatively small numbers of data (approximately 50) were available at each site, a regression of salinity against frequency of occurrence of a given low salinity value was made, in order to estimate the frequency of extreme low salinity values.

5.2.4.2. Distribution

The abundance of *P. vulgata* and *P. depressa* was plotted against distance from the site nearest the mouth of the estuary, for the east and west sides of the Plentzia Estuary and the west side of the Mundaka Estuary (Figure 5.6). The percentage of *P. vulgata* compared to the total abundance of both species is also given in each case.

In chapter 4 it was seen that on the open coast of northern Spain, the index of log relative abundance of *P. vulgata* and *P. depressa,* $\log_{10}$ (*Pv/Pd*), shows a negative linear relationship with temperature. To see whether there was a similar relationship in estuaries, $\log_{10}$ (*Pv/Pd*) was plotted against distance from the mouth of the estuaries (Figure 5.7). Clearly this could only be done for sites at which both species were observed. Linear regression analysis was performed on this index of relative abundance and also on *Pv/(Pv+Pd),* the proportion of *P. vulgata* compared to the total abundance of both species (Figure 5.8).

5.2.4.3. Mortality

It was noted that *P. vulgata* at both sites tended to migrate to the underside of boulders (presumably a reaction to heat stress), while *P. depressa* remained on the upper surface.

Although this meant that individuals of *P. vulgata* were somewhat harder to find than *P. depressa,* it was nonetheless assumed that the number of marked limpets found in a thorough search of each site area was a reliable estimate of the overall survival rate in each group. Numbers of individuals surviving after 2 and 30 days are shown in Figure 5.6.

Individuals that survived for the first two days were assumed to have re-established themselves after the translocation process. Mortality between day 2 and day 30 was therefore used to test (using G-tests) the hypothesis that mortality for each species was independent of experimental treatment (whether limpets were returned to their original site or moved to the other site).

5.2.4.4. Shell Growth

For the limpets in each group that survived until day 30 of the experiment, Ford-Walford regression plots were made of shell growth (difference in length between day 2 and day 30) against initial length on day 2 of the experiment (Figure 5.10). Straight lines were fitted to the data and the slope and standard error of the slope were estimated for each species at each site. The slope of each line gave an indication of the growth rate. Tests of homogeneity of slope of the regression lines were made between experimental and control groups for each species (Fowler *et al.*, 1998).

5.3. Results

5.3.1. Physical factors

5.3.1.1. Temperature

Summer (July–Sept) temperatures were on average about 0.6°C lower at Arketas than at San Sebastian. Part of this difference can be accounted for by distance along the coast, because of the known east-west gradient in temperature (see Chapter 2): this accounts for a difference of approximately 0.2°C. This indicates that average summer SST at Arketas is about 0.4°C cooler than on the open coast at Mundaka. Since Arketas is about 2500m upriver of Mundaka, this represents on average a change in temperature of 0.16°C per kilometre, although there is no evidence that this change occurs monotonically.

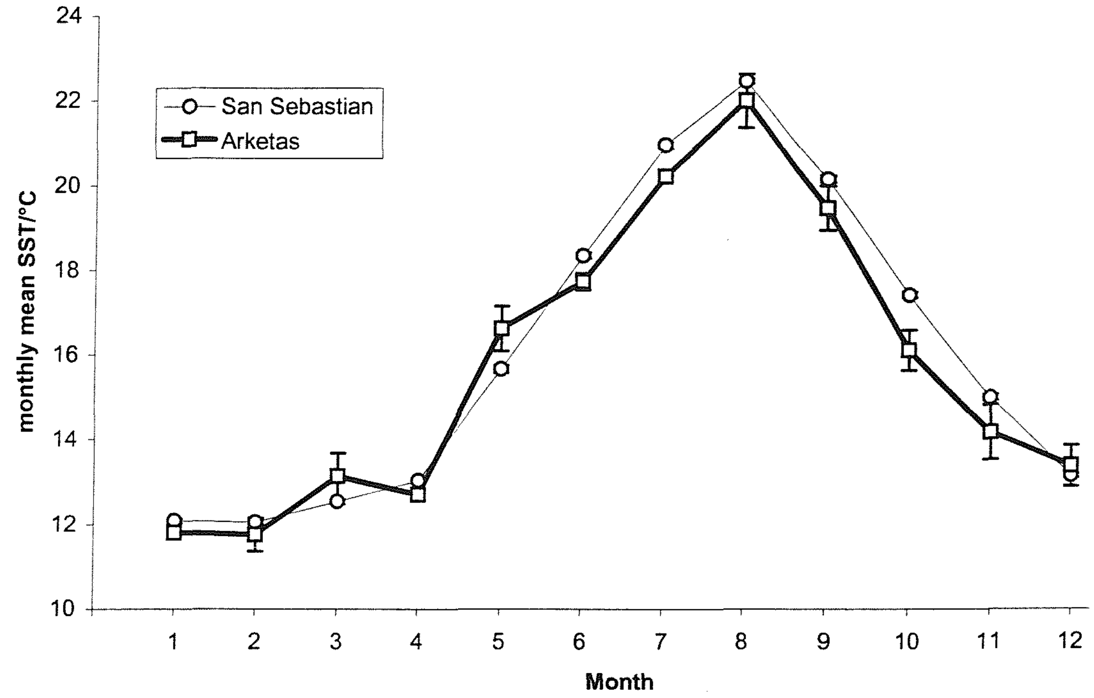


Figure 5.4. Monthly mean sea surface temperatures for 1990–2000 at Arketas, 2500m above the mouth of the Mundaka Estuary (AZTI Foundation: J. Franco, pers. comm.) and at San Sebastian Aquarium, 60km east of Mundaka (Borja *et al.*, 2000).

5.3.1.2. Salinity

Mean salinity at Arketas within 1.5 hours before or after high tide during 1990–2000 was 33.96 ppt, only 1.6 different from fully marine salinity of 35.6. This represents a change of salinity with distance up the estuary of approximately 0.64 per kilometre, although there is no evidence that this change occurs monotonically.

Figure 5.5 shows the frequency with which low values of salinity were observed at each of the three sites sampled by AZTI Foundation. The value plotted against 20 on the x-axis, for example, is the minimum salinity that can be expected to occur once in every 20 tidal cycles. Exponential decay regression curves were fitted to the data. The curves were then extrapolated to predict the frequency with which very low values of salinity would occur at each site (an arbitrary value of 3.5 was chosen, representing 10% of fully marine salinity). Salinity of 3.5 or less should occur at Arketas once every 169 tidal cycles, at Kanala once every 93 tidal cycles, and at Murueta once every 38 tidal cycles.

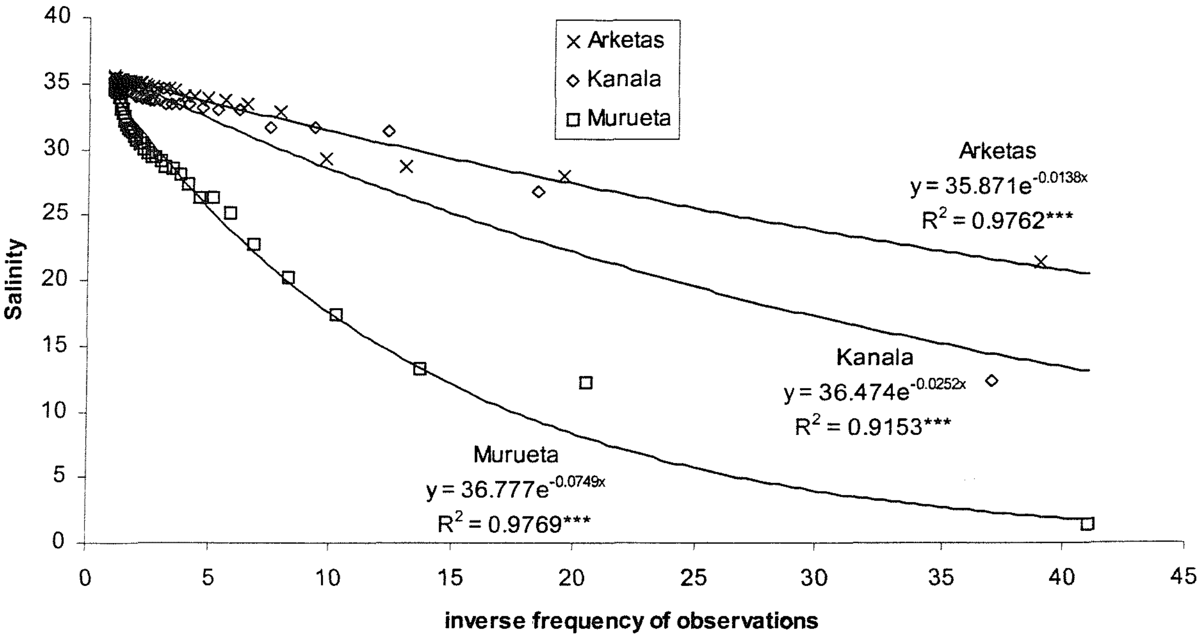


Figure 5.5. Inverse frequency of low values of salinity recorded at three sites in the Mundaka Estuary in 1990–2000 (AZTI Foundation: J. Franco, pers. comm.) The sites were respectively 2.5 km above the mouth of the river (Arketas), 5 km (Kanala) and 7.5 km (Murueta). Exponential decay curves (asymptotic to zero) were fitted to the values at each site. The regression in each case was significant ($p<0.001$).

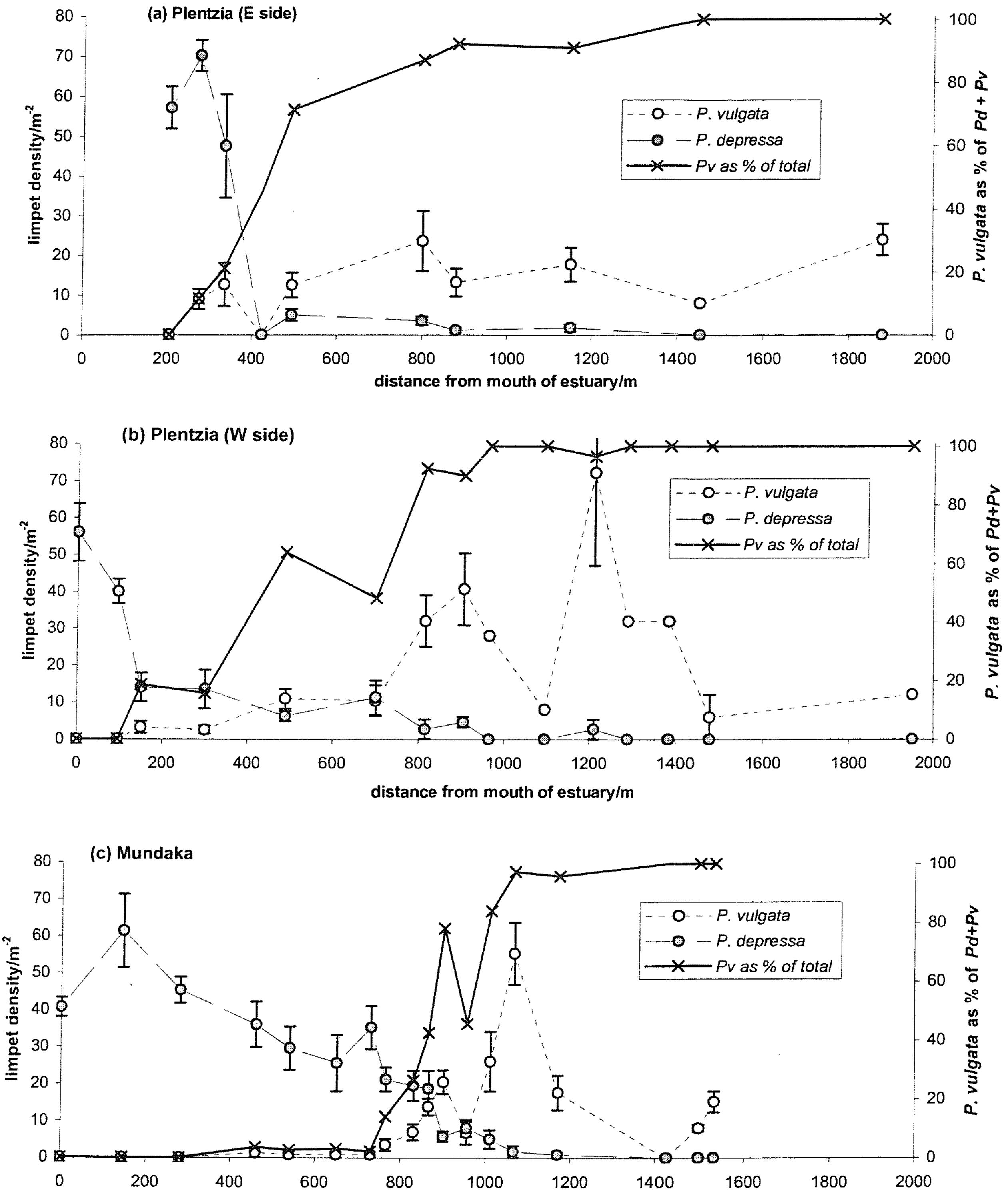


Figure 5.6. Abundance (in individuals/m^2) and relative abundance of *P. vulgata* and *P. depressa*, in the Plentzia (a–b) and Mundaka (c) Estuaries. Error bars give standard error. No error bars are given where only 1 quadrat was sampled due to lack of available rock.

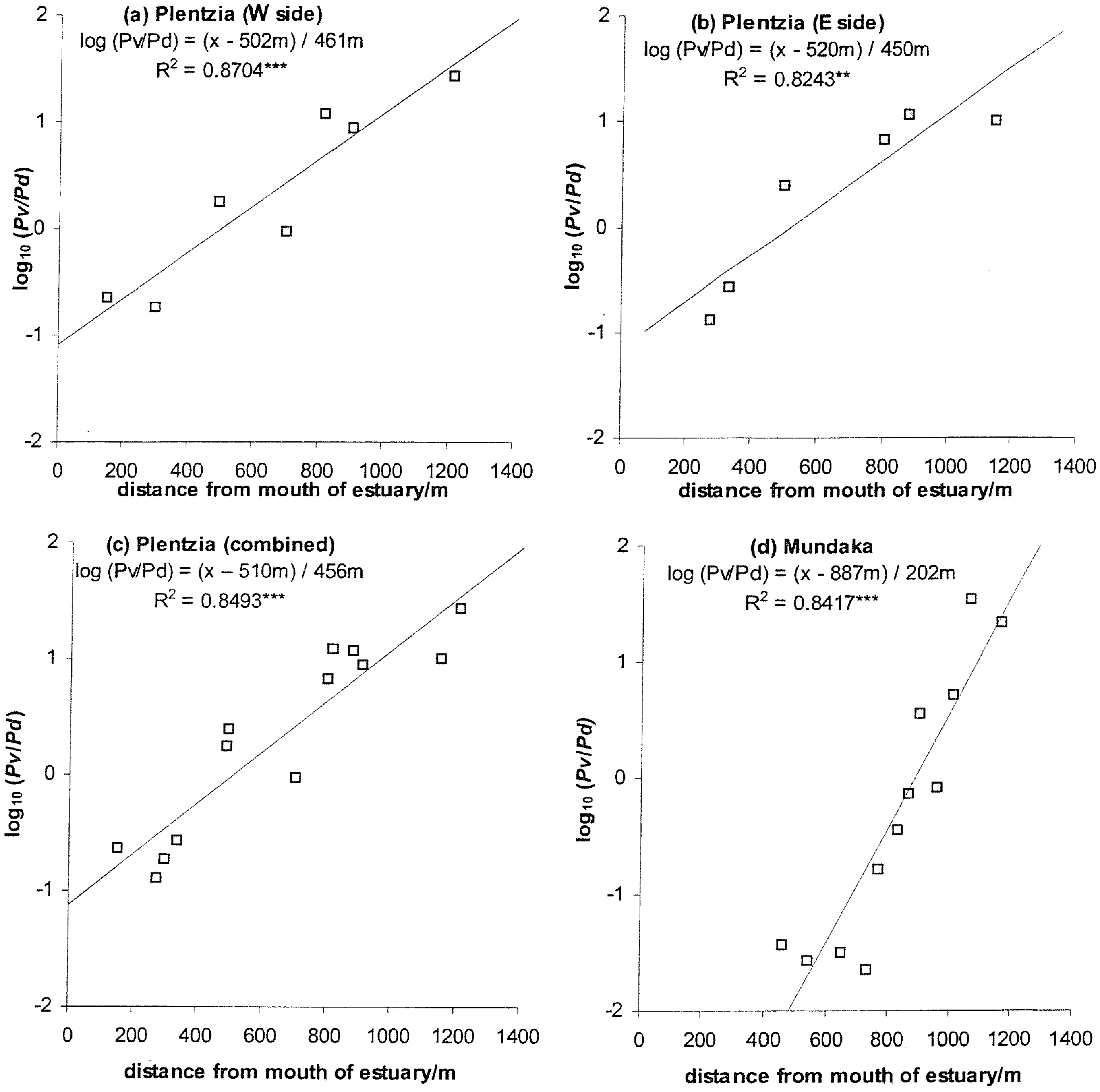


Figure 5.7. Plots of log relative abundance of *P. vulgata* and *P. depressa*, $\log_{10}$ (*Pv/Pd*), against distance from the mouths of the Plentzia (a: W side; b: E side; c: both sides combined) and Mundaka (d) Estuaries. All regressions were significant. (a: $F_{(1,5)}=33.6$, $p=0.002$; b: $F_{(1,4)}= 19.1$, $p=0.012$; c: $F_{(1,11)}=62.0$, $p<0.00001$; d: $F_{(1,10)}=53.2$, $p=0.000026$.)

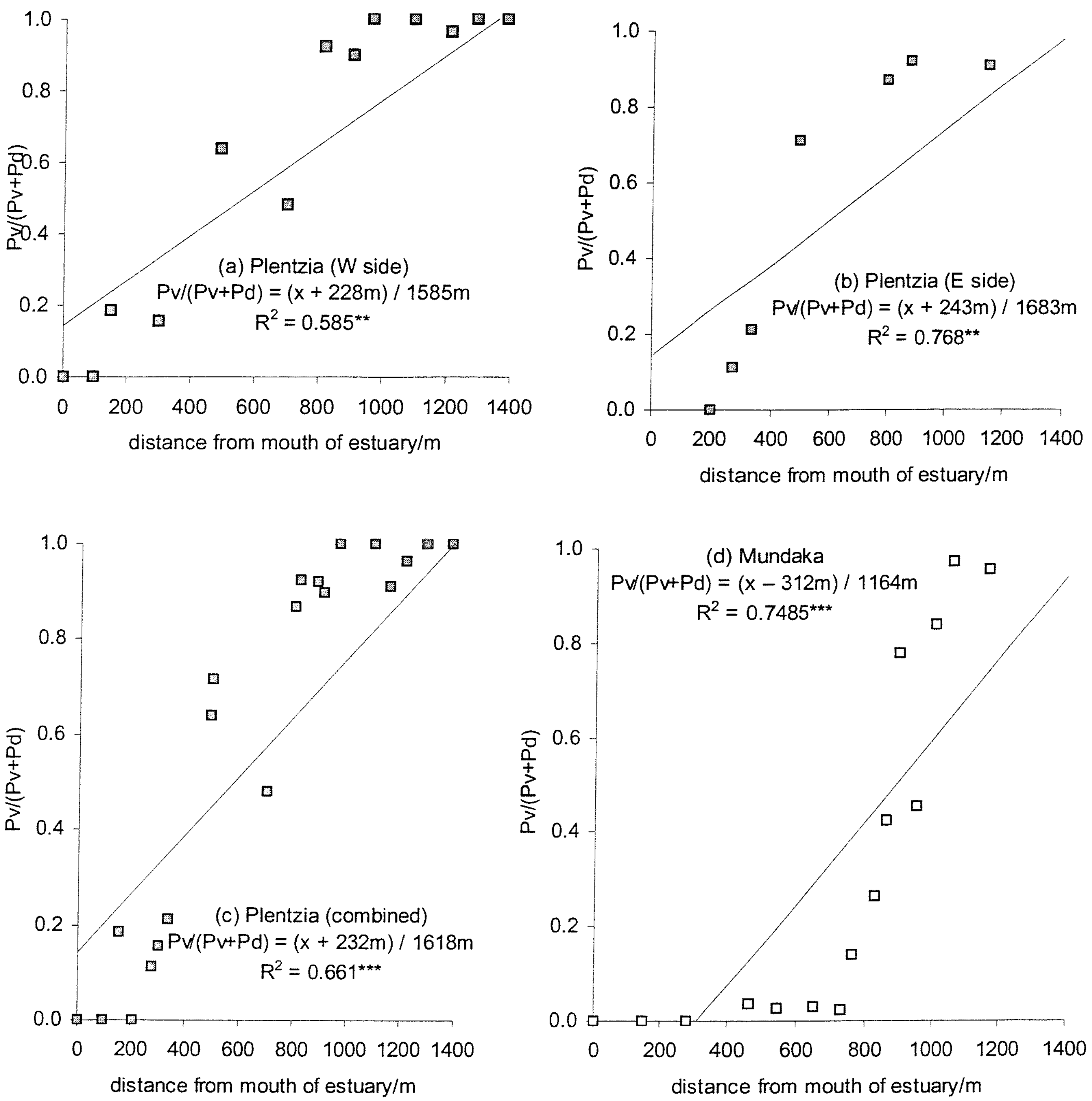


Figure 5.8. Regression plots of relative abundance of *P. vulgata* and *P. depressa*, *Pv/(Pv+Pd)*, against distance from the mouths of the Plentzia (a: W side; b: E side; c: both sides combined) and Mundaka (d) Estuaries. All regressions were significant. (a: $F_{(1,13)}$= 48.3, p=0.00001; b: $F_{(1,7)}$=16.3, p=0.005; c: $F_{(1,22)}$=37.1,p<0.00001; d: $F_{(1,15)}$=44.6, p<0.0001.)

5.3.2. Distribution

The pattern of distribution in both estuaries is seen to be similar. *P. depressa* is abundant in the lower estuary, becoming scarcer upstream (Figure 5.6). *P. vulgata* is rare or absent at the mouth of the estuary, becoming more common upstream, peaking at around 1200m from the mouth before falling in abundance again (although this peak is less clear on the east side of the Plentzia Estuary). There is a marked difference between the two estuaries in the position at which the transition from dominance of *P. depressa* to *P. vulgata* takes place. On both sides of the Plentzia Estuary the transition happens 100–800m from the river mouth, whereas in the Mundaka Estuary it takes place between 700 and 1100m.

A positive linear relationship for both relative abundance of the two species, $Pv/(Pv+Pd)$, and log relative abundance, $\log_{10}(Pv/Pd)$, with distance from the mouth of each estuary was found. The fit of the regression lines against distance from the river mouth for $\log_{10}(Pv/\mathrm{Pd})$ was better than for $Pv/(Pv+Pd)$: see Figures 5.7 and 5.8. The relationship between $\log_{10}(Pv/Pd)$ and distance from the mouth of each estuary is given in the following equations:

Mundaka: $\log_{10}(Pv/Pd) = (x - 887\text{m}) / 202\text{m}$ [$R^2 = 0.8417^{***}$] [5.1a]

Plentzia (W side): $\log_{10}(Pv/Pd) = (x - 502\text{m}) / 461\text{m}$ [$R^2 = 0.8704^{***}$] [5.1b]

Plentzia (E side): $\log_{10}(Pv/Pd) = (x - 520\text{m}) / 450\text{m}$ [$R^2 = 0.8243^{**}$] [5.1c]

Plentzia (combined): $\log_{10}(Pv/Pd) = (x - 510\text{m}) / 456\text{m}$ [$R^2 = 0.8493^{***}$] [5.1d]

The equations for both sides of the Plentzia Estuary (equations 5.1b and 5.1c) are very similar and a combined equation (5.1d) was calculated. The point at which the expected abundance of *P. vulgata* and *P. depressa* is equal is situated 510m from the mouth of the Plentzia Estuary; the distance over which there is a tenfold change in relative abundance is 456m. In the Mundaka Estuary, the point at which expected abundance is equal is further inside the estuary (887m from the mouth) but the transition is more rapid: a tenfold change in relative abundance takes place over just 202m. The positive linear relationship between $\log_{10}(Pv/Pd)$ and distance from the mouth of the estuary in both the Plentzia and Mundaka Estuaries suggests that the transition from predominance of *P. depressa* to *P. vulgata* is comparable to that on the open coast, where a negative linear relationship of $\log_{10}(Pv/Pd)$ with temperature is seen (see Chapter 4).

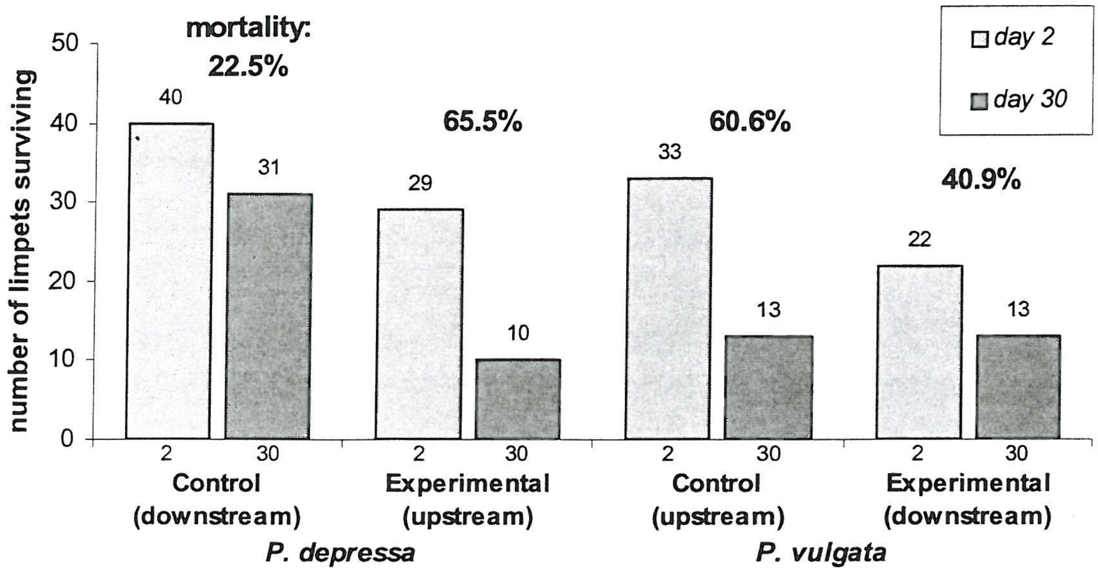


Figure 5.9. Number of limpets surviving on day 2 and day 30 of a transplantation experiment carried out on two species of limpets at two sites in the Mundaka Estuary (Basque coast, northern Spain) in April–May 2002. 50 limpets of each species were translocated to each site on day 0 of the experiment.

5.3.3. *Translocation experiment*

5.3.3.1. Survival

During the first two days after translocation (days 0–2), mortality was high among both the experimental groups, those limpets that were moved to the other site, and the control groups, those removed then returned to their original site; there was no difference between the two groups for either species (G-test: *P. depressa*: $G_1 = 1.03$, $p = 0.31$; *P. vulgata*: $G_1 = 1.42$, $p = 0.23$). The high mortality in the first two days was due to failure of limpets to re-attach after translocation, a common problem in translocation experiments (Hawkins, pers. comm.) For this reason, analysis of both mortality and growth was based on the numbers surviving on day 2.

During the following 28 days (days 2–30), numbers of *P. depressa* declined from 40 to 31 at the control (downstream) site (22.5% mortality), and from 29 to 10 at the experimental (upstream) site (66.5% mortality). For *P. vulgata,* mortality was 60.6% at the control (upstream) site compared with 40.9% at the experimental site. There was no significant difference between sites for either species (G-test: *P. depressa:* $G_1 = 3.60$, $p = 0.06$; *P. vulgata:* $G_1 = 0.72$, $p = 0.40$). (See Figure 5.9).

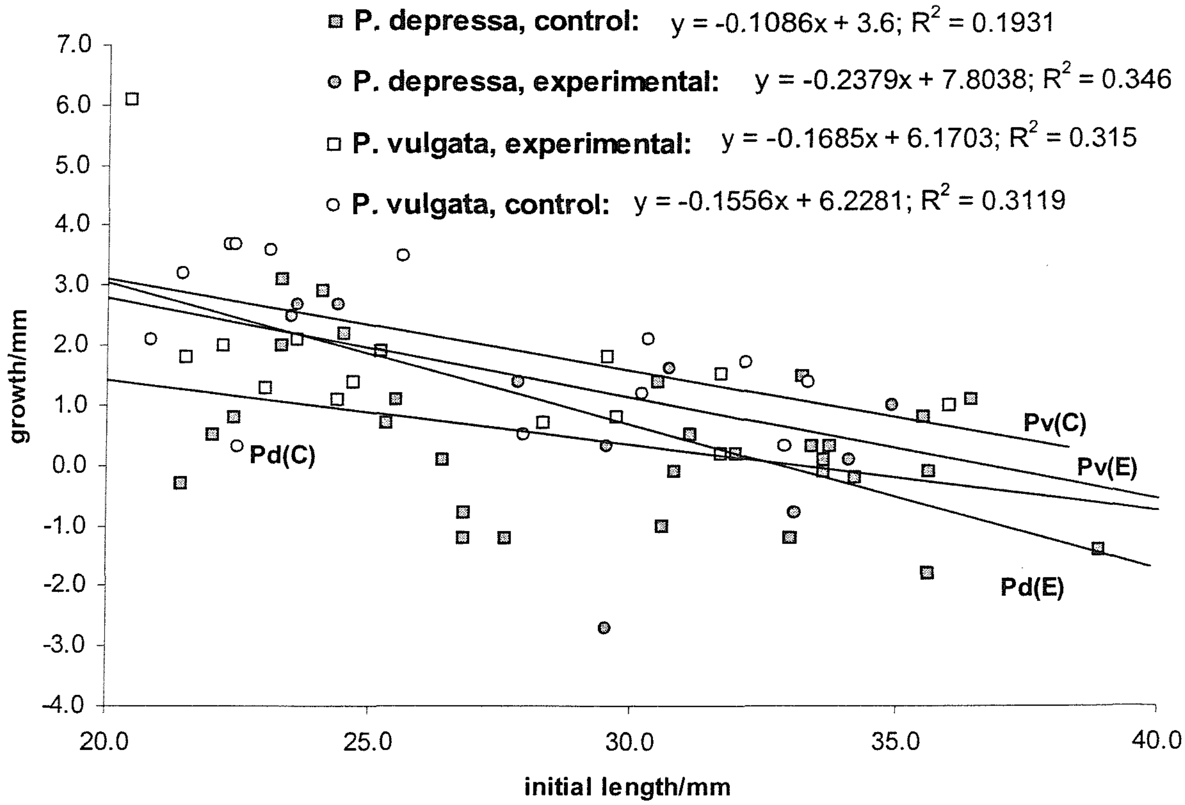


Figure 5.10. Ford-Walford plot of shell growth against initial length for two species of limpets (*Patella vulgata* and *P. depressa*) at two sites in the Mundaka Estuary (Basque coast, northern Spain) in April–May 2002. **Initial length** gives shell length on day 2 of the experiment; **growth** represents difference between length on day 30 and day 2. Equations of regression lines fitted by the least-squares method are given. **Pd(C)** is the regression line for the control group of *P. depressa*, etc. Tests for homogeneity of slope between regression lines for control and experimental groups gave no significant difference for either species. (*P. depressa*: $F_{(1,37)}$=1.11, p=0.299; *P. vulgata*: $F_{(1,22)}$=0.016, p=0.901)

5.3.3.2. Shell Growth

Tests for homogeneity of slope between regression lines for control and experimental groups gave no difference for either species (Figure 5.10) (*P. depressa*: $F_{(1,37)}$=1.11, p=0.299; *P. vulgata*: $F_{(1,22)}$=0.016, p=0.901). Thus the experiment did not find any difference between the growth rate of either species at its original site and its growth rate at the other site, suggesting that translocation did not have affect the growth rate of either species. Note that because of measurement errors negative growth rates were observed for some individuals of *Patella depressa.* If these individuals are ignored the results do not change: there is still no difference between slopes of the regression lines for the experimental and control groups. ($F_{(1,23)}$=2.63, p=0.12).

5.4. Discussion

5.4.1. Physical gradients and the mechanisms by which they act

Although it has long been known that *P. vulgata* is more common in estuaries in the inner Bay of Biscay than it is on the coast (Fischer-Piette, 1955a), this is the first time that the distribution patterns of *P. vulgata* and *P. depressa* in estuaries in Spain have been described quantitatively. In both estuaries studied, there was a strong correlation between log relative abundance of the two species and distance upstream from the mouth of the estuary: a relationship that mirrors the response of the same two species to the gradient of summer sea surface temperature on the north coast of Spain (see Chapter 4).

Two related questions can be asked about the mechanisms responsible for maintaining the observed distribution patterns of *P. vulgata* and *P. depressa* in these estuaries. First, what physical factors make estuaries comparably favourable habitats for *P. vulgata* and thus permit this species to thrive in estuaries when it is rare on the open coast? Second, by what means and on what stage(s) of their life cycles is the differential action of these physical factors on the two species expressed?

The main physical factors known to affect the relative abundance of limpet species are wave exposure (Southward and Orton, 1954; Orton *et al.*, 1956; Orton and Southward, 1961; Ballantine, 1961a), temperature (Lewis *et al.*, 1982; Bowman and Lewis, 1986; Lewis, 1986) and salinity (De Pirro *et al.*, 1999). No data were available on wave exposure in either of the two estuaries studied, but their physical configuration (Mundaka being much more open to wave action than Plentzia, which is protected by a breakwater and opens onto a sheltered bay) and the structure of soft sediments (predominantly sandy in Mundaka, muddy in Plentzia) both indicate greater wave action in the Mundaka Estuary. The transition from dominance of *P. depressa* to *P. vulgata* takes place further upriver in Mundaka than in Plentzia: the abundance of the two species is equal at a point

890m from the river mouth in Mundaka but only 510m from the river mouth in Plentzia. This is consistent with the hypothesis that wave action or some factor correlated with it, such as sedimentation rate, is partly responsible for maintaining the observed distribution of the two species.

The frequency of very low values of salinity was found to increase with distance up the Mundaka Estuary. Low salinity (approximately 3.3 for 24 hours) is known to cause differential mortality in two other limpet species, *P. ulyssiponensis* and *P. caerulea* (De Pirro *et al.*, 1999). Differential mortality due to low salinity is thus a potential mechanism for maintaining the observed distribution of *P. vulgata* and *P. depressa* in estuaries.

The variation of mean values of salinity and water temperature with distance up the Mundaka Estuary (about 0.64 and 0.16°C per kilometre, respectively), however, appear too small to account for the observed distribution of limpets. Based on the relationship between summer sea surface temperature and log relative abundance of *P. vulgata* and *P. depressa* derived in Chapter 4 (Equation 4.1), the temperature change necessary to produce a tenfold change in relative abundance of the two species on the open coast is 0.71°C. Since the present study found a tenfold change in relative abundance of the two species over a distance of between 200 and 450m (Equations 5.1a–d), it can be seen that the temperature gradient with distance up the estuary would need to be 10–20 times steeper than the observed gradient to fully account for the distributional patterns of the two species in estuaries, in terms of the response to temperature gradients observed on the open coast. However, it seems that variation of temperature with distance up the estuary could potentially account for approximately 5–10% of the variation in abundance of the two species.

Other physical factors correlated with distance up the estuary are likely to be important. These might include lack of suitable nursery grounds for *P. depressa* (Bowman, 1981) or possible greater intolerance of *P. depressa* to silt (Hawkins, pers. comm.)

The experimental part of the present study did not allow any firm conclusions to be reached about the mechanisms responsible for maintaining the observed distribution of the two species in the estuaries studied, perhaps because of the small sample sizes used.

No significant differences in either growth or mortality were observed. This could, however, be due to the initial sample sizes and the number of limpets that survived the initial translocation process being too small. The results for growth indicate that both species grew well at both experimental and control sites. This suggests that differences in growth rates are unlikely to account for the observed distribution pattern. In order to detect differences in mortality caused by extremes of low salinity, a long-term study over more than one year, including monitoring of salinity during the study, would be needed. Monitoring of siltation would also be required to know whether this factor might be one cause of the observed distribution. It may also be that differences in another stage of the life cycle (e.g. settlement or survival of juveniles) are mainly responsible for maintaining the observed distribution. Other possible mechanisms, not investigated in this study, include competition between the two species (Boaventura *et al.*, 2002b; Roberts, 2002), differences in reproductive success (Lewis, 1986; Bowman and Lewis, 1986; Guerra and Gaudencio, 1986), positive interactions with other species, notably fucoid algae (Burrows and Lodge, 1950; Southward and Southward, 1978; Hartnoll and Hawkins, 1985; Johnson *et al.*, 1998; Burrows and Hawkins, 1998), or susceptibility to predation (Coleman *et al.*, 1999).

Studies of competition between *P. vulgata* and *P. depressa* in northern Portugal (Boaventura *et al.*, 2002b), where *P. vulgata* is near its southern limit, concluded that interspecific competition was very unlikely to be the factor preventing *P. vulgata* from extending its range further south. However, it is difficult to draw generalised conclusions from this study because competitive ability varies between environments.

Physical factors affecting the reproduction and settlement are a possible mechanism for maintaining the distribution of these species in estuaries. Reproductive failure due to low summer temperatures is thought to set the northern limits of several species of grazing gastropods, notably *Patella depressa* in north Wales (Lewis, 1986; Bowman and Lewis, 1986). The southern limit of *P. vulgata* in the southwest Iberian Peninsula may also be set by reproductive failure due to high winter temperatures (Guerra and Gaudencio, 1986). It is not known to what extent factors such as low salinity or wave exposure can affect reproduction or settlement.

Several species of fucoid algae are present in the Mundaka and Plentzia estuaries (see Chapter 3), notably *Fucus spiralis, F. vesiculosus* and *Ascophyllum nodosum.* They are mainly present in isolated patches, however, and their abundance in the areas examined in this study is quite low. In these estuaries, therefore, it is unlikely that fucoid algae play an important role in providing shelter for *P. vulgata* (Burrows and Lodge, 1950; Southward and Southward, 1978; Hartnoll and Hawkins, 1985; Johnson *et al.*, 1998; Johnson and Hawkins, 1998; Burrows and Hawkins, 1998; Jenkins *et al.*, 1999a,b) since there are many boulders and other sheltered areas available, particularly in the Mundaka estuary.

5.4.2. Interpretation of distribution patterns with reference to palaeoecological studies

Consideration of palaeoecological studies helps to place the distribution patterns observed in the present study into a historical context. Analysis of shells deposited in middens by prehistoric cave dwellers in northern Spain indicates that during the last Ice Age, around 20,000 years BP (before the present), limpet populations on the north coast were mainly or entirely composed of *Patella vulgata* (Ortea, 1986; Southward *et al.*, 1995). *P. depressa* appeared in the middens at about 15,000 BP, but in small proportions (less than 10% of all limpets). *P. vulgata* continued to predominate until approximately 9,000 BP. This date corresponds with the end of the Ice Age, when global temperatures rose by about 5°C (Stauffer, 1999; Petit *et al.*, 1999). There was then a comparatively rapid decline in *P. vulgata* and a simultaneous rise in the proportion of *P. depressa.* By 6,500 BP, *P. depressa* was the predominant species while *P. vulgata* comprised less than 10% of all limpets (Ortea, 1986; Southward *et al.*, 1995). Analysis of other species found in the middens rules out the hypothesis that this rapid shift in species composition was due to gathering on more exposed areas of the coast (Southward *et al.*, 1995). Present-day limpet gatherers appear to show a relative preference for *P. vulgata* over *P. depressa* (personal communication from fishermen in Ribadesella, Asturias). If prehistoric gatherers showed a similar preference it could have influenced the proportion of species in the middens. Nonetheless it seems likely that the ratio of species in the middens is a fairly accurate reflection of populations found on the coast.

Thus until about 9,000 BP, *Patella depressa,* if present at all in northern Spain, was probably restricted to exposed habitats on the open coast, as it is today near its northern limits in Britain (Orton and Southward, 1961), while *P. vulgata* was probably abundant and widespread, as it is today in northern Europe (Orton *et al.*, 1956; Ballantine, 1961b). By about 6,500 BP, *P. vulgata* would have become restricted mainly to sheltered habitats. Episodes of sea level rise linked with warming (Stauffer, 1999) took place on the Basque coast around 8000 BP and 3000 BP (Cearreta, 1998). This created the drowned river valleys (*rías*) along the north coast of Spain, providing significant areas of estuarine habitat which then became refuges for *P. vulgata* and other northern species (Fischer-Piette, 1955a).

Present-day populations of *P. vulgata* in estuaries in northern Spain, therefore, probably represent relicts of a widespread Ice Age population. These estuarine refugee populations are likely to have become reproductively isolated during unfavourable (warm) periods and then connected again during favourable (cool) periods, which should be reflected in their genetic structure. Evidence of past genetic bottlenecks, probably due to climatic factors, has been observed in northern Spanish populations of *F. serratus,* another boreal species (Coyer *et al.*, 2003). This presents a possible avenue for future investigation.

5.4.3. Lessons for design of future studies

The present study had several shortcomings that would need to be overcome in order for future studies to be more productive. There were no long-term data on physical conditions at the experimental sites, so extrapolations had to be made from existing data sets. The use of autonomous data loggers could provide much more extensive data on physical factors.

The number and size of the experimental groups was limited by both the size of the available populations, and the need to set up the experiment on evening low tides, when the limpets were actively feeding and could be removed with minimum shock. The original intention was to carry out repeated studies of mortality and shell growth during a period of several months. This would have allowed for analysis of survival functions using a standard life-table (Begon *et al.,* 1996) and estimation of confidence limits for survival times. In the event the experiment was terminated after one month because of low survival in three of the four groups. Using larger groups with replication of groups and sites could have permitted the continuation of the study for a longer period and allowed more sensitive detection of differences in growth and mortality.

The west shore of the Mundaka estuary on which the translocation experiment was carried out had some drawbacks. The limited area of habitat available meant that limpet populations were relatively small. As a boulder shore it was difficult to work on and potentially unstable. Also, some of the limpets moved underneath boulders, making them hard to find and measure. If possible, it would be better to use estuaries with significantly larger areas of bedrock shore.

Nonetheless, this study has shown that estuaries have the potential to be used as tractable systems for experimental studies of the response of cold- and warm-temperate rocky shore species to environmental gradients. If the practical difficulties can be resolved and given the right set of estuaries, there is ample scope for productive experimentation.

Chapter 6: Response of selected rocky shore species to climate change: Predictions using a graphical model

6.1. Introduction

Climate change is already occurring and is likely to accelerate. Even if humans take immediate, drastic action to reduce emissions of greenhouse gases, substantial, rapid change over the coming century is inevitable (Houghton *et al.*, 2001). It is therefore important to forecast the likely responses of natural ecosystems to projected future climate scenarios, so as to plan for, adapt to and perhaps to mitigate the effects of climate change.

This chapter develops a graphical method for forecasting the response of rocky shore species to projected climate scenarios, based on their existing ranges and known temperature tolerances. This approach is applied to forecast the responses of 18 common species in the northeast Atlantic to three climate scenarios. The scenarios were derived from Intergovernmental Panel on Climate Change (IPCC) forecasts and observed trends during 1982–2001. This introduction briefly reviews the relevant knowledge about the effects of climate on rocky shore species and communities before giving the detailed objectives of the chapter.

The majority of studies that attempt to predict the response of ecosystems to climate change do so on the basis of the "climate envelope" approach (Davis *et al.*, 1998a,b) , which is based on the assumption that species or ecosystems will move to locations comparable to their present-day climate and environment. Despite its drawbacks, discussed in Chapter 1, this remains the most widely used approach (see reviews by Gitay *et al.,* 2002; Walther *et al.*, 2002; Parmesan and Yohe, 2003). It has previously been applied to rocky shore species (Breeman 1990; Hiscock *et al.*, 2001, 2004). To date, however, few quantitative estimates have been made of changes in distribution of rocky shore species in response to specific climate change scenarios.

The effects of climate on rocky shore species have been extensively studied over a long period of time (Orton, 1920; Allee, 1923; Hutchins, 1947; Southward, 1958; Lewis *et al.*, 1982; Lüning, 1984; Lewis, 1986; Breeman, 1988; Lüning, 1990; Hoek *et al.*, 1990; see review in Chapter 1). The consensus is that on large temporal and spatial scales (decades and hundreds of kilometres), temperature is the overriding climatic factor affecting rocky shore organisms. Other important factors include day length (Breeman, 1988) and wind, indirectly via wave action (Ballantine, 1961a) and wind-induced upwelling (Menge *et al.*, 1997; Shkedy and Roughgarden, 1997; Connolly and Roughgarden, 1999; Menge, 2000).

From the point of view of studying the impact of climate change, perhaps the most significant effect of temperature is in limiting the range of rocky shore species. Temperature is the ultimate factor determining the geographical limits of most rocky shore species (Orton, 1920; Allee, 1923; Hoek, 1982; Breeman, 1988; Lüning, 1990), although other, proximate causes typically determine the exact position of their limits. These can include physical barriers or lack of suitable habitat (Crisp and Southward, 1953, 1958; Herbert *et al.*, 2003), coupled with the role of currents and larval dispersal (Gaylord and Gaines, 2000; Andrew and Viejo, 1998). Populations that already experience suboptimal climatic conditions are likely to be the first to respond to warming or cooling: thus range limits are the first place to look for the effects of climate change (Lewis, 1996; Herbert *et al.*, 2003). Data on the ranges and limits of species are often more readily available than for other characteristics of the species such as abundance, reproduction or spatial distribution. Range shifts are also a useful way of describing the effects of climate change to the general public. It is therefore not surprising that the effects of climate change on rocky shore species have often been discussed in terms of extension or retreat of their range (Breeman, 1990; Weaver and Green, 1998; Hiscock *et al.*, 2001, 2004).

The geographical limits of rocky shore species are normally established by interaction between the thermal requirements of their life cycles, and spatial and temporal variations in climate (Hutchins, 1947; Hoek, 1982; Breeman, 1988, 1990; see review in Chapter 1). In general, two types of limit can be distinguished (Hutchins, 1947): "survival limits", caused by mortality of the more hardy stages of the life cycle, and "repopulation limits", caused by failure to complete the life cycle at a more temperature-sensitive stage, such as reproduction, larval settlement, or early growth. Organisms are thought to adjust their life cycles so that thermally sensitive stages take place at the most favourable time of year for them (Hoek, 1982; Bowman and Lewis, 1986). Therefore, in temperate climates, limits set by failure to repopulate tend to be associated with high winter temperatures (e.g. the southern limit of *Laminaria* *hyperborea* in Spain, which is set by winter temperatures too warm for initiation of blade growth: Bolton and Lüning, 1982) or with low summer temperatures (e.g. the northern limits of many warm-water invertebrates in Britain, including *Gibbula umbilicalis, Chthamalus montagui,* and *Osilinus lineatus*, which appear to be set by reproductive failure: Lewis, 1986). Conversely, survival limits are typically set by high summer or low winter temperatures (e.g. the northern limits of *Saccorhiza polyschides* in the eastern North Sea, which appear to be set by winter mortality: Norton, 1970).

For many species of macroalgae, distribution coincides approximately with the experimentally determined temperature requirements for the species (Breeman, 1988; Lüning, 1984). For example, experimental studies of the thermal tolerance of the lower shore kelp *Laminaria hyperborea* (Gunnerus) Foslie indicate that the adult can survive maximum sea water temperatures of approximately 20–21°C for a week (Lüning, 1984) while the most temperature-sensitive phase of the life cycle, the formation of new blades, is inhibited by temperatures above 15°C (Bolton and Lüning, 1982). These values coincide approximately with the extreme monthly average sea surface temperatures near the southern limits of this species, in northwest Spain (August and February) and Brittany (August only).

Species that live higher on the shore are likely to be limited by air, rather than sea, temperatures (e.g. fucoid algae: Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985). If so, their experimentally determined temperature tolerances while immersed may not coincide with observed range limits. This can be seen for four species of fucoid algae whose temperature tolerances were tested by immersing them in sea water at controlled temperatures for a week (Lüning, 1984). *Fucus serratus* L. survived at 25°C but died at 28°C. *Ascophyllum nodosum* (L.) Le Jolis survived at 25°C but sometimes died and sometimes survived at 28°C, and *F. vesiculosus* L. and *Fucus spiralis* L. both survived at 28°C but died at 30°C. If sea temperature were the limiting factor, therefore, all four species should be able to live at San Sebastián (Gipúzkoa, Spanish Basque Country), where the absolute maximum sea temperature recorded since 1947 (Borja *et al.*, 2000) is 25.3°C, and where the mean August temperature for 1947–1989 was just 21.5°C. In fact, *F. spiralis* is the only one of the four found at San Sebastián. The other three species mentioned have been absent from Gipúzkoa and from the French Basque coast since at least the 1950s, probably longer. *F. serratus* has not been found living within 150km of San Sebastián during the 20th century, and all three species are restricted to the most favourable habitats (sheltered estuaries) throughout the inner Bay of Biscay (Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959; Ibañez, 1990; see also Chapter 3). Although sea temperature is broadly correlated with the distribution of these and many other cold-temperate rocky shore species within the Bay of Biscay, some other factor must be responsible for setting their actual limits. Air temperature is a likely candidate factor (Schonbeck and Norton, 1978), although biological interactions such as grazing (Hawkins *et al.*, 1992) could also play a role.

The response of species to climate change will often depend on what factors limit their expansion at present. Population studies of the gastropod *Gibbula umbilicalis* (da Costa) (Lewis *et al.*, 1982; Kendall and Lewis, 1987) and the barnacle *Chthamalus montagui* Southward (Lewis *et al.*, 1982) concluded that the northern limits of both species in northern Scotland are probably set by failure to consistently reproduce and hence lack of recruitment, due to low summer temperatures in the 1970s and early 1980s. Yet until recently neither species had extended its range down the east coast of Britain (Crisp *et al.*, 1981; Southward *et al.*, 1995), where summer temperatures are higher but winter temperatures lower than they are in northern Scotland. This could be due to limitation by lower winter temperatures on the east coast, possibly affecting the larval or newly settled juvenile stages (Kendall *et al.* 1987a, 1987b). Recent observations suggest, however, that both *Gibbula umbilicalis* and *Chthamalus montagui* may be extending their range in Scotland (N. Miezskowska, pers. comm.)

In order to predict the responses of species to climate change, therefore, it is advisable to compare experimental predictions of limiting factors (where they exist) with those estimated from the actual spatial distributions of species. This can be done by drawing the range of a species on charts of summer and winter sea surface temperature and seeing at which isotherms the limits fall (Hoek *et al.*, 1990). However, this requires the use of two charts per species and it cannot easily be applied to predict species response to climate change scenarios. It is possible to use a single chart by superimposing summer and winter isotherms but this tends to be confusing.

This chapter describes a graphical method I have developed for estimating the temperature limits of rocky shore species, using a transformation of species distribution data from physical space (axes of latitude and longitude) to climate space (axes of winter and summer temperature). This allows visualisation of the temperature requirements of species in a single graphical representation, thus making it easy to project responses to climate change scenarios. The approach is used to estimate the upper or lower temperature limits of 18 common cold- and warm-temperate rocky shore species in the northeast Atlantic, based mainly on their observed spatial distribution, but also, where available, on predictions from experimental studies. Predictions are then made of the range shifts of these 18 species under three different climate change scenarios.

6.2. Methods

6.2.1. Temperature requirements of rocky shore species

The climate data used in this part of the study were from the Reynolds SST data set (based on satellite observations from November 1981 to the present), obtained from the website of the NOAA-CIRES Climate Diagnostics Centre at www.cdc.noaa.gov. Winter temperatures were defined as January–March averages and summer temperatures as July–September averages. Charts were generated of both summer and winter sea surface temperatures between 30°N and 70°N, 15°W and 15°E, for each year from 1982 to 2001 inclusive. The temperatures were read visually off the charts at 62 selected points along the coastline of North Africa and Europe, including Britain and Ireland. Figure 6.1 is a sample chart showing temperatures for summer 2001.

After thus obtaining mean winter and summer sea surface temperatures for 1982–2001 for each of these 62 points, the data were plotted on a single figure with winter temperature on the x-axis and summer temperature on the y-axis (see Figure 6.2). Inverted axes were used so as to put northern Europe at the top of the figure. Straight lines were used to interpolate between adjacent points. National borders and 1- and 3-degree intervals of latitude are also indicated. The resulting map of Europe has in effect been stretched so that the summer and winter isotherms are straight and perpendicular. Because winter temperatures in Europe generally increase in a northeast-southwest direction, while summer temperatures increase in a north-south direction, Figure 6.2 still resembles a normal map of Europe. Regional climatic anomalies, such as the summer maximum on the Basque coast and the winter minimum in the North Sea, can be seen clearly.

The current distribution of 18 selected rocky shore species was then plotted (see Figures 6.13 to 6.30) on axes of summer against winter temperature, based on my observations (described in Chapter 3) and other sources (Fischer-Piette, 1955; Fischer-Piette and Gaillard, 1959; Crisp and Fischer-Piette, 1959; Lewis, 1964, 1986; Crisp *et al.*, 1981; Guerra and Gaudencio, 1986; Lüning, 1990; Southward *et al.*, 1995; Barnes, 1996; Hayward *et al.*, 1996; Santos, 2000; Herbert *et al.*, 2003; S. J. Hawkins and N. Miezskowska, pers. comm.). The temperature requirements of each species (Table 6.1) were estimated from distribution and any relevant experimental or biogeographical studies (Lewis *et al.*, 1982; Lewis, 1986; Bowman and Lewis, 1986; Kendall and Lewis, 1987; Lüning, 1984; Breeman, 1988)

For the warm-water species examined (*Pollicipes pollicipes, Balanus perforatus, Chthamalus montagui, Patella rustica, Patella depressa, Patella ulyssiponensis, Gibbula pennanti, Gibbula umbilicalis,* and *Osilinus lineatus*) it was found that existing distribution patterns could generally be best explained by a combined winter and summer limit, even for those species where a summer limit has been suggested (e.g. *Osilinus lineatus, Chthamalus montagui, Gibbula umbilicalis* and *Patella ulyssiponensis*: Lewis *et al.*, 1982). Both winter and summer limits were therefore estimated for these species. On the other hand, for many cold-water species (*Nucella lapillus, Pelvetia canaliculata, Fucus vesiculosus, Fucus serratus, Fucus distichus distichus,* and *Alaria esculenta*) it was found that a summer temperature limit sufficed to explain their distribution. In the interests of simplicity these species were therefore modelled with a summer temperature limit only.

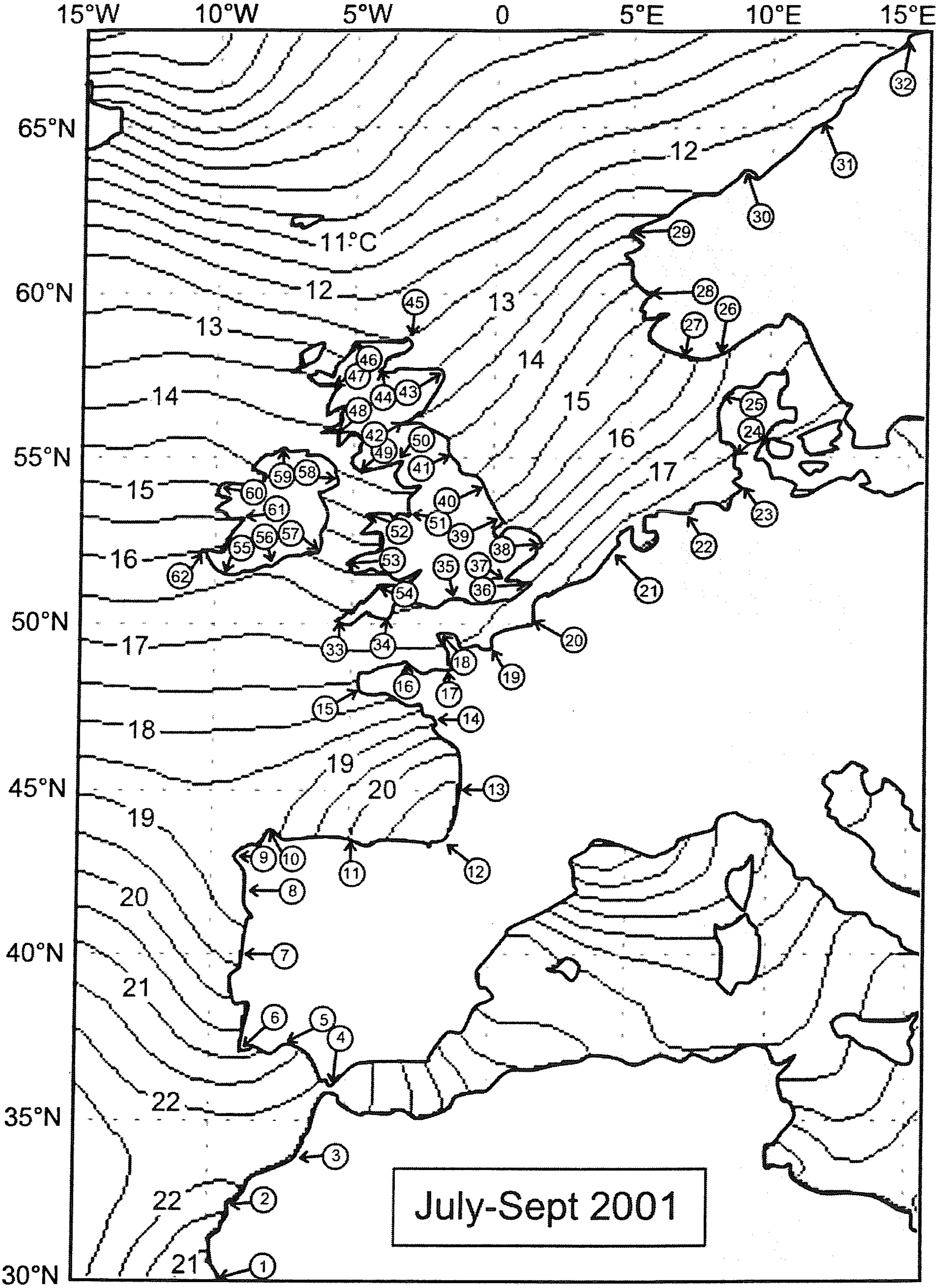


Figure 6.1. Sample chart showing sea surface temperatures in the northeast Atlantic during July–September 2001, in degrees Celsius. Numbers in circles with arrows show the 62 points along the coast where temperature was read off. Chart based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003).

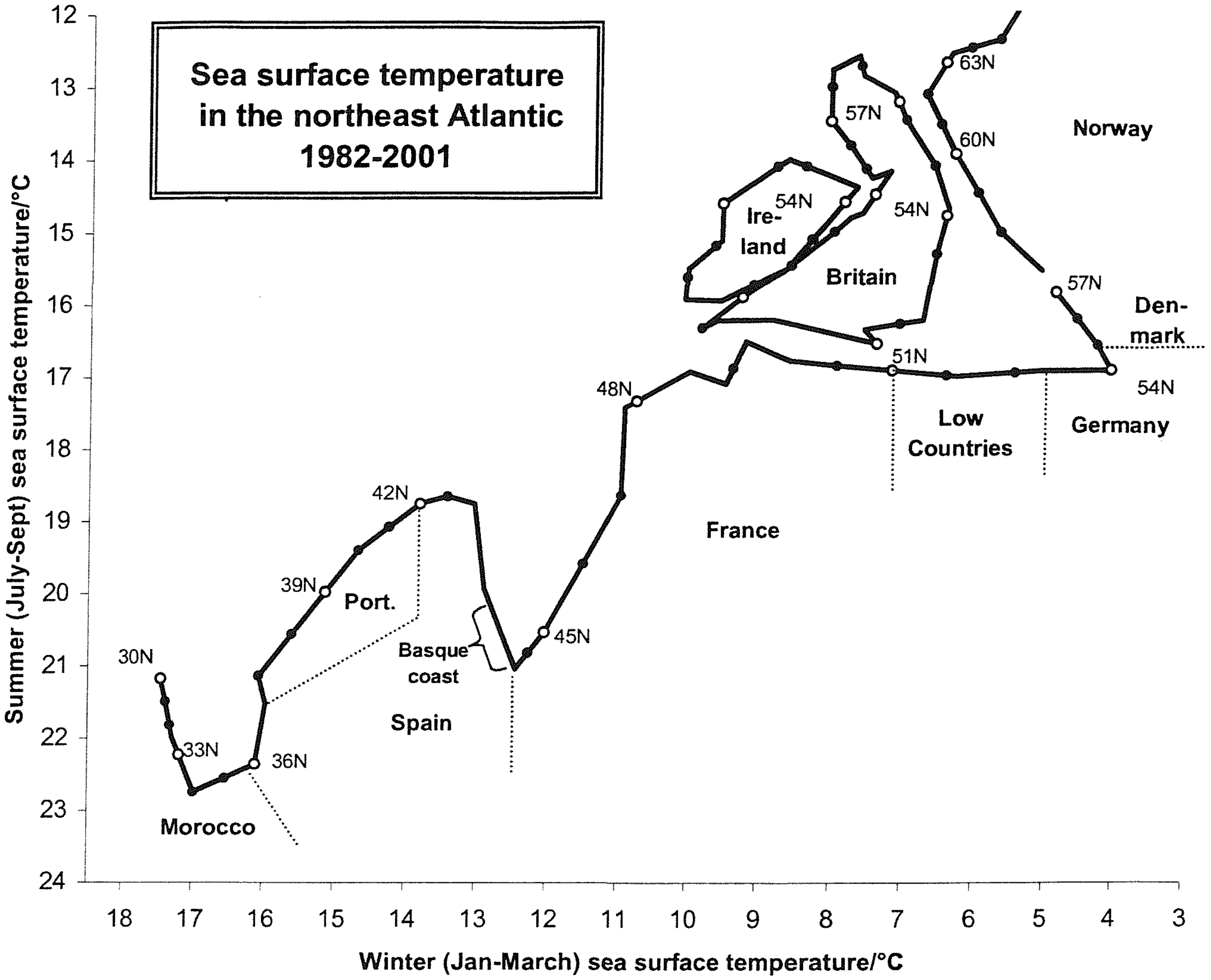


Figure 6.2. Mean summer (July–September) sea surface temperatures for 1982–2001 on the y-axis against corresponding winter (January–March) temperatures on the x-axis, sampled at 62 points along the northeast Atlantic coast between 30°N and 66°N (shown in Figure 6.1). Note inverted axes. Closed circles represent 1-degree intervals of latitude and open circles 3-degree intervals. Based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003).

Table 6.1. Distribution limits and estimated temperature requirements for 18 rocky shore species common in the northeast Atlantic. Species are listed in order of temperature ranges from warmest to coldest. **Southern spp.:** Northern distribution limits of warm-temperate species with minimum temperature limits in winter and (in parentheses) summer. **Northern spp.:** Southern distribution limits of cold-temperate species with maximum temperature limits in summer and (in parentheses) winter, where information was available. Temperature requirements are seasonal means (January–March and July–September) estimated from distribution and any relevant experimental studies, based on 1982–2001 mean sea surface temperatures (NOAA-CIRES Climate Diagnostics Centre, 2003): see Figures 6.13 through 6.30. **Present limits** are based on my observations (described in Chapter 3) and other studies (Fischer-Piette, 1955; Fischer-Piette and Gaillard, 1959; Crisp and Fischer-Piette, 1959; Crisp *et al.*, 1981; Guerra and Gaudencio, 1986; Lewis, 1986; Lüning, 1990; Southward *et al.*, 1995; Barnes, 1996; Hayward *et al.*, 1996; Santos, 2000; Herbert *et al.*, 2003; S. J. Hawkins and N. Miezskowska, pers. comm.)

	Species	Present northern limits	Min temp.
Southern spp.	*Patella rustica*	Basque coast, C Portugal, NW Spain	12.5°C (18.75°C)
	Pollicipes pollicipes	SW Cornwall, W Brittany	9.5°C (16°C)
	Gibbula pennanti	N Brittany, Channel Isles	9°C (16.5°C)
	Balanus perforatus	SW Wales, SE England, N France	7.5°C (15.75°C)
	Patella depressa	Normandy, Isle of Wight, N Wales	7.5°C (14.75°C)
	Osilinus lineatus	Normandy, S England, N Wales, N Ireland	7.5°C (14°C)
	Chthamalus montagui	Normandy, Isle of Wight, NE Scotland	7°C (12.5°C)
	Gibbula umbilicalis	N France, Isle of Wight, N Scotland	7°C (12.5°C)
	Patella ulyssiponensis	Normandy, NE England, W Norway	6°C (12.5°C)

	Species	Present southern limits	Max temp.
Northern spp.	*Patella vulgata*	S Portugal	21.5°C (16°C)
	Nucella lapillus	S Portugal, N Spain, SW France	21°C
	Pelvetia canaliculata	S Portugal	21°C
	Fucus vesiculosus	S Portugal, Basque coast, W France	20.5°C
	Semibalanus balanoides	N Portugal, N Spain, W France	20.5°C (14.5°C)
	Fucus serratus	N Portugal, N Spain, S Brittany	19.5°C
	Laminaria hyperborea	N Portugal, NW Spain, Brittany	19°C (14°C)
	Alaria esculenta	Brittany, Cornwall, S Norway, E England	16.5°C
	Fucus distichus ssp. *distichus*	W Ireland, Scotland, S Norway	16°C

6.2.2. Climate scenarios

Projections were made of future expansion or retreat in distribution for the 18 selected species, under three climate scenarios, two for 2025 and one for 2050, as follows:

> **Scenario 1** (Figure 6.3): A scenario for 2025 based on regional trends projected by the Intergovernmental Panel on Climate Change (IPCC) models A2 and B2 (Houghton *et al.*, 2001). Both these models predict that compared with global trends, northern Europe will experience "much greater than average" winter warming and "greater than average" summer warming, while southern Europe and north Africa will experience "greater than average" winter warming and "much greater than average" summer warming (ibid, Figure 3.2). Given that the projected global mean temperature increase for the period 1990 to 2025 is from 0.4 to 1.1°C (ibid, §3.6), "greater than average" and "much greater than average" were interpreted as rises of 1.0°C and 1.5°C respectively, based on 1982–2001 means. These rises were varied with latitude: at 30°N (Morocco) warming was set at 1.0°C in winter and 1.5°C in summer; at 70°N (northern Norway) it was 1.5°C in winter and 1.0°C in summer. At intermediate points the warming was calculated by linear interpolation based on latitude, so that at 50°N, for example, it was 1.25°C in both summer and winter. This and scenario 3 are both based on "best guess" projections of median temperature rises.
>
> **Scenario 2** (Figure 6.5): An alternative scenario for 2025 based on extrapolation of observed trends for 1982–2001. For each of the 62 points sampled, the summer and winter trends were calculated as the slope (in °C per year) of a straight line fitted by the least-squares method to the data for each year 1982–2001. Summer and winter temperatures and the resulting trendlines for four of the sample points are shown in Figure 6.4. These trendlines were extrapolated forwards to give projected temperatures for 2025.
>
> **Scenario 3** (Figure 6.6): A scenario for 2050 based on the IPCC's climate models A2 and B2 (Houghton *et al.*, 2001). As with Scenario 1, warming was varied linearly with latitude: warming at 30°N was set at 2.2°C in winter and 3.0°C in summer, while at 70°N it was 3.0°C in winter and 2.2°C in summer.

For each of these three scenarios, projected summer sea surface temperatures were plotted against projected winter temperatures (Figures 6.3, 6.5 and 6.6). Based on the estimated temperature limits in Table 6.1, the projected distribution for each species under each scenario was plotted, again on temperature axes (Figures 6.13 to 6.30). The present-day and projected future distributions for each species were then plotted on a standard distribution map with latitude and longitude axes (Figures 6.7 to 6.12).

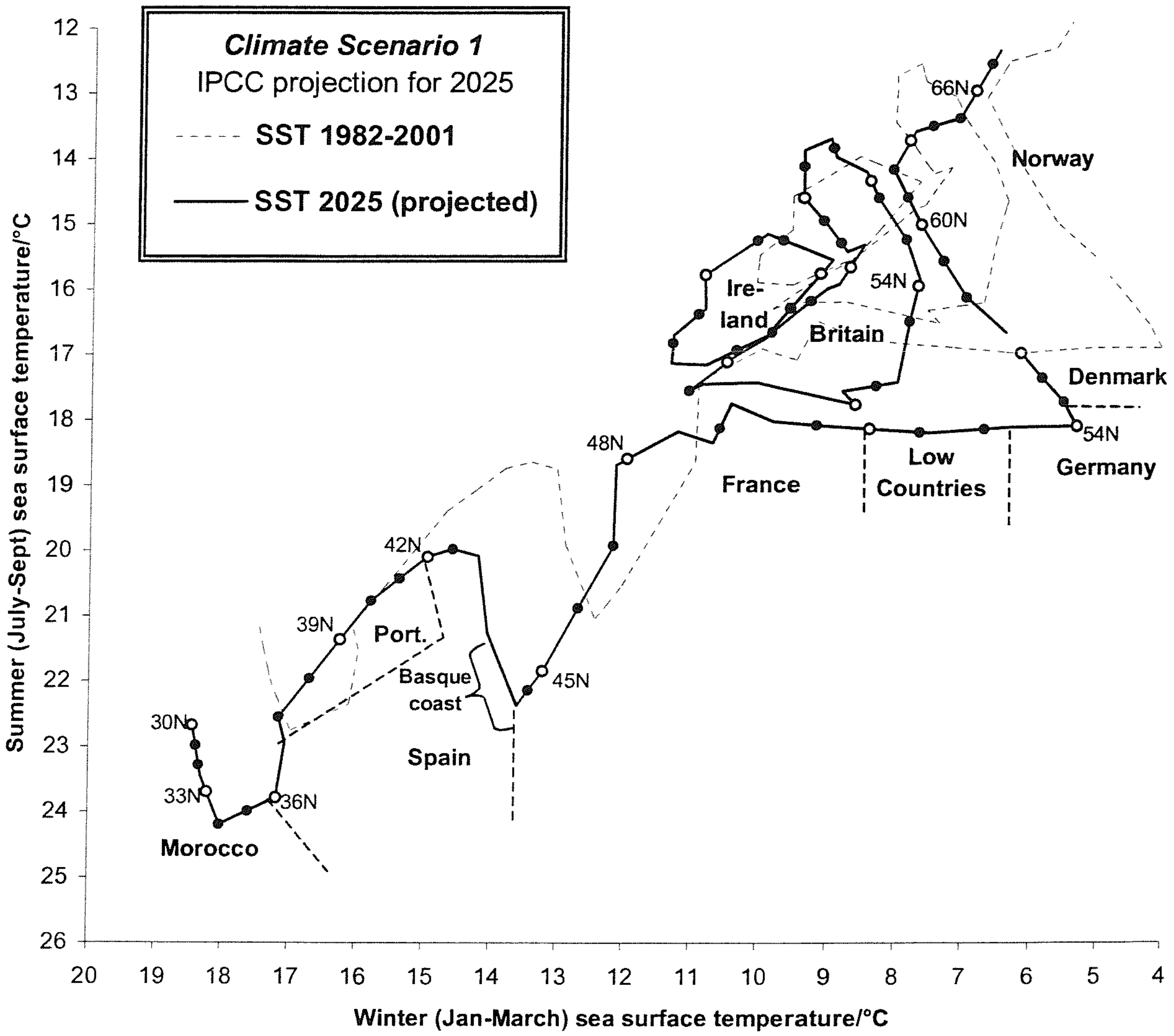


Figure 6.3. Projected summer (July–September) sea surface temperatures on the y-axis against winter (January–March) sea surface temperatures on the x-axis, for the northeast Atlantic coast between 30°N and 66°N, under a climate scenario for 2025 based on scenario models A2 and B2 of the IPCC (Houghton *et al.*, 2001). Under this scenario warming is dependent on latitude: at 30°N, winter temperature rises by 1.0°C and summer T by 1.5°C, while at 70°N, winter T rises by 1.5°C and summer T by 1.0°C, all based on averages for 1982–2001 (dashed curve). Projections for intermediate latitudes are based on linear interpolation between these extremes. Closed circles represent 1-degree intervals of latitude and open circles 3-degree intervals. Note inverted axes. Based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003).

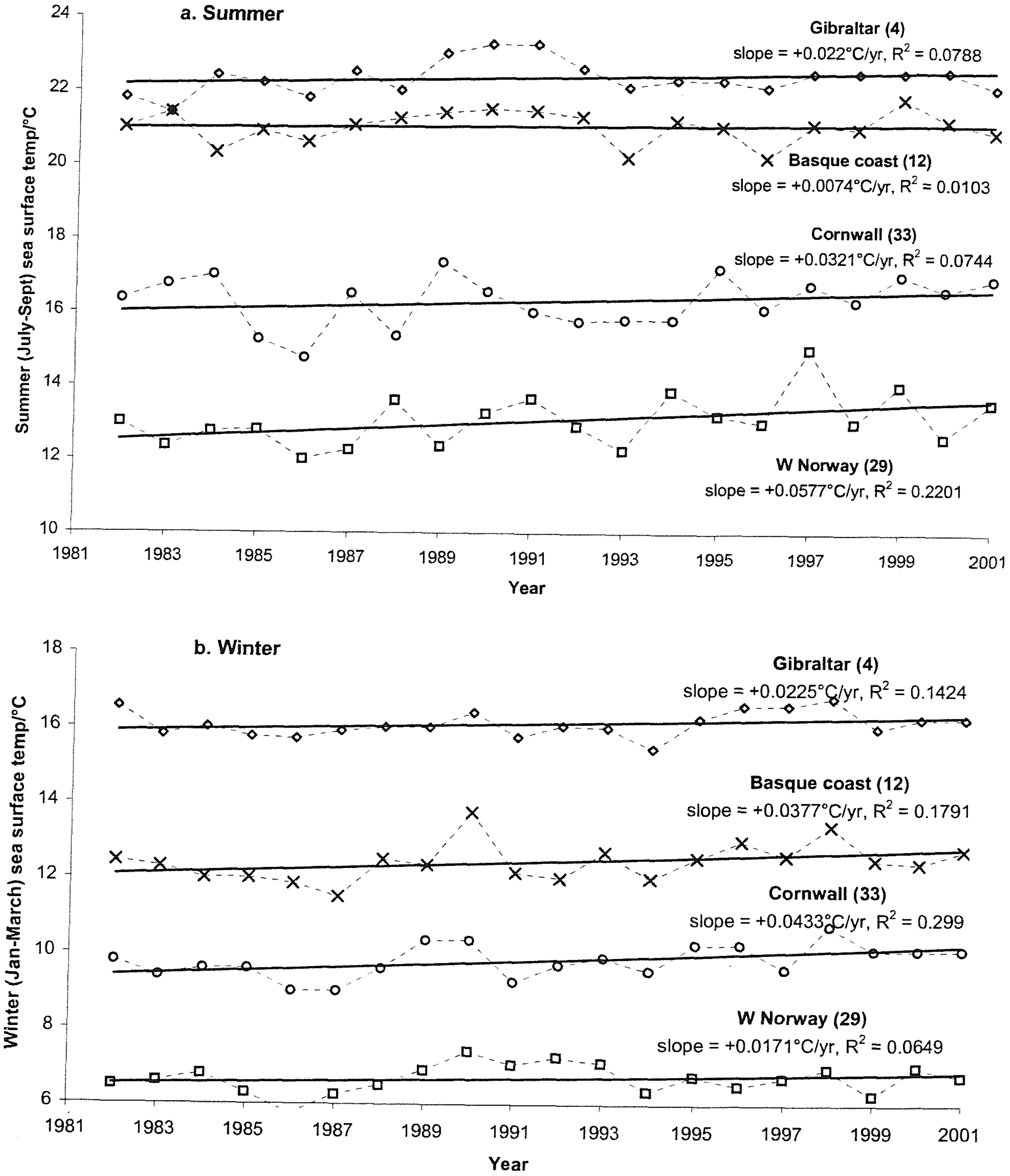


Figure 6.4. a. Summer (July–September) and b. winter (January–March) sea surface temperatures for 1982–2001 at four sample points on the northeast Atlantic coast. Locations (numbers in parentheses) are given in Figure 6.1. Straight lines are fitted to the data by the least-squares method. Data from the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003).

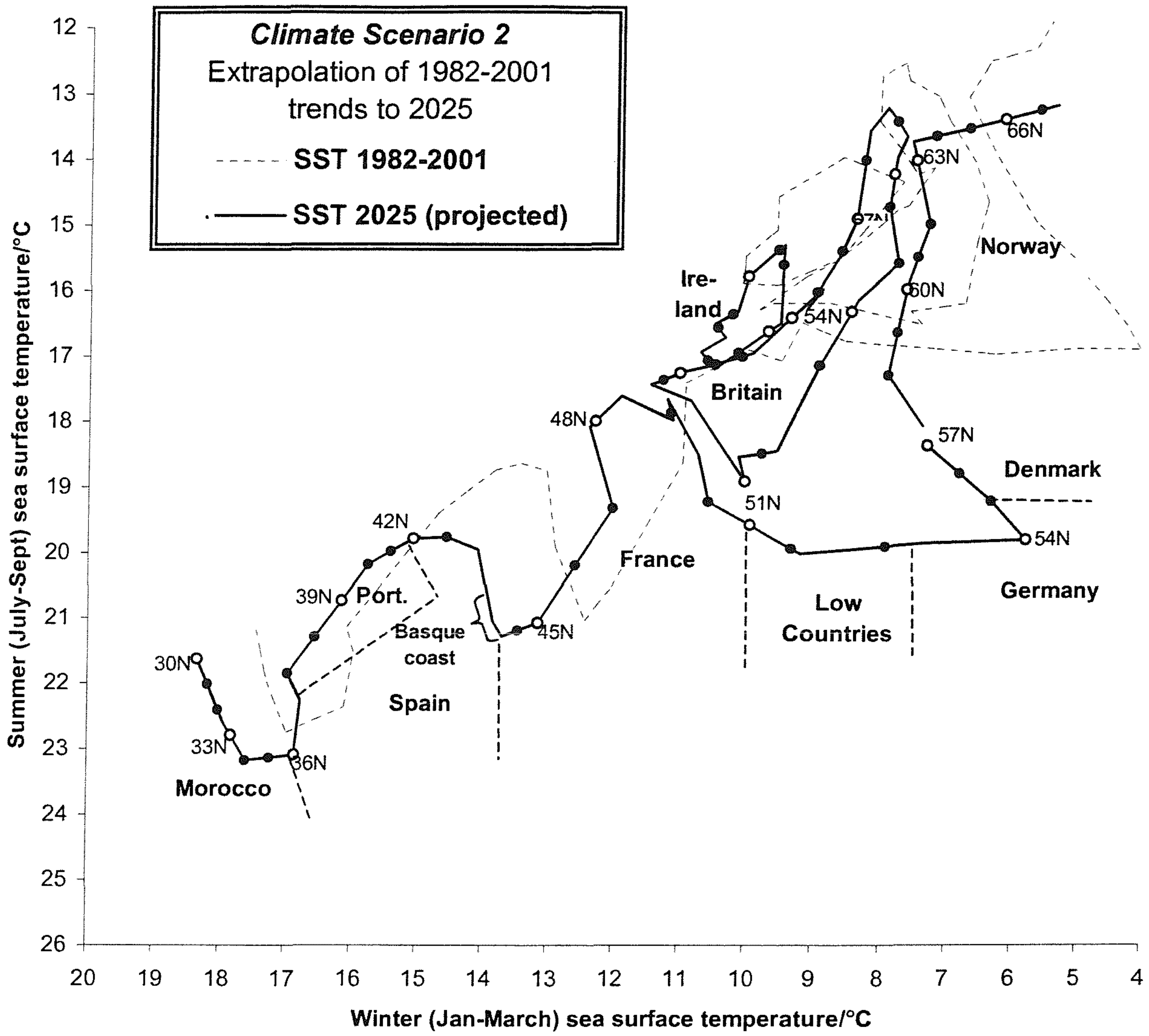


Figure 6.5. Projected summer (July–September) sea surface temperatures on the y-axis against winter (January–March) sea surface temperatures on the x-axis, for the northeast Atlantic coast between 30°N and 67°N, under a climate scenario for 2025 based on extrapolation of trends during 1982–2001. For each of the 62 points at which temperatures were sampled (see figure 6.1), the trends in winter and summer temperatures were calculated as the slope of a straight line fitted by the least-squares method to values for 1982–2001. These trendlines were then extrapolated forwards to give projected temperatures for 2025. Note inverted axes. Closed circles represent 1-degree intervals of latitude and open circles 3-degree intervals. Based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003).

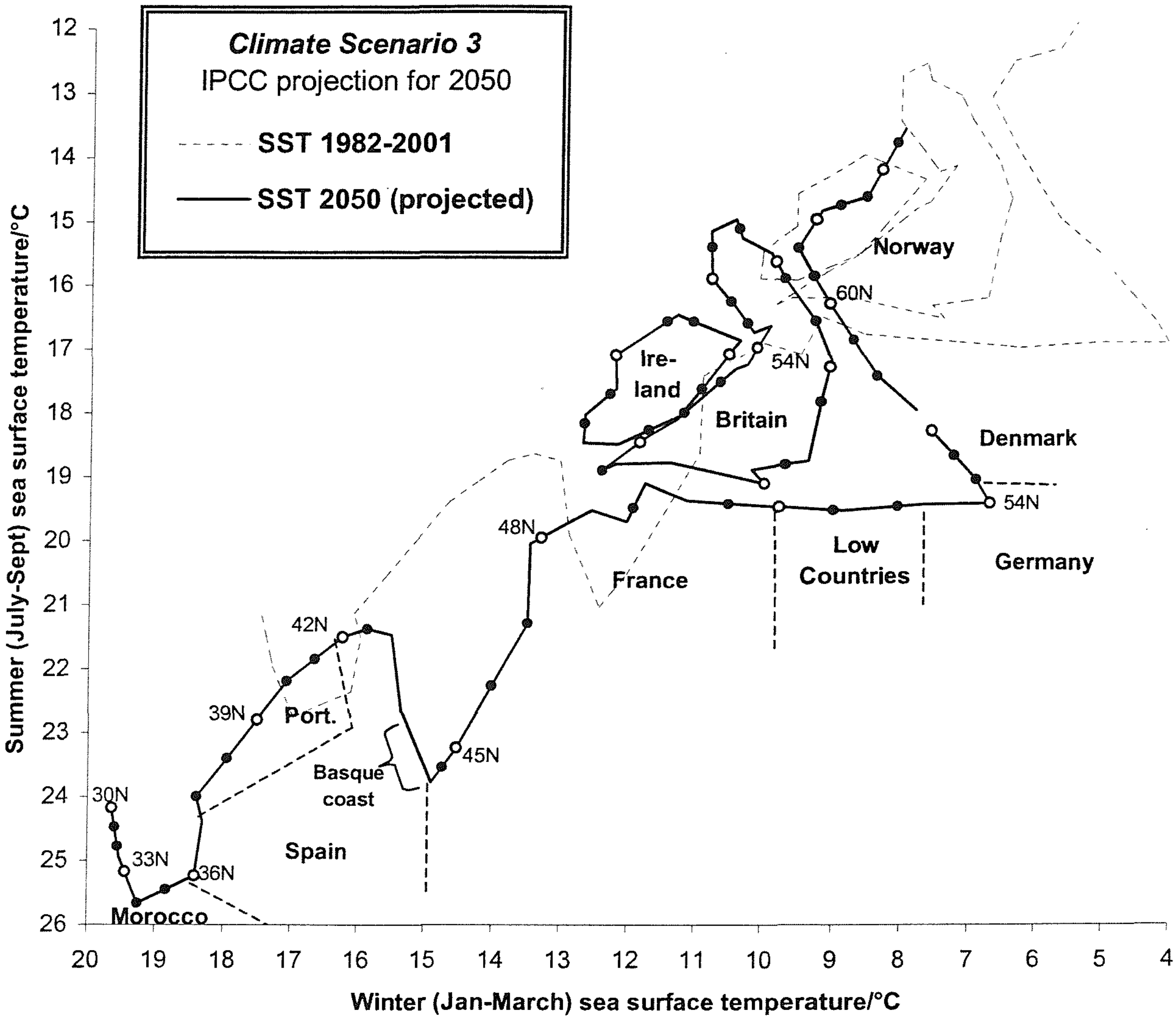


Figure 6.6. Projected summer (July–September) sea surface temperatures on the y-axis against winter (January–March) sea surface temperatures on the x-axis, for the northeast Atlantic coast between 30°N and 66°N, under a climate scenario for 2050 based on scenario models A2 and B2 of the Intergovernmental Panel on Climate Change (Houghton *et al.*, 2001). Under this scenario warming is dependent on latitude: at 30°N, winter temperature rises by 2.2°C and summer T by 3.0°C, while at 70°N, winter T rises by 3.0°C and summer T by 2.2°C, all based on averages for 1982–2001 (dashed curve). Projections for intermediate latitudes are based on interpolation between these extremes. Note inverted axes. Closed circles represent 1-degree intervals of latitude and open circles 3-degree intervals. Based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003).

Table 6.2. Summary of projected changes in sea temperatures by 2025 and 2050 for selected European coastal localities. **Locality** gives the name of the locality in question. **1981-2001** gives the average winter and summer sea surface temperatures for 1982–2001 at that locality. The other three columns give the projected winter and summer SSTs at that locality under the three climate scenarios described in §6.2.2, together with the names of the localities, if any, whose 1982–2001 winter and summer SSTs best approximate to the projected values. For example, under the 2050 IPCC climate scenario, the climate of Bergen is projected to resemble the present-day climate of south Devon, and the climate of Lands End to resemble the present-day climate of northern Galicia. * Projected climate not closely approximated by present-day climate at any European locality. These localities (in the Bay of Biscay, eastern English Channel and southern North Sea) have a winter-summer temperature range of 8°C or more, compared with about 5–7°C at most coastal locations in western Europe. + Cabo Fisterra in Galicia, Spain is not to be confused with Finisterre in Brittany, France.

	Mean sea surface temperatures (winter, summer)			
Locality	**1981–2001**	***2025 (IPCC)***	***2025 (Trends)***	***2050 (IPCC)***
Bergen	6.2, 13.9	7.6, 15.1 (N Wales)	7.6, 16.0 (Essex)	9.1, 16.3 (S Devon)
Orkney	7.7, 12.5	9.0, 13.7 (Donegal)	7.9, 13.2 (Skye)	10.4, 15.0 (SW Ireland)
Donegal	8.6, 14.0	9.9, 15.2 (Galway)	9.4, 15.3 (Galway)	11.3, 16.5 (Finisterre+)
Anglesey	7.8, 14.8	9.1, 16.0 (Devon)	9.9, 17.0 (Cherbourg)	10.4, 17.4 (Finisterre+)
Lands End	9.8, 16.3	11.1, 17.6 (Finisterre+)	11.3, 17.4 (Finisterre+)	12.4, 18.9 (N Galicia)
SW Jutland	4.0, 16.9	5.3, 18.1 (Netherlands)	5.8, 19.8 *	6.7, 19.4 *
Calais	7.2, 16.9	8.4, 18.1 *	9.9, 19.6 (Nantes)	9.8, 19.5 (Bordeaux)
Brest	10.7, 17.3	12.0, 18.6 (mid-Biscay)	12.3, 18.0 (mid-Biscay)	13.3, 20.0 (Santander)
Basque coast	12.4, 21.0	13.6, 22.4 *	13.7, 21.3 *	14.9, 23.8 *
Cabo Fisterra+	13.4, 18.6	14.6, 20.0 (C Portugal)	14.5, 19.8 (C Portugal)	15.9, 21.4 (Faro)
Lisboa	15.1, 20.0	16.2, 21.4 (SW Portugal)	16.1, 20.7 (SW Portugal)	17.5, 22.8 (Rabat)

6.3. Results

6.3.1. Expansion of warm-water species

6.3.1.1. Patella rustica

The limpet *Patella rustica* (Figures 6.7 and 6.13) is a high-shore species preferring exposed locations. It appears now to be absent from the north-west Iberian Peninsula between central Portugal, about 39.5°N (Santos, 2000), and northern Galicia (pers. obs., see Chapter 3). During the mid-20th century it was present, albeit uncommon, throughout this area (Fischer-Piette and Gaillard, 1959). It is evidently limited by low summer temperatures (estimated minimum of 18.75°C) and may have been affected by the increasing trend in upwelling during the 20th century. As a high-shore species *P. rustica* is likely to be particularly affected by the environment during emersion, including factors such as air temperature and cloud cover.

Its northern limit is on the French Basque coast (Fischer-Piette and Gaillard, 1959). Its expansion northwards here could be limited either by lack of suitable habitat along the predominantly sandy southwest coast of France, or by low winter temperatures, but not by summer temperatures, which are higher here than in Galicia. Its minimum winter temperature requirement is therefore unknown, but no greater than 12.5°C.

By 2025 *P. rustica* is expected to expand to the entire northwest Iberian Peninsula, but this expansion may be limited by local summer climatic conditions dependent on upwelling intensity, if the rising trend in upwelling observed during the 20th century continues (Bakun, 1990; see Chapter 2.)

By 2025 it will also be theoretically able to live in western France north of the Gironde, and in Brittany by 2050 (possibly further north depending on its winter temperature limit). Its northward expansion will therefore depend mainly on whether it is able to disperse as far as the Gironde, overcoming the lack of rocky shore habitat in the intervening area.

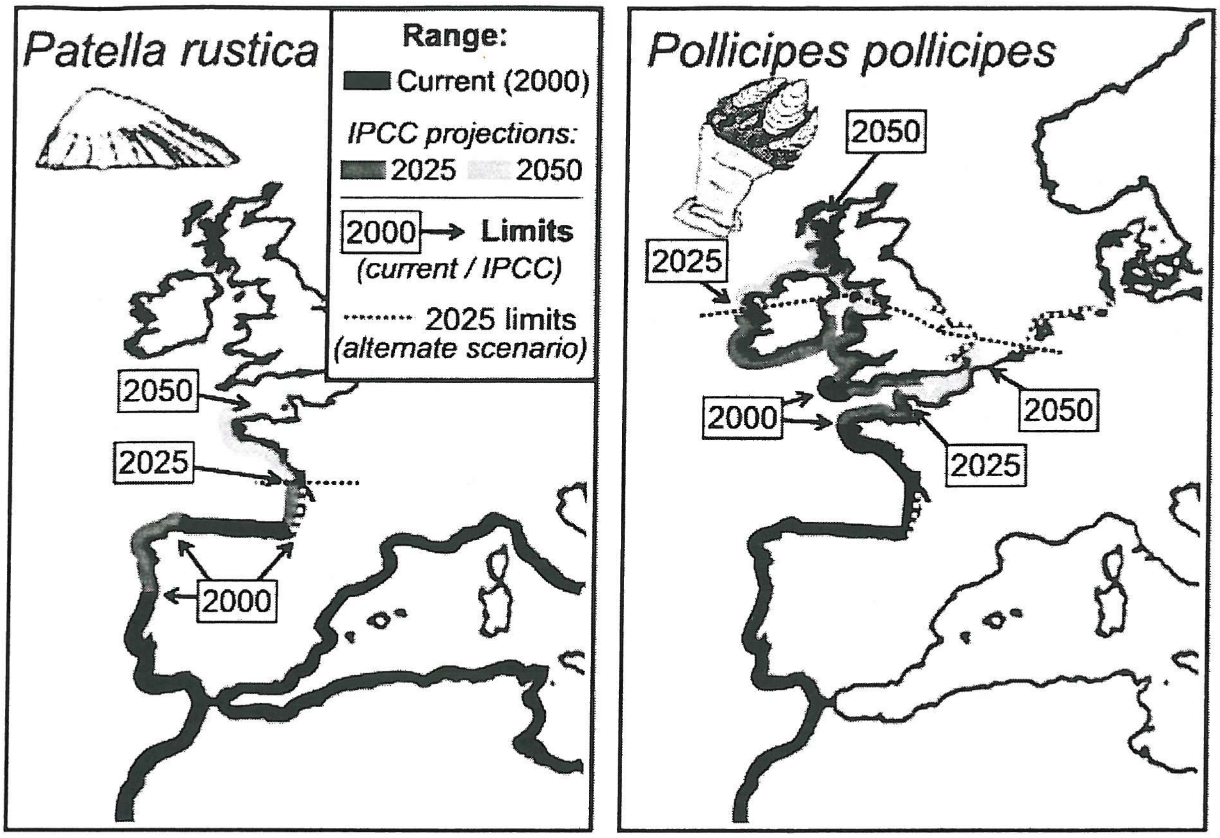


Figure 6.7. Current distribution (2000) and projected expansion (by 2025 and 2050) of two species of warm-temperate rocky shore invertebrates, the limpet *Patella rustica* (left) and the stalked barnacle *Pollicipes pollicipes,* in the northeast Atlantic, based on the three climate scenarios described in §6.2.2. Dotted coastline indicates areas with very little rocky shore habitat. Dotted lines indicate limits in 2025 under an alternative scenario based on projected trends for 1982–2001 (see §6.2.2). Illustrations adapted from (Southward *et al.*, 1995). For sources, see Table 6.1.

6.3.1.2. Pollicipes pollicipes

The stalked barnacle *Pollicipes pollicipes* (Figures 6.7 and 6.14) is found on very exposed shores from west Africa as far north as northwest Brittany and very occasionally Cornwall (Fischer-Piette, 1936; Crisp and Fischer-Piette, 1959; Barnes, 1996; Cruz and Hawkins, 1998; Cruz and Araujo, 1999). It breeds in late spring and summer throughout its European range: in Portugal (Cruz and Hawkins, 1998; Cruz and Araujo, 1999), Spain (Molares, *et al.*, 1994) and northwest France (Cruz and Hawkins, 1998). Summer temperature is therefore probably a key factor limiting its northward expansion. Its eastward expansion along the English Channel may be limited by winter temperatures. As a species that favours exposed habitat, its most likely route of expansion will be to southwest Wales and then southern Ireland. Its theoretical limits are projected to be in Galway and north Wales by 2025, and west Scotland by 2050. Its expansion up the English Channel and in the Irish Sea north of St David's head in Wales is likely to be limited by lack of suitable wave-exposed habitat, not temperature.

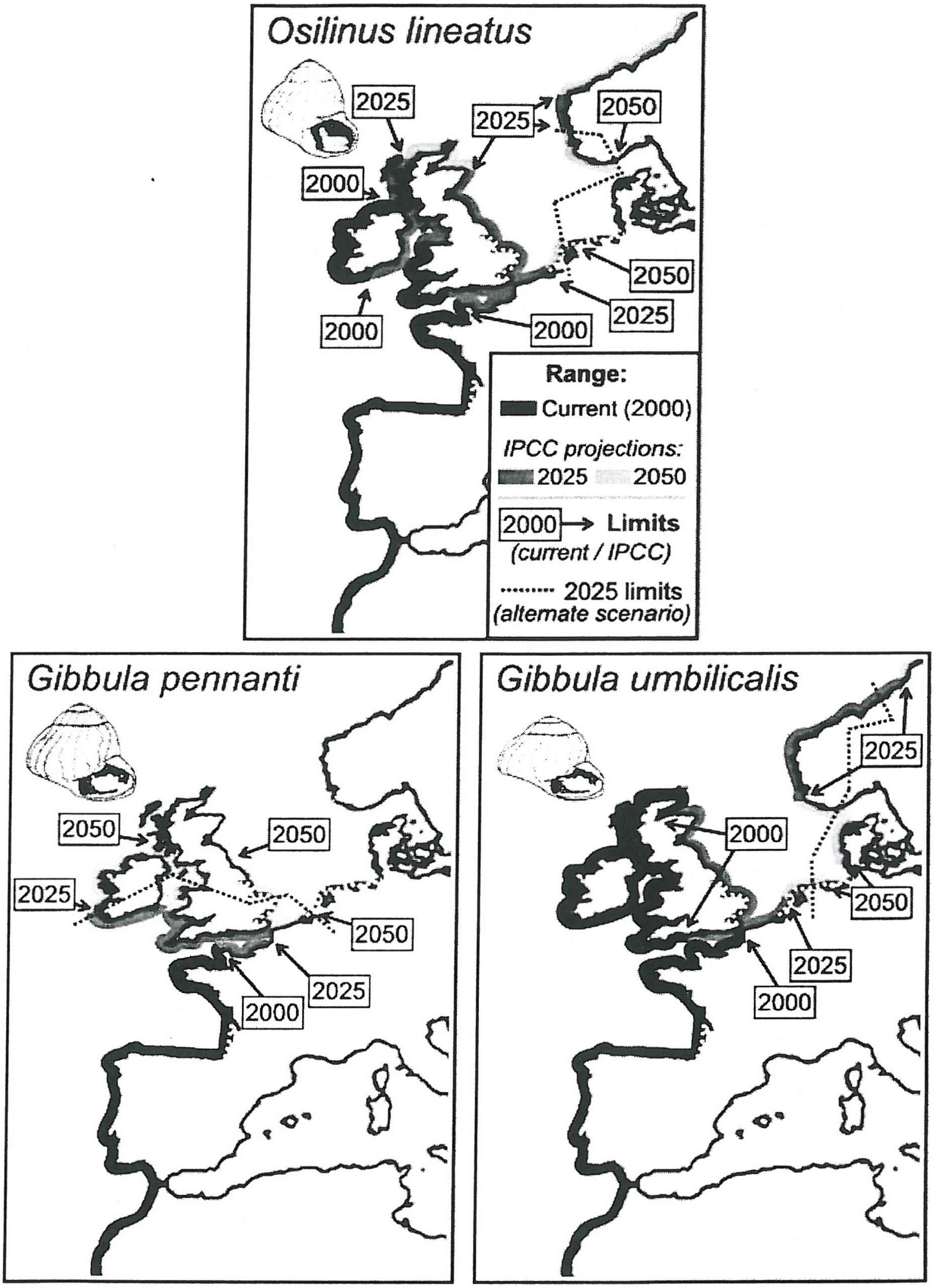


Figure 6.8. Current distribution (2000) and projected expansion (by 2025 and 2050) of three species of warm-temperate trochids: *Osilinus lineatus* (top), *Gibbula pennanti* (bottom left) and *Gibbula umbilicalis* (bottom right) in the northeast Atlantic, based on the three climate scenarios described in §6.2.2. Dotted coastline indicates areas with very little rocky shore habitat. Dotted lines indicate limits in 2025 under an alternative scenario based on projected trends for 1982–2001 (see §6.2.2). Illustrations adapted from (Southward *et al.*, 1995). For sources, see Table 6.1.

6.3.1.3. *Gibbula pennanti, Gibbula umbilicalis* and *Osilinus lineatus*

The trochid snails *Osilinus lineatus* (formerly known as *Monodonta lineata*) (Figures 6.8 and 6.15), *Gibbula pennanti* (Figures 6.8 and 6.16) and *Gibbula umbilicalis* (Figures 6.8 and 6.17) are ecologically similar species with different temperature tolerances. There has been little work on *G. pennanti* but its biology is similar to that of *G. umbilicalis* (Fischer-Piette and Gaillard, 1956). *G. pennanti* has not, however, crossed the English Channel from the Channel Islands and France to Britain. Studies on the reproduction of both *Gibbula umbilicalis* and *Osilinus lineatus* indicate that their northward expansion in the British Isles is limited by low summer temperatures leading to reproductive failure (Garwood and Kendall, 1985; Kendall, 1987; Kendall and Lewis, 1987; Kendall *et al.*, 1987).The location of the limit of *G. umbilicalis* in the extreme northeast of Scotland suggests, however, that this species is also limited by winter temperatures, perhaps affecting survival of juveniles. This would explain why it has not, at least until very recently (Miezskowska and Kendall, pers. comm.) extended its range down the east coast of Scotland and northern England, where summer temperatures are warmer, but winter temperatures colder, than they are in northeast Scotland.

All three species are likely to expand eastward along the English Channel and southern North Sea although their progress will probably be slowed by the lack of suitable habitat. *G. pennanti* may spread to southwest Britain and Ireland from its present northern limit in Normandy; if so it could theoretically reach the whole of Ireland, Wales and western England by 2050. *O. lineatus* could reach northwest Scotland by 2025 and the whole of the British Isles by 2050. *G. umbilicalis* has recently extended its range in the English Channel (Frost, Moschella and Hawkins, pers. comm.). Where suitable habitat exists, it could in theory spread to the whole of the British Isles, including Orkney and possibly Shetland, by 2025. All three species will also become theoretically able to live in western Norway by 2050, but the barrier of the North Sea makes it unlikely that they will reach there.

6.3.1.4. *Balanus perforatus, Chthamalus montagui* and *C. stellatus*

The barnacles *Balanus perforatus* (Figures 6.9 and 6.18), *Chthamalus montagui* (Figures 6.9 and 6.19) and *Chthamalus stellatus* (not shown, but similar distribution to *C. montagui*) (Southward, 1976) are warm-water species whose northern limits in the British Isles are thought to be set by low summer temperatures causing reproductive failure (Crisp *et al.*, 1981; Lewis 1986; Burrows *et al.*, 1992; Herbert *et al.*, 2003). Their eastern limits in the English Channel and northern Scotland (*Chthamalus*: see remarks on *G. umbilicalis*, above), however, are more plausibly related to winter temperature. *B. perforatus* has extended its range some 150km eastward along both sides of the English Channel since the 1960s (Herbert *et al.*, 2003) when all three species suffered severe cold-related mortality (Crisp, 1964).

Both species of *Chthamalus* could in theory expand to the whole coast of Britain and also western Norway by 2025; *B. perforatus* could reach northern Scotland by 2025 and all of Britain and western Norway by 2050. Speed of dispersal may limit their expansion. Limits to dispersal may have prevented *B. perforatus* from reaching Ireland (Crisp and Southward, 1953). Its absence there could also be due to low summer temperatures and thus low reproductive output near its limit.

Rapid dispersal has been seen in another intertidal barnacle, the invasive species *Elminius modestus* (Crisp 1958; Fischer-Piette and Forest, 1961; Barnes and Barnes, 1965). *E. modestus* arrived in Britain at Southampton in the early 20th century and subsequently dispersed both along the coast at a rate of about 20–30 km per year (Crisp 1958), and to remote locations via ships. However, *Chthamalus stellatus, C. montagui* and *Balanus perforatus* do not grow well on ships. *B. perforatus* seems to be able to extend its range during periods of favourable climate when "stepping stones" of artificial habitat are available, as it has done in recent years in the English Channel (Herbert *et al.*, 2003). *C. stellatus* probably has greater powers of dispersal than *C. montagui,* with a longer larval life (Burrows, 1988; Burrows *et al.*, 1999), explaining the presence of *C. stellatus* on isolated islands in the northeast Atlantic, including Shetland (Crisp and Southward, 1981).

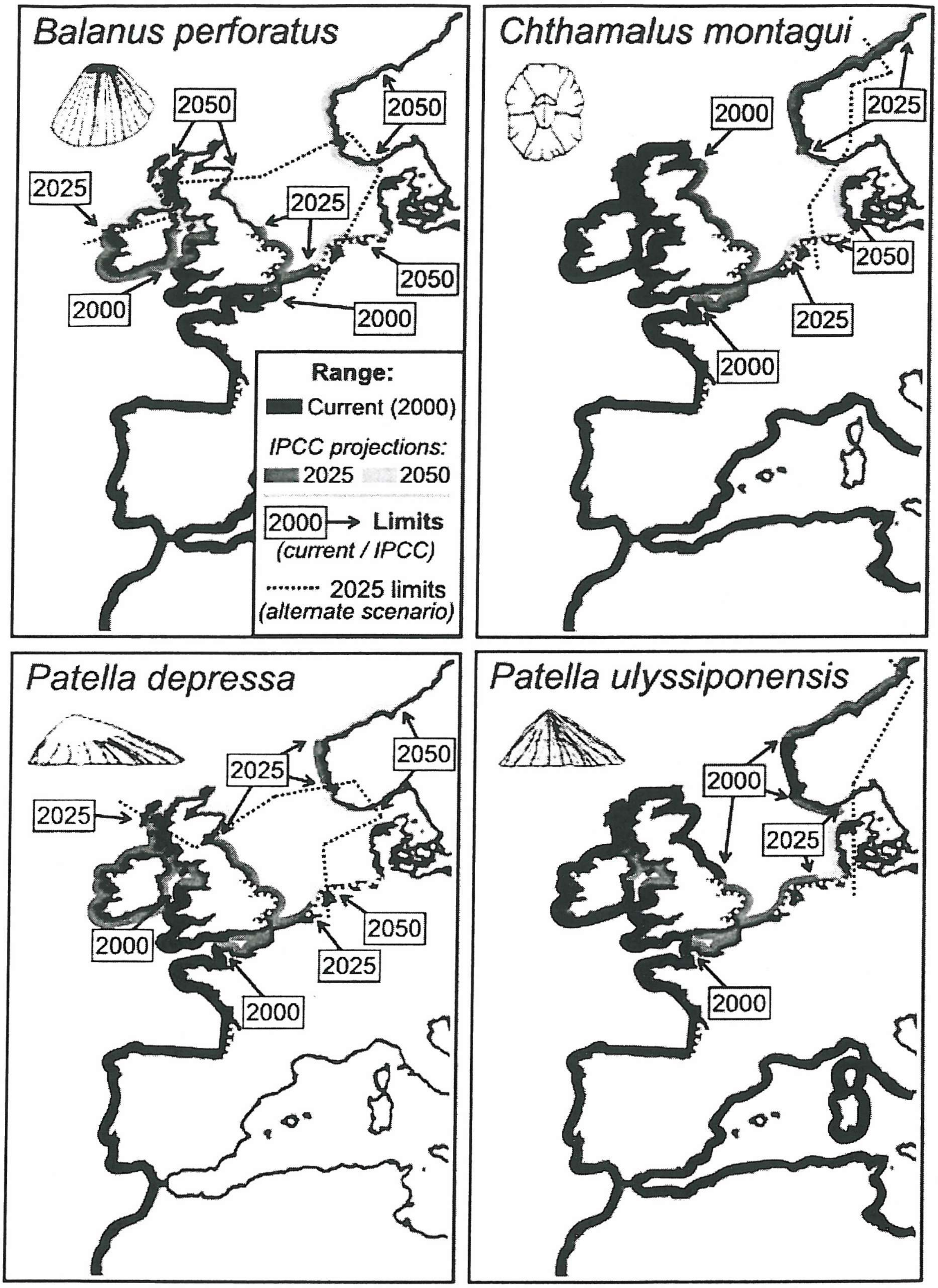


Figure 6.9. Current distribution (2000) and projected expansion (by 2025 and 2050) of four warm-temperate invertebrate species: the barnacles *Balanus perforatus* (top left) and *Chthamalus montagui* (top right), and the limpets *Patella depressa* (bottom left) and *Patella ulyssiponensis* (bottom right), in the northeast Atlantic, based on the three climate scenarios described in §6.2.2. Dotted coastline indicates areas with very little rocky shore habitat. Dotted lines indicate limits in 2025 under an alternative scenario based on projected trends for 1982–2001 (see §6.2.2). Illustrations adapted from (Southward *et al.*, 1995). For sources, see Table 6.1.

6.3.1.5. *Patella depressa* and *Patella ulyssiponensis*

The limpets *P. depressa* (Figures 6.9 and 6.20) and *P. ulyssiponensis* (Figures 6.9 and 6.21) are mainly warm-temperate species that have northern and eastern limits in the British Isles. *P. ulyssiponensis* also lives in south-western Norway (Lewis, 1964); *P. depressa* is absent from Ireland (Crisp and Southward, 1953). Studies of the reproduction of *P. ulyssiponensis* suggest that it is limited in northeast England by frequent reproductive failure due to low summer temperatures (Bowman and Lewis, 1986). The same may well be true of *P. depressa,* which also breeds mainly in summer in Britain. Also, the abundance of *P. depressa* compared with that of its competitor *P. vulgata* shows a positive correlation with summer temperatures in both northern Spain and the English Channel (see Chapter 4). Both *P. depressa* and *P. ulyssiponensis* are therefore likely to have northern limits set by low summer temperatures.

There is little evidence, on the other hand, that low winter temperatures play a role in setting the limits of these species. The abundance of *P. depressa* compared to *P. vulgata* in the English Channel shows no clear relationship with winter temperatures (Crisp and Southward, 1958; see also Chapter 4). *P. ulyssiponensis* is able to live in southwest Norway and *P. depressa* in north Wales, where winter temperatures are, respectively, 3°C (SW Norway) and 1.5°C (N Wales) lower than on the Isle of Wight, the eastern limit for both species in the Channel (Herbert, 2001).

It is clear that non-climatic factors such as dispersal and lack of habitat play a major role in setting the distribution of these species. The absence of *P. depressa* from Ireland, despite favourable climatic conditions, is further evidence of this. Despite being present in southwest Wales, it has never managed to cross the 80km-wide St George's Channel between Wales and Ireland (Crisp and Southward, 1953). Reasons for this might include the prevailing direction of currents (alongshore rather than offshore), or low reproductive output at its range limit (Crisp and Southward, 1953) as well as more limited dispersal than other limpet species (Hawkins, pers. comm.)

P. ulyssiponensis is projected to expand to the whole Atlantic coast of northwest Europe by 2025, apart from the southeast North Sea where it may be temporarily limited by winter temperatures. Its limits will be set mainly by dispersal or lack of habitat (wave-exposed shores) rather than by climate. *P. depressa* is likely to expand up the west coast of Britain and could potentially reach western Scotland by 2025, and the whole of Britain by 2050. Its actual rate of expansion is again likely to be limited by dispersal and habitat. It is unlikely to reach Norway, even though climatic projections indicate that it will be able to live there by 2025, and its expansion from Wales to Ireland and also the Isle of Man and Scotland is likely to be delayed by physical barriers.

6.3.2. Retreat of cold-water species

6.3.2.1. Patella vulgata

In the limpet *Patella vulgata* (Figures 6.10 and 6.22) the timing of reproduction shows clear latitudinal trends (Bowman and Lewis, 1986; Lewis, 1986), and it has been suggested that spawning in this species is triggered by sea water temperatures falling below 12°C (Bowman and Lewis, 1986), which may lead to reproductive failure towards the southern end of its range in southern Portugal (Guerra and Gaudencio, 1986). On the north coast of Spain there is a significant inverse relationship between the abundance of *P. vulgata* and summer temperature (see Chapter 4), possibly due to competition for food resources between *P. vulgata* and *P. depressa*, which is greatest in summer (Thompson *et al.* 2000; Jenkins *et al.*, 2001; Boaventura *et al.*, 2002b). The southern limit of *P. vulgata* is thus probably set by both winter and summer temperatures.

By 2025, *P. vulgata* is projected to disappear from southern Portugal and the inner Bay of Biscay, areas where it is now fairly rare (Guerra and Gaudencio, 1986; Santos, 2000; Boaventura *et al.*, 2002b; see also Chapter 4). It may continue to persist in estuarine refuges (Fischer-Piette, 1955a, 1958; Fischer-Piette and Gaillard, 1959; see Chapter 5). In western France its limit will retreat northwards, probably as far as southern Brittany by 2050. By 2050 it will probably also be restricted to a relatively small area of northwest Spain and perhaps northern Portugal. Its long-term prospects in this area will be largely dependent on whether the increasing trend in upwelling intensity during the 20th century continues (Bakun, 1990; see also Chapter 2). Even in a scenario of increased upwelling, however, rises in winter temperature could eventually eliminate *P. vulgata* from the Iberian Peninsula entirely, although this is unlikely to happen before 2050.

6.3.2.2. *Nucella lapillus*

The southward extension of the dog whelk *Nucella lapillus* (Figures 6.10 and 6.23) is apparently limited by summer temperature, as it is absent from the inner Bay of Biscay but comparatively common in northwest Spain (Fischer-Piette, 1953, 1955a). This species declined markedly throughout Europe in the 1980s due to tributyltin (TBT) pollution (Gibbs *et al.*, 1987; Oehlmann *et al.*, 1998; Spence *et al.*, 1990; Douglas *et al.*, 1993), although subsequent recovery has occurred (Birchenough *et al.*, 2002; Santos *et al.*, 2002; Hawkins *et al.*, 2002). It appears to have become rare on the west coast of France since 1955 (see Chapter 3), possibly for this reason. Climate change is likely to reduce its range further in France and may eliminate it from the northwest Iberian Peninsula entirely by 2050, although as with *Patella vulgata* this is likely to depend on the intensity of upwelling.

6.3.2.3. *Semibalanus balanoides*

The southern limits of the cold-water barnacle *Semibalanus balanoides* (Figures 6.10 and 6.24) in north America are thought to be set by high winter temperatures (Hutchins, 1947; Barnes, 1953, 1961; Barnes and Powell, 1966), and the onset of reproduction appears to be triggered by low temperatures (Crisp and Lewis, 1984). It is therefore likely that winter temperatures also play a role in setting its southern limits in Europe. This species is absent from the inner Bay of Biscay, probably due to high summer temperatures.

As with *Nucella lapillus,* the southern limit of *S. balanoides* in France is likely to retreat to southern Brittany, and it is likely to disappear from the Iberian Peninsula by 2050. Increased local upwelling, particularly in estuaries (Nogueira *et al.*, 1997) which are the preferred habitat of this species (Barnes *et al.*, 1972) could, however, delay its disappearance.

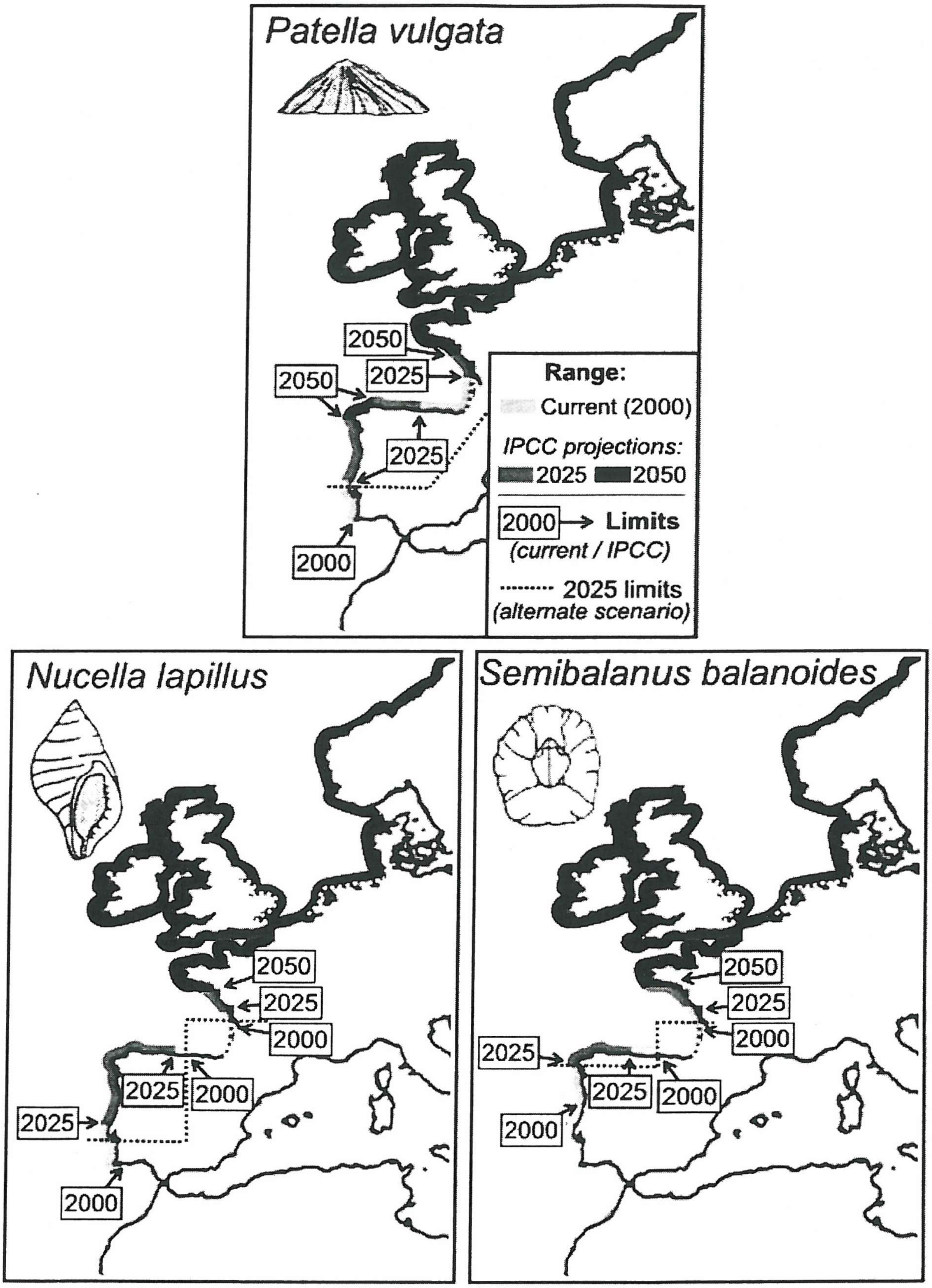


Figure 6.10. Current distribution (2000) and projected retreat (by 2025 and 2050) of three species of cold-temperate rocky shore invertebrates, *Patella vulgata* (top), *Nucella lapillus* (bottom left) and *Semibalanus balanoides* (bottom right), in the northeast Atlantic, based on the three climate scenarios described in §6.2.2. Dotted coastline indicates areas with very little rocky shore habitat. Dotted lines indicate limits in 2025 under an alternative scenario based on projected trends for 1982–2001 (see §6.2.2). Illustrations adapted from (Southward *et al.*, 1995). For sources, see Table 6.1.

6.3.2.4. ***Pelvetia canaliculata*** **and** ***Fucus vesiculosus***

In the inner Bay of Biscay, the upper-shore fucoid *Pelvetia canaliculata* (Figures 6.11 and 6.25) has persisted throughout the twentieth century in isolated patches in favourable habitats (Fischer-Piette, 1957). Its abundance has, however, fluctuated considerably with variations in climate (see Chapter 3). Projected rises in summer temperature are likely to reduce its abundance still further and it is likely to disappear as a major component of Iberian rocky shore communities by 2050. Nonetheless its high resistance to desiccation stress (Dring and Brown, 1982; Pfetzing *et al.*, 2000) means that the species is likely to persist in isolated patches. As an upper shore species that is probably limited mainly by air temperatures (Schonbeck and Norton, 1978) it is unlikely to benefit much from any increase in the intensity of upwelling.

The mid-shore fucoid *Fucus vesiculosus* (Figures 6.11 and 6.26) has a similar distribution to *P. canaliculata* but it is slightly less tolerant of high temperatures, and considerably less resistant to desiccation stress (Dring and Brown, 1982; Pfetzing *et al.*, 2000). It is likely to disappear from the Iberian Peninsula by 2050, although increased upwelling could allow it to persist on the open coast. It could also persist in estuarine refuges as it does today in southern Portugal (Santos, 2000; Ladah, 2003). In France both species are likely to retreat as far as S Brittany.

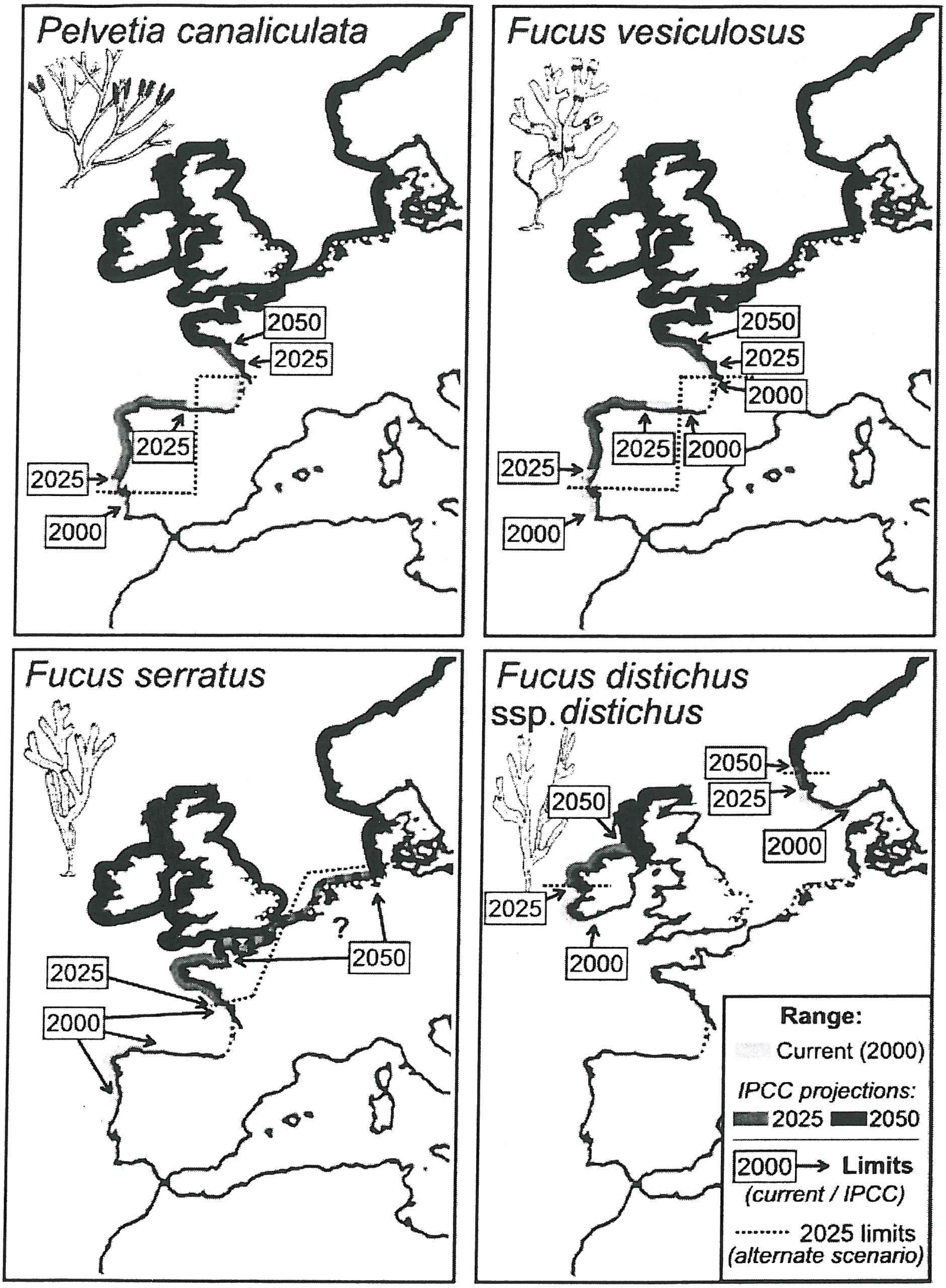


Figure 6.11. Current distribution (2000) and projected retreat (by 2025 and 2050) of four species of cold temperate-boreal fucoid algae: *Pelvetia canaliculata* (top left), *Fucus vesiculosus* (top right), *Fucus serratus* (bottom left) and *Fucus distichus* ssp. *distichus* (bottom right), in the northeast Atlantic, based on the three climate scenarios described in §6.2.2. Dotted coastline indicates areas with very little rocky shore habitat. Dotted lines indicate limits in 2025 under an alternative scenario based on projected trends for 1982–2001 (see §6.2.2). **?** indicates that projected temperature is marginal for *F. serratus* over an extended area of coast. Illustrations adapted from (Southward *et al.*, 1995). For sources, see Table 6.1.

6.3.2.5. *Fucus serratus*

The lower-shore fucoid *Fucus serratus* (Figures 6.11 and 6.27) is more sensitive to high summer temperatures than the other species of fucoid algae found on the Iberian Peninsula. As a lower-shore species, however, it is likely to benefit most from any increase in the intensity of upwelling. Its range has actually increased on the north coast of Spain since 1980 (Arrontes, 1993, 2002) despite increasing summer temperatures (see Chapter 2). It is not clear whether this is due to increased upwelling; the only upwelling indices that have been calculated for the region in question (near Cabo Peñas in Asturias) do not show a rising trend during the last 20 years (see Chapter 2).

The continued persistence of *F. serratus* in Spain is likely to be dependent on increased upwelling leading to local cooling in summer. Otherwise it is projected to disappear from the Iberian Peninsula by 2025. In France and the Low Countries summer temperatures are likely to become marginal for *F. serratus* by 2050 and it is likely to be restricted to particularly favourable habitats across a 1500km section of coast stretching from western Brittany to Denmark.

6.3.2.6. *Fucus distichus* ssp. *distichus*

The boreal fucoid alga *Fucus distichus* ssp. *distichus* (Figures 6.11 and 6.28) is found on the exposed western coasts of Ireland, Scotland and Norway. Its southern limits may be set either by high summer temperatures (Bird & McLachlan, 1976) or by the interaction of temperature with day length, as observed in other boreal algae (Breeman, 1988). It is projected to retreat northwards and by 2050 its range is likely to be restricted to Scotland and, in Norway, to the area north of Bergen.

6.3.2.7. *Laminaria hyperborea* and *Alaria esculenta*

The kelps *Laminaria hyperborea* (Figures 6.12 and 6.29) and *Alaria esculenta* (Figures 6.12 and 6.30) are boreal species whose southern limits have been recorded in northern Portugal (*L. hyperborea:* Santos, 2000) and the extreme west of Brittany (*A. esculenta:* Fischer-Piette, 1949). *Laminaria hyperborea* appears to be limited in the northwest Iberian Peninsula both by high winter temperatures – it requires temperatures under 15°C to initiate blade growth (Bolton and Lüning, 1982) – and by lethal summer temperatures of 20–21°C (Lüning, 1984). Thus it is likely to disappear from the Iberian Peninsula by 2025, even in a scenario of increased upwelling. By 2050, as with *Fucus serratus,* it is likely to disappear from the 1500km section of coast of from Brittany to Denmark, due to summer warming.

Alaria esculenta disappeared from much of the western English Channel coast of Britain in the 1950s and has not reappeared since then except in isolated patches such as in the subtidal on the Eddystone rock (Hawkins, pers. comm.). This species is projected to retreat in Ireland, Britain and Norway. By 2050 it is likely to be restricted to northern Ireland, Scotland, northeast England, and Norway north of Stavanger.

Both species are likely to be progressively replaced by the more southern kelp *Laminaria ochroleuca* over parts of their present range.

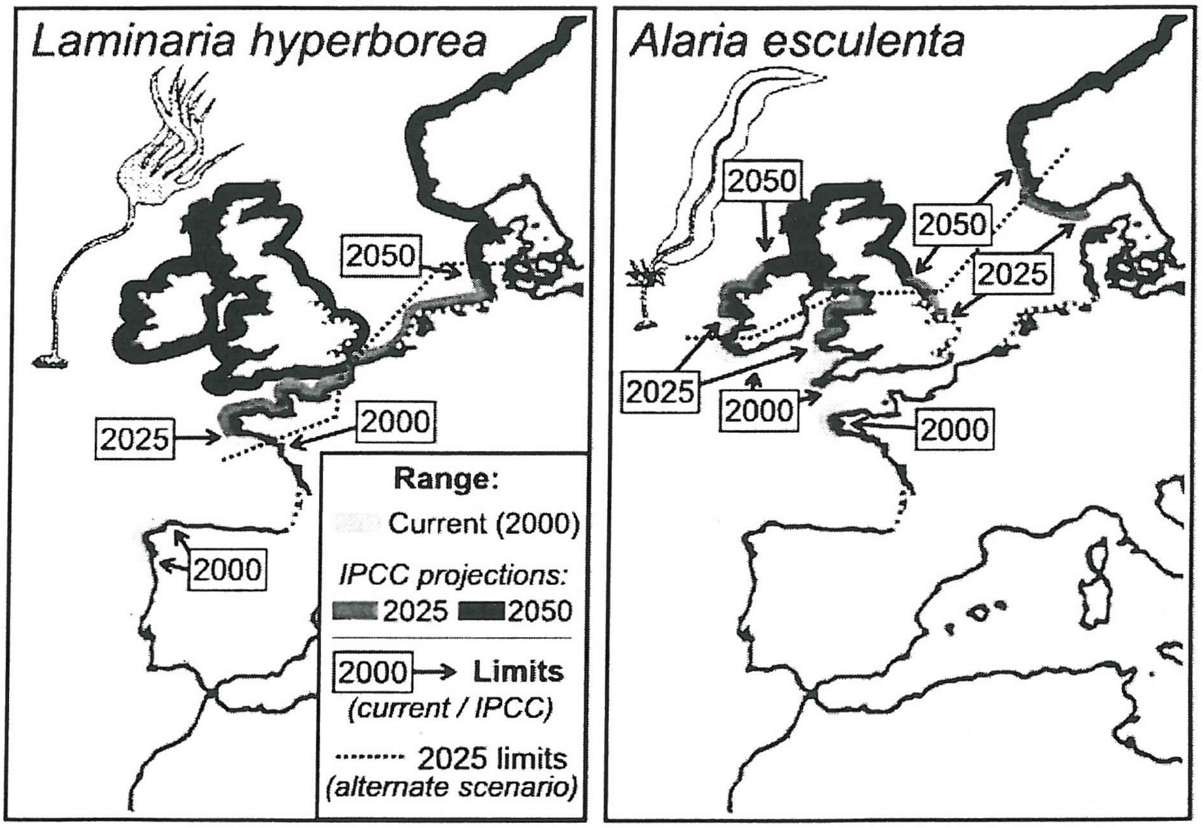


Figure 6.12. Current distribution (2000) and projected retreat (by 2025 and 2050) of two species of boreal kelp, *Laminaria hyperborea* (left) and *Alaria esculenta* (right), in the northeast Atlantic, based on the three climate scenarios described in §6.2.2. Dotted coastline indicates areas with very little rocky shore habitat. Dotted lines indicate limits in 2025 under an alternative scenario based on projected trends for 1982–2001 (see §6.2.2). Illustrations adapted from (Southward *et al.*, 1995). For sources, see Table 6.1.

6.4. Discussion

6.4.1. Spatial variation in sea temperature in the NE Atlantic

During the 20th century, poleward range shifts have been observed in many species, at an average rate of 6.1 km per decade (review by Parmesan and Yohe, 2003). The assumption behind this average seems to be that shifts in species distribution will take place at a speed primarily determined by the rate of global warming. However, the large-scale variations in spatial patterns of temperature highlighted in this chapter mean that poleward shifts in species distribution (Parmesan and Yohe, 2003) are by no means a universal response to warming.

Breeman (1990) discusses how rates of change of temperature with latitude on the Atlantic coasts of North America and Europe will affect the response of marine algae to climate change in these areas. The rate of change of temperature with distance is an important indicator of how rapidly species are likely to expand or retreat. Perhaps counter-intuitively, areas where temperature changes very rapidly with distance will see the least dramatic shifts in species range due to warming over time. Breeman (1990) points out that this means that ranges of marine organisms in the eastern Atlantic will, in general, move further in response to climate change than those in the western Atlantic.

On the Pacific coast of North America, in contrast, the temperatures experienced by rocky shore organisms do not vary in a predictable way with latitude (Denny and Paine, 1998; Helmuth *et al.*, 2002). Instead, tidal, seasonal and diurnal cycles interact to create “hot spots” where organisms are likely to suffer extreme high temperatures much more frequently than elsewhere (Helmuth *et al.*, 2002).

Apart from these studies there has been little consideration of how spatial variations in climate will mediate the effects of climate change on rocky shore communities. However, spatial variations in sea surface temperatures along the coastline of the northeast Atlantic (Figure 6.2) show several notable features with respect to the biogeography of rocky shores and the likely effects of climate change upon them.

The general trend of both summer and winter sea surface temperatures in the region is, of course, to decrease from south to north. However, these trends are by no means uniform. Many areas do indeed show a steady decrease in both winter and summer temperatures with increasing latitude. These include the west coast of Portugal and Spain (a decrease of about 2.5°C in both summer and winter temperatures from Cabo de San Vicente, 37°N, to Cabo Fisterra, 43°N); the west coast of France (a decrease of 3°C in summer and 1.75°C in winter from the Gironde, 45.5°N, to Cherbourg, 49.5°N); and the west coast of England and Wales (a decrease of 2.2°C in summer and 2.6°C in winter from Land's End, 50°N, to the Solway Firth, 55°N). In these areas, warming is indeed likely to lead to a steady, northward shift of species range as both winter and summer limits move northwards. This pattern may, of course, be altered by factors that impede dispersal of rocky shore organisms, such as physical barriers, absence of suitable habitat, or adverse currents.

In other areas of the coast, there is a steep spatial gradient in temperature during one season but little or no change in the other. On the north coast of Spain, there is an increase of 2.5°C in summer temperatures over a distance of 500km from northern Galicia (8°W) to the French border (1.75°W), together with a much smaller decrease (about 0.6°C) in winter temperatures. Another such area is the English Channel and south coast of the North Sea, where winter temperatures decrease rapidly, by more than 5°C from Cherbourg, 49.5°N, to northwest Germany, 54°N, while summer temperatures remain almost unchanged.

In these areas, climate change could have dramatic, large-scale effects on certain species, as temperatures become marginal for their continued survival over large areas of coast simultaneously. This could lead, for example, to the disappearance of *Laminaria hyperborea* and *Fucus serratus* from the southern English Channel and North Sea (some 1500km of coastline) as a result of summer warming of about 1.5°C.

Other areas show an inverse trend in summer and winter temperatures. This is the case on the west coast of Germany, Denmark and Norway from 54°N to 62°N, and also in Scotland (east and west coasts) and northeast England. All these areas show a decrease in summer temperatures as usual, but an increase in winter temperatures, from south to north. Northwest Morocco is another area where there are inverse trends in temperature, but here summer temperatures decrease from north to south while winter temperatures do the opposite: these patterns may be related to upwelling.

In these areas, species with different temperature requirements can shift in opposite directions as a result of climate change. In theory, *Patella ulyssiponensis* could expand southwards along the southwest coast of Norway (due to winter warming, although its expansion may be limited by lower salinity in this region due to freshwater runoff) while *Alaria esculenta* retreats northwards along the same coast (due to summer warming). *Alaria* is also likely to retreat northwards in eastern England and Scotland, while species such as *Chthamalus montagui, Chthamalus stellatus* and *Gibbula umbilicalis* could expand southwards in the same area (range extensions in *Gibbula* and *C. stellatus* have already been observed: N. Miezskowska, pers. comm.)

In some areas variations in temperature and other conditions on local scales can outweigh large-scale variations. Coastal upwelling, in particular, is the result of the interaction between wind and coastal topography (Sverdrup, 1938), and thus varies on relatively small (hundred metre to kilometre) spatial scales (Molina, 1972; Prego and Varela, 1998; Alvarez-Salgado *et al*., 2000). This variation is likely to have a major influence on the response to climate change of rocky shore species in upwelling areas, especially low on the shore.

6.4.2. Climate change scenarios, limitations and uncertainties

The three climate change scenarios considered in this chapter are very simplified views of possible future changes in climate. In the first place, they only consider changes in temperature; climate change is likely to involve a whole rage of changes in other climatic variables as well. In particular, changes in wind speed and direction, and consequently wave action and the incidence of storms, are likely to have significant impacts on coastal ecosystems, including rocky shores. Many of the species studied in this chapter are limited in their range not only by temperature but also by their tolerance for particular conditions of wave exposure. IPCC models project increases in the incidence of storms in some regions (Houghton *et al.,* 2001) which would result in an increase in disturbance events on rocky shores (see §1.3). Data for the north coast of Spain for 1972–1994 (Puertos del Estado, 2003), however, indicate a decline in wave height during this period. In any case, wave action is a key climatic factor that should be incorporated in any future revision of this model. Other important factors that could be incorporated include cloud cover and extreme values of air temperature.

Also, climate models by their nature are subject to large uncertainties. IPCC projections of average global temperature rise over the period 1990–2050 vary by a factor of 3.25, from 0.8°C to 2.6°C (Houghton *et al.*, 2001). This range of uncertainty is based on unknowns in the response of the global climate system to anthropogenic changes under "business-as-usual" scenarios (Houghton *et al.*, 2001). Estimates by different researchers of the 90% confidence limits for IPCC climate scenarios have produced similar (or slightly smaller) ranges to those used by the IPCC, which do not have probabilities attached to them (Reilly *et al.*, 2001; Wigley and Raper, 2001).

These uncertainties are reflected in the rates of regional warming used in the IPCC-based scenarios for 2025 and 2050 considered in this chapter. Thus, if a threefold uncertainty factor is used, the amount of warming projected in the 2025 scenario could occur as early as 2010 or as late as 2050, while the 2050 scenario could occur as early as 2025 or as late as 2095. Thus the overall global rate of warming is one major uncertainty in projections of climate change and its effects on ecosystems.

The second climate scenario for 2025 used in this chapter (Scenario 2), based on observed trends in summer and winter temperatures for 1982–2001 at 62 points on the northeast Atlantic coast, demonstrates the extent to which local trends can deviate from regional averages. Scenario 2 predicts a similar overall rate of warming to that in the IPCC scenario for 2025 (Scenario 1), but considerably greater warming in certain areas, notably the southern North Sea, English Channel and Irish Sea, and less in others, particularly the Bay of Biscay. Thus local variations in warming are another important source of uncertainty in climate change scenarios.

The IPCC scenarios do not take into account certain large, non-linear feedbacks that are difficult to assign probabilities. One example is a shift in the thermohaline circulation system (Broecker, 1997; Allen *et al.*, 2001; Clark *et al.*, 2002) which could alter the course of the Gulf Stream and lead to very rapid cooling in northern Europe. In this case the spatial patterns of climate in Europe would come to resemble those of eastern North America, with very sharp latitudinal gradients in temperature. It has been suggested that a shift in the thermohaline system could occur by 2100 if current rates of anthropogenic greenhouse gas emissions continue (Broecker, 1997).

6.4.3. Projected changes in distribution of rocky shore species

The projections made in this chapter of changes in the distribution of rocky shore species as a result of climate scenarios are themselves subject to uncertainties. They are based on the "climate envelope" approach, which relies on several assumptions. It assumes that the temperature requirements of each species are known, whereas in fact this is true for very few species. Although many studies have been made of the temperature tolerance of different stages of the life cycles of rocky shore organisms (e.g. Evans, 1948; Southward, 1958, 1964; Sandison, 1967; Foster, 1969; Newell *et al.*, 1971; Moss and Sheader, 1975; Lüning, 1984; Crisp and Lewis, 1984; Hoek, 1982; Hoek *et al.*, 1990; Wiencke *et al.*, 1994), the body temperatures experienced by organisms on the rocky shore may bear little relation to the temperatures recorded by meteorological stations (Southward, 1958; Helmuth, 1999). In most cases, therefore, the effective climatic requirements of a species (the range of conditions needed to sustain a viable population) can only be estimated by comparing the actual distribution of that species with climate data, as has been done in the present chapter. The main difficulty with this approach is that information on the distribution of rocky shore species is not always of high quality. Data may be decades old: in some cases the present study has had to rely on species distribution data from the 1950s (e.g. Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959). Data are often patchy, particularly in remote areas (Norton, 1978). Records of a species may not always represent the presence of a viable population, but rather transient individuals that are not reproductively active (Crisp and Fischer-Piette, 1959), and may also reflect variation due to species interactions (Davis *et al.*, 1998) or other non-climatic factors. These problems serve to emphasise the often-noted need for regular surveys to create baselines on which to base estimates of the effects on communities of change in climate or other external factors (Lewis, 1976, 1996; Norton, 1978; Hawkins and Hartnoll, 1983; Hawkins *et al.*, 1986; Southward *et al.*, 1995).

Knowing the temperature requirements of a species, its potential range (the area in which it could theoretically live) under a given climate change scenario can be projected using a method such as the one presented in this chapter. However, its true range under those conditions will not necessarily conform to its potential range.

Cold-water species with long life spans (over 5 years) are likely to survive, perhaps for decades, in areas where they are only able to reproduce in particularly favourable years, whereas short-lived species will tend to retreat much more quickly in response to warming (Hiscock *et al.*, 2004). Their ability to disperse, I would argue, is not likely to influence the rate at which cold-water benthic species will retreat in response to warming: the main consideration is not whether species are able to reach new areas but whether they are able to maintain a viable population in the areas where they already live.

The rate at which the ranges of warm-water species expand in response to warming will depend on a number of factors, also discussed by Hiscock *et al.* (2004). Species with limited dispersal ability, for instance because their larvae are either benthic or else pelagic with a very short life span, will expand slowly. Species that under good conditions are able to disperse effectively may nonetheless be limited in practice by other factors. Near their northern limits, many rocky shore invertebrate species exist as sparse populations and experience frequent reproductive failure: examples include *Gibbula umbilicalis,* (Kendall and Lewis, 1987; Kendall *et al.*, 1987), *Osilinus lineatus* (Kendall, 1987; Kendall *et al.*, 1987), *Patella ulyssiponensis* (Lewis, 1986; Bowman and Lewis, 1986) and *Chthamalus montagui* (Lewis *et al.*, 1982; Lewis, 1986). These species are likely to expand more slowly than the rate of warming would indicate, because of the limited supply of larvae, at least until populations near the limits have increased in abundance. Water currents (Gaylord and Gaines, 2000; Hiscock *et al.*, 2004), depending on their direction and speed, can either reduce or enhance the effective dispersal ability of species; in some cases currents can have a greater effect on species distribution than climate itself (Gaylord and Gaines, 2000). All these factors can alter the effective rate of dispersal of rocky shore species.

Unfortunately, few data are available with which to make quantitative comparisons between dispersal rates and the rate at which climate is expected to change. The best data are perhaps for invasive species such as the barnacle *Elminius modestus,* which after its introduction in the 1940s spread around the coast of Europe at a rate of 20–30km per year (Crisp, 1958). For comparison, a rate of warming of 0.4°C per year (the average rate under the two IPCC scenarios used in this chapter), on the north coast of Spain, would mean summer isotherms moving westward by about 8km per year, whereas winter isotherms would move eastward by about 30km per year. Thus in this area a species limited by low winter temperatures would have to expand at more than three times the rate of a species limited by low summer temperatures, in order to keep up with the expected rate of climate change.

Another key consideration in the response of warm-water species to rising temperatures is the existence of barriers to expansion (Crisp and Southward, 1953; Hiscock *et al.*, 2004). Barriers for rocky shore species can include seas, channels, and areas with little suitable habitat, such as those areas dominated by sandy shores including southwest France, the eastern English Channel, and the southern North Sea. If the effective distance that a species is able to disperse in a single year is less than the width of a sea barrier that it must cross, then its expansion may be halted indefinitely. Thus the projections made in this chapter of the effects of climate change on rocky shore species include many uncertainties, which must be taken into account when interpreting them. Nonetheless, on a broad scale, they provide first-level estimates of how the distribution of these species is likely to alter in the future.

6.4.4. Comparative evaluation of climate envelope models at species and ecosystem levels

As discussed in Chapter 1, there are two paradigms for modelling how ecosystems will respond to climate change. The "ecosystem movement" paradigm (Gitay *et al.*, 2002) assumes that ecosystems will shift more-or-less intact to locations with climatic conditions that resemble their present-day environment. Essentially, then, this means applying a climate envelope model (Davis *et al.*, 1998a,b) at the level of whole ecosystems. This approach has the important advantage of simplicity, and although many criticisms of it can be made (reviewed in Chapter 1; see also Gitay *et al.*, 2002), it remains a standard with which more sophisticated models need to be compared. Climate-related whole-ecosystem shifts have been shown to occur in plankton (Beaugrand *et al.*, 2002a, b), which have short life spans and no barriers to dispersal, making them likely to respond rapidly and homogeneously to climate change. Most ecosystems, however, do not share these characteristics.

The graphical method developed in this chapter, in contrast, applies the climate envelope model at the level of species, using a two-dimensional envelope with axes of summer and winter temperature. This approach involves making many more predictions (considering tens or hundreds of species compared to only one ecosystem at a given location), but makes it possible to incorporate a variety of factors that cannot be addressed at the ecosystem level. These include the differential responses of species to different climatic factors: a range limit for a given rocky shore species is typically set by either summer or winter temperature, but seldom both. These differential responses lead to inaccuracies in an ecosystem-level approach under climate scenarios such as those considered in this chapter, which project different amounts of warming in winter and summer. Factors such as ability to disperse, barriers to expansion, and lags due to organism life-spans, can also be considered at species level much more readily than at the level of ecosystems.

Thus modelling at the species level, while more laborious, can be considerably more accurate in forecasting species responses to climate change than modelling at the ecosystem level. However, in order to make forecasts of ecosystem responses of climate change, it is necessary to take the results of species-level modelling a step further by considering how the assemblage of species projected for a given location will interact with each other and with their environment, and how changes in climate will affect these interactions.

For example, the northward expansion of southern species is likely to mean an increase in the number of species of grazers found on many northern European rocky shores. *Patella vulgata* will remain common throughout northern Europe, but southern species such as *Patella ulyssiponensis, P. depressa, Gibbula pennanti, G. umbilicalis* and *Osilinus lineatus* will expand. Shores that now have only two or three main species of grazers may soon have five or six. The likely consequence will be more consistent exploitation of food resources, in both space and time, with fewer fluctuations in exploitation due to variable recruitment of grazers. Algae will have fewer opportunities to "escape" grazing pressure by growing to adult size (Southward, 1964; Hawkins and Hartnoll, 1985; Jenkins *et al.*, 1999a, b), and as a result there will be a reduction in the abundance of algae. Indirect effects such as this are likely to modify considerably the direct effects of temperature on rocky shore species. However, predicting the effect on communities of changes in biological interactions under altered climatic conditions is a complex problem that cannot be fully addressed here.

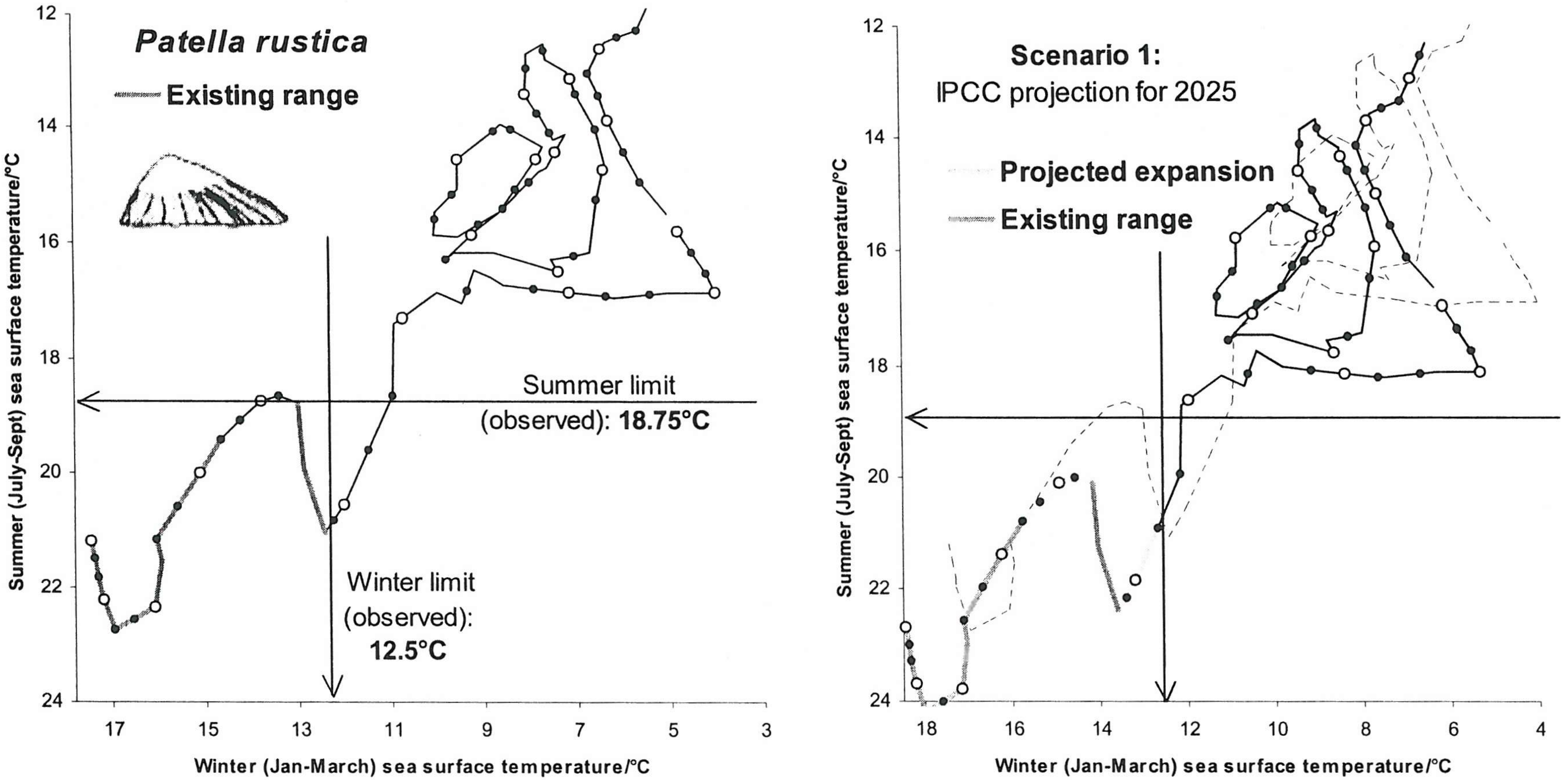


Figure 6.13. Graphical modelling of the temperature limits of *Patella rustica* L. and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

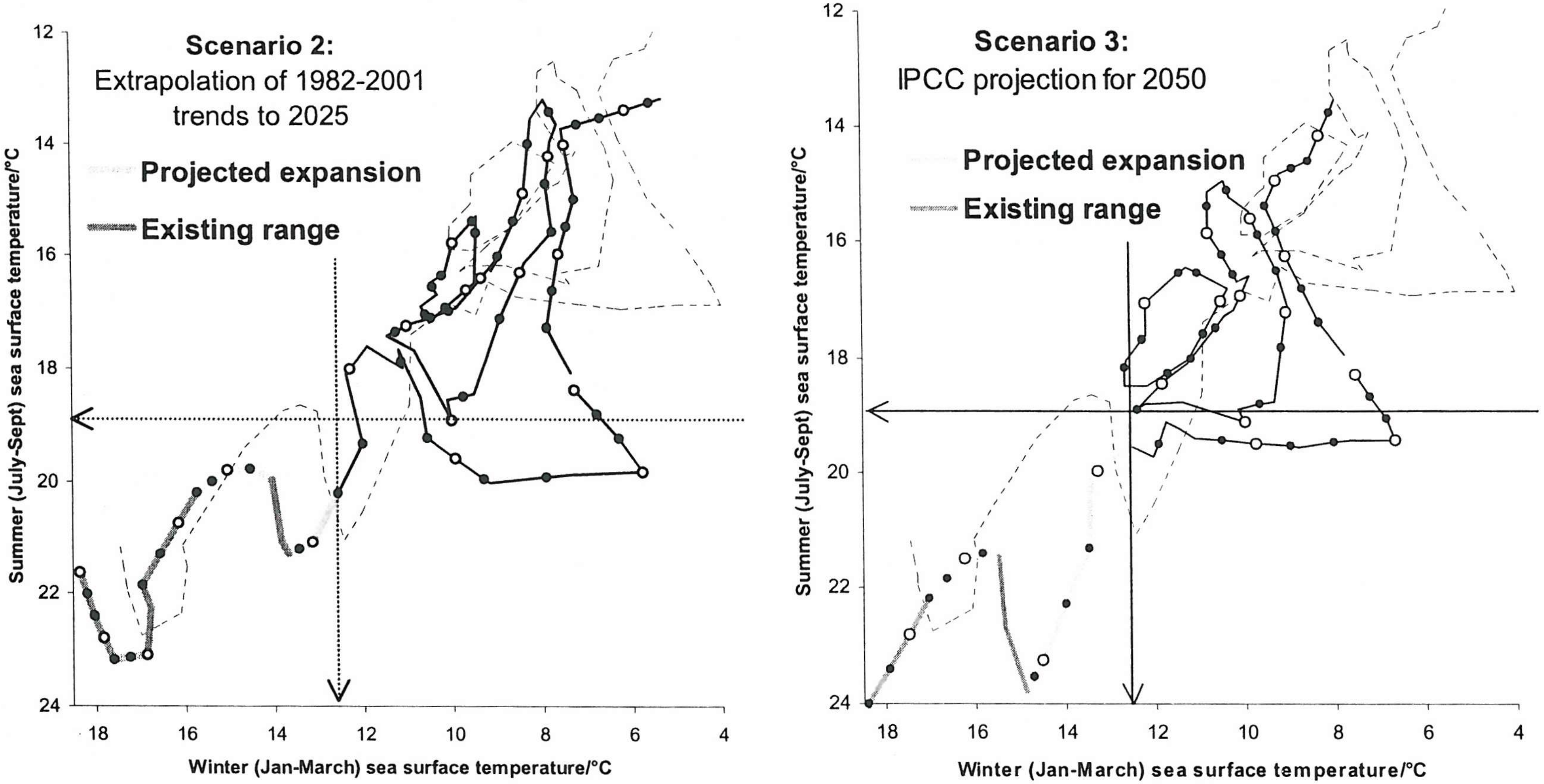


Figure 6.13 (continued). Graphical modelling of the temperature limits of *Patella rustica* L. and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

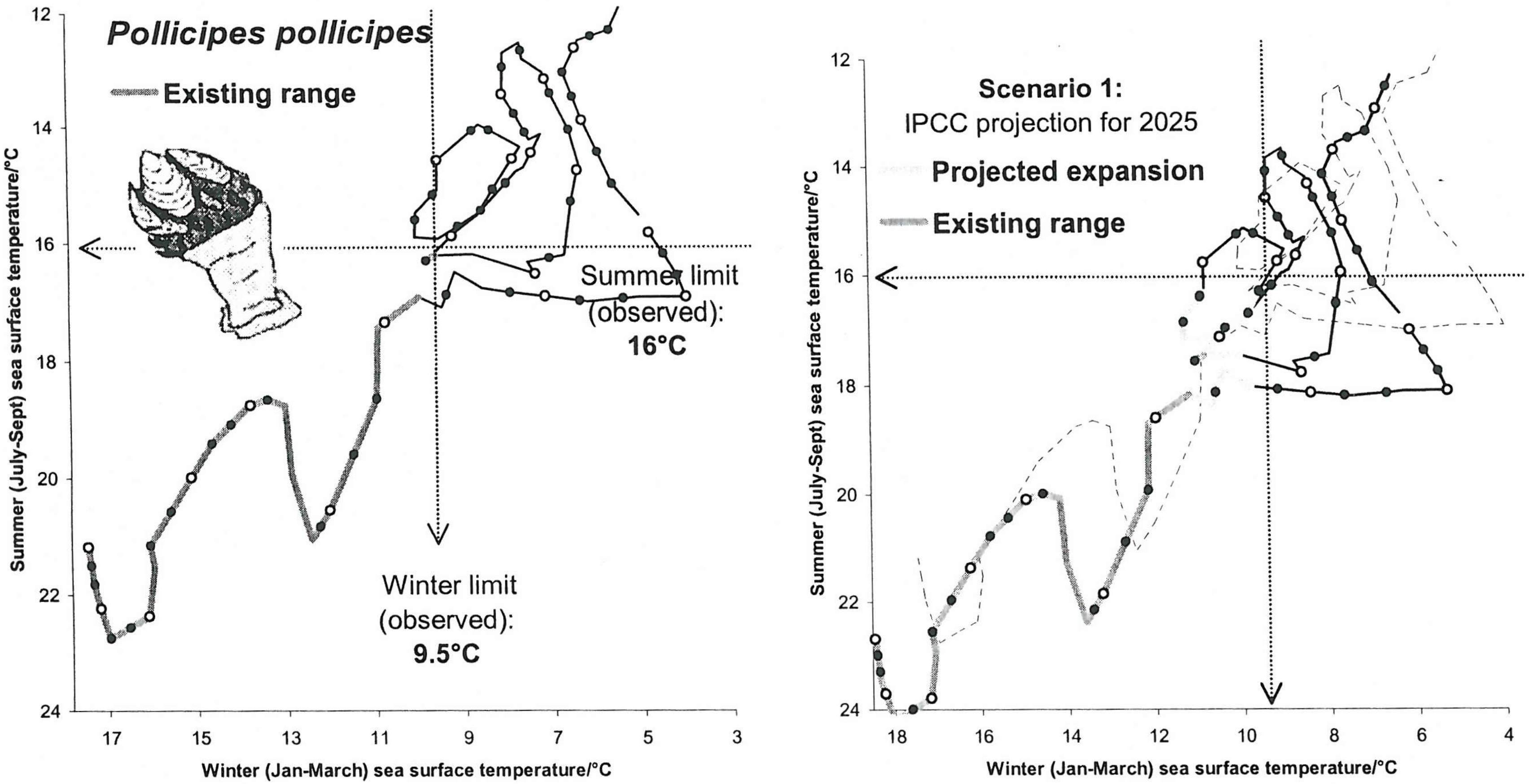


Figure 6.14. Graphical modelling of the temperature limits of *Pollicipes pollicipes* Gmelin and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

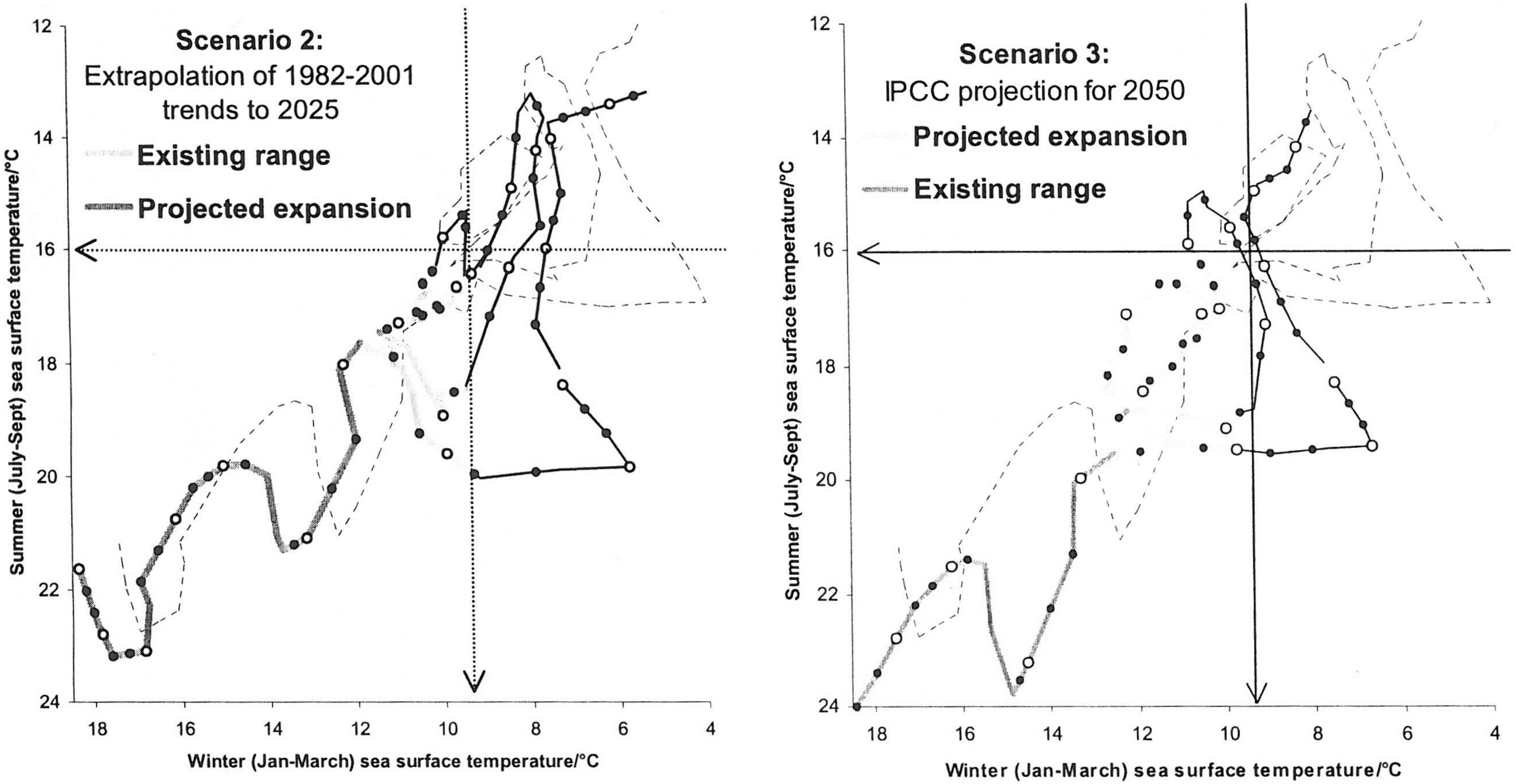


Figure 6.14 (continued). Graphical modelling of the temperature limits of *Pollicipes pollicipes* Gmelin and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

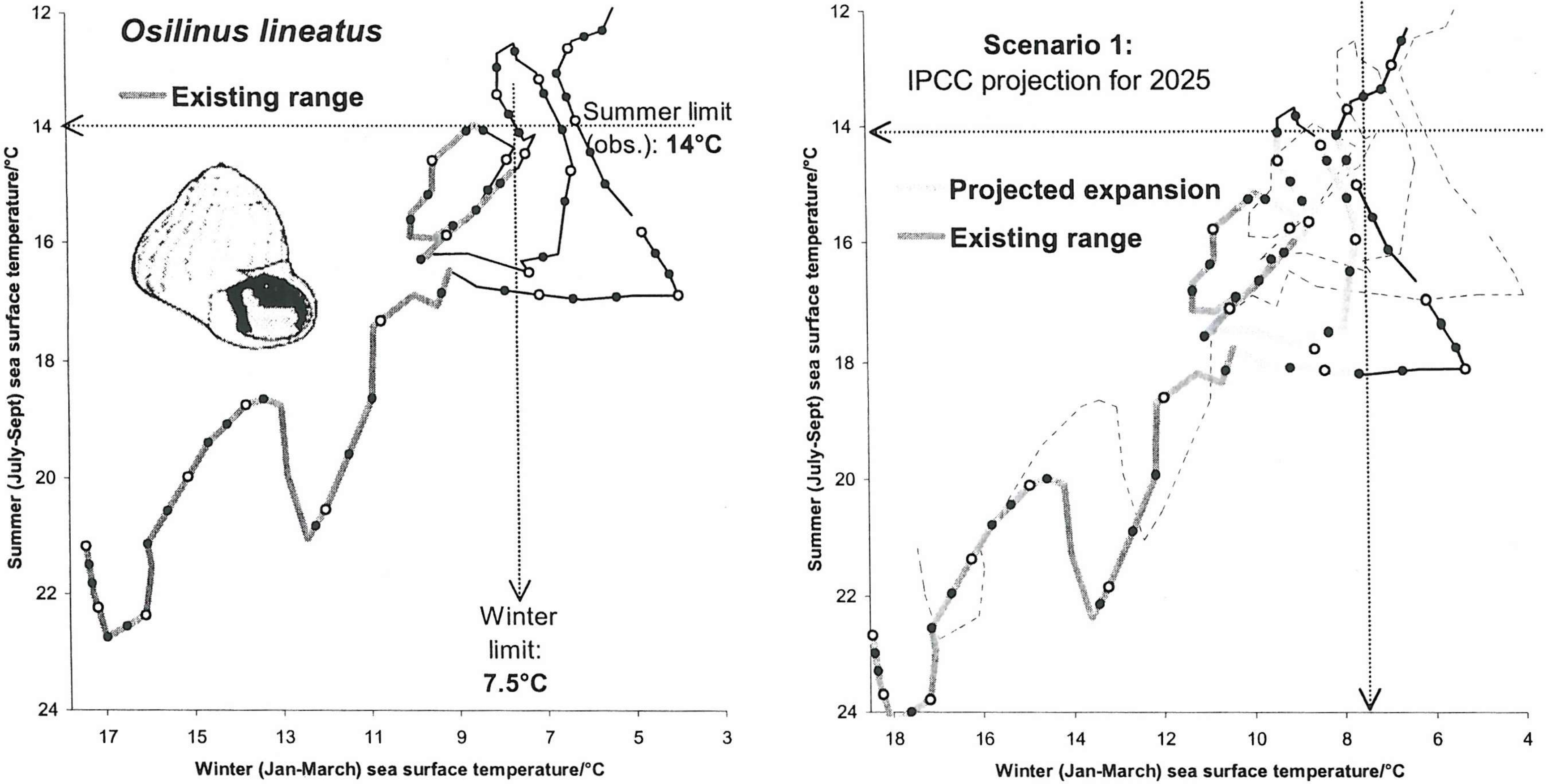


Figure 6.15. Graphical modelling of the temperature limits of *Osilinus lineatus* and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

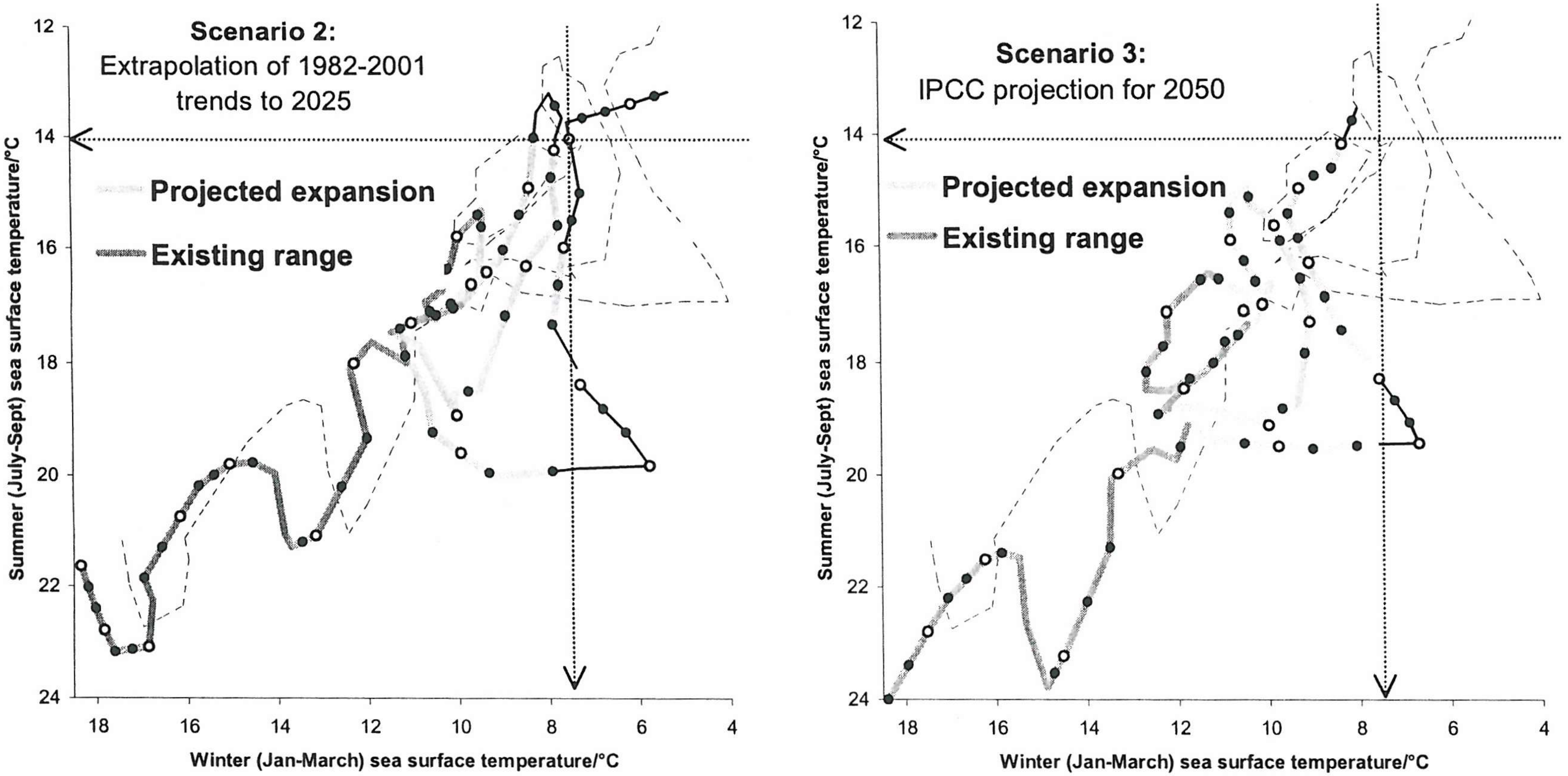


Figure 6.15 (continued). Graphical modelling of the temperature limits of *Osilinus lineatus* and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

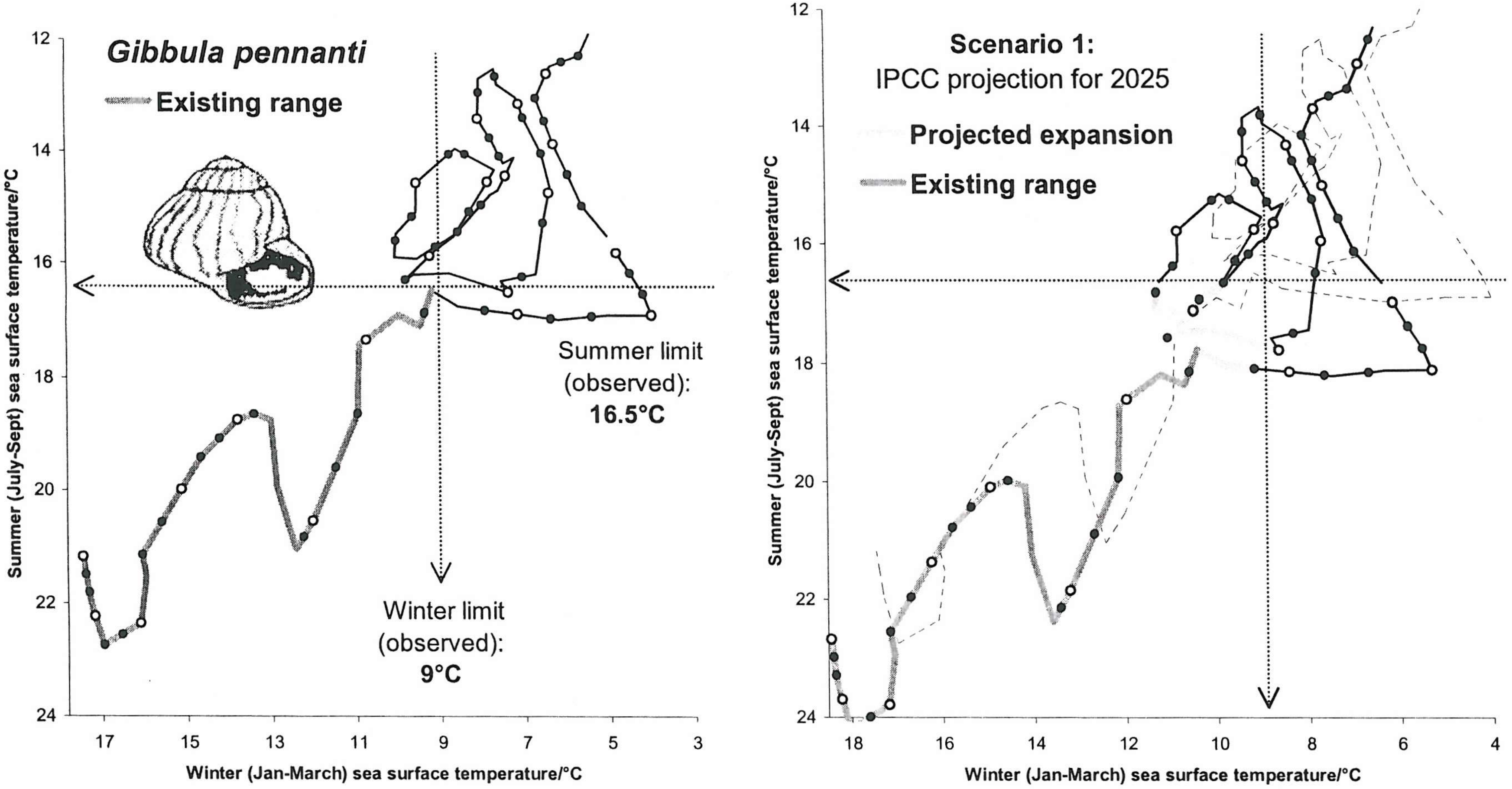


Figure 6.16. Graphical modelling of the temperature limits of *Gibbula pennanti* (Philippi) and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

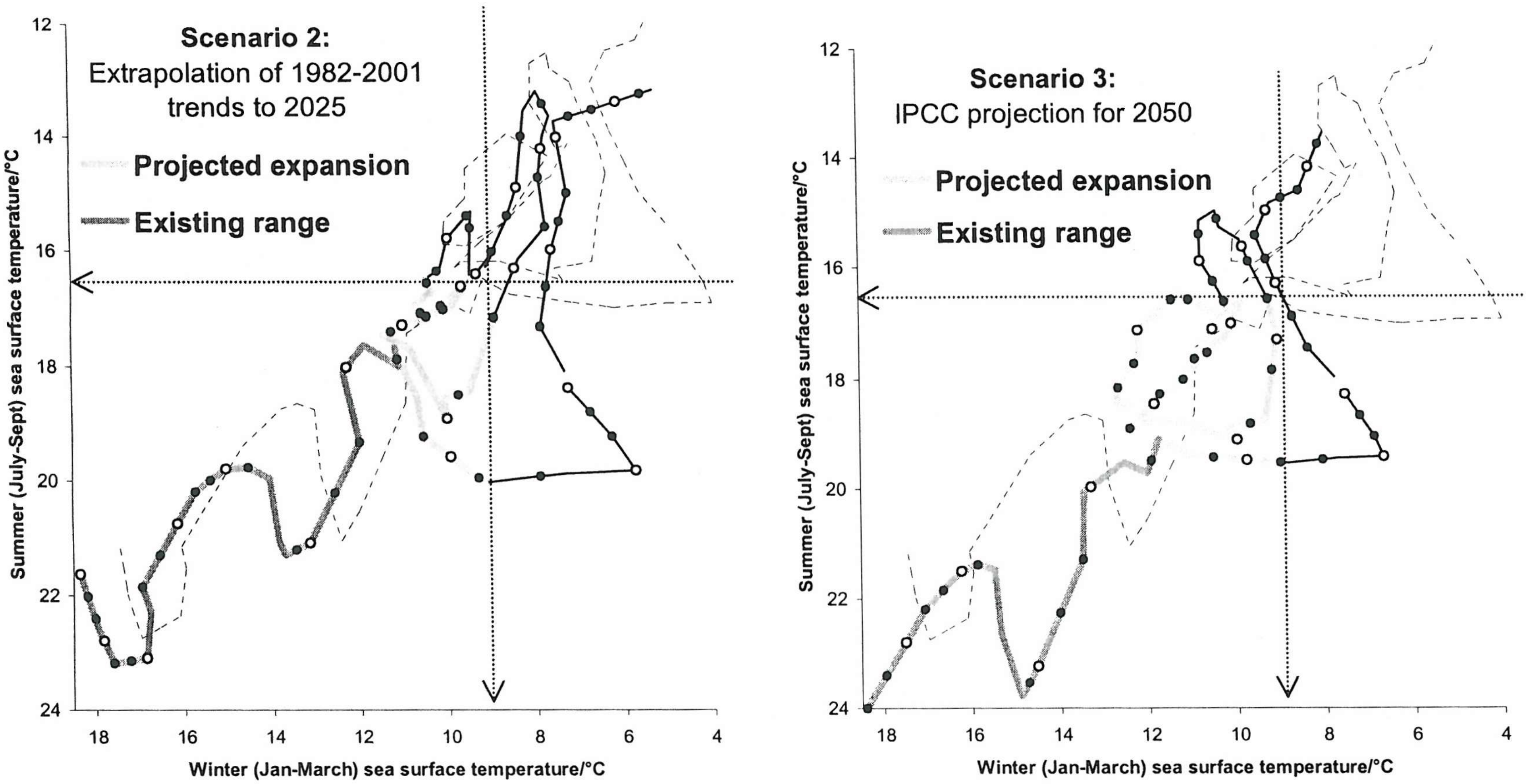


Figure 6.16 (continued). Graphical modelling of the temperature limits of *Gibbula pennanti* (Philippi) and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

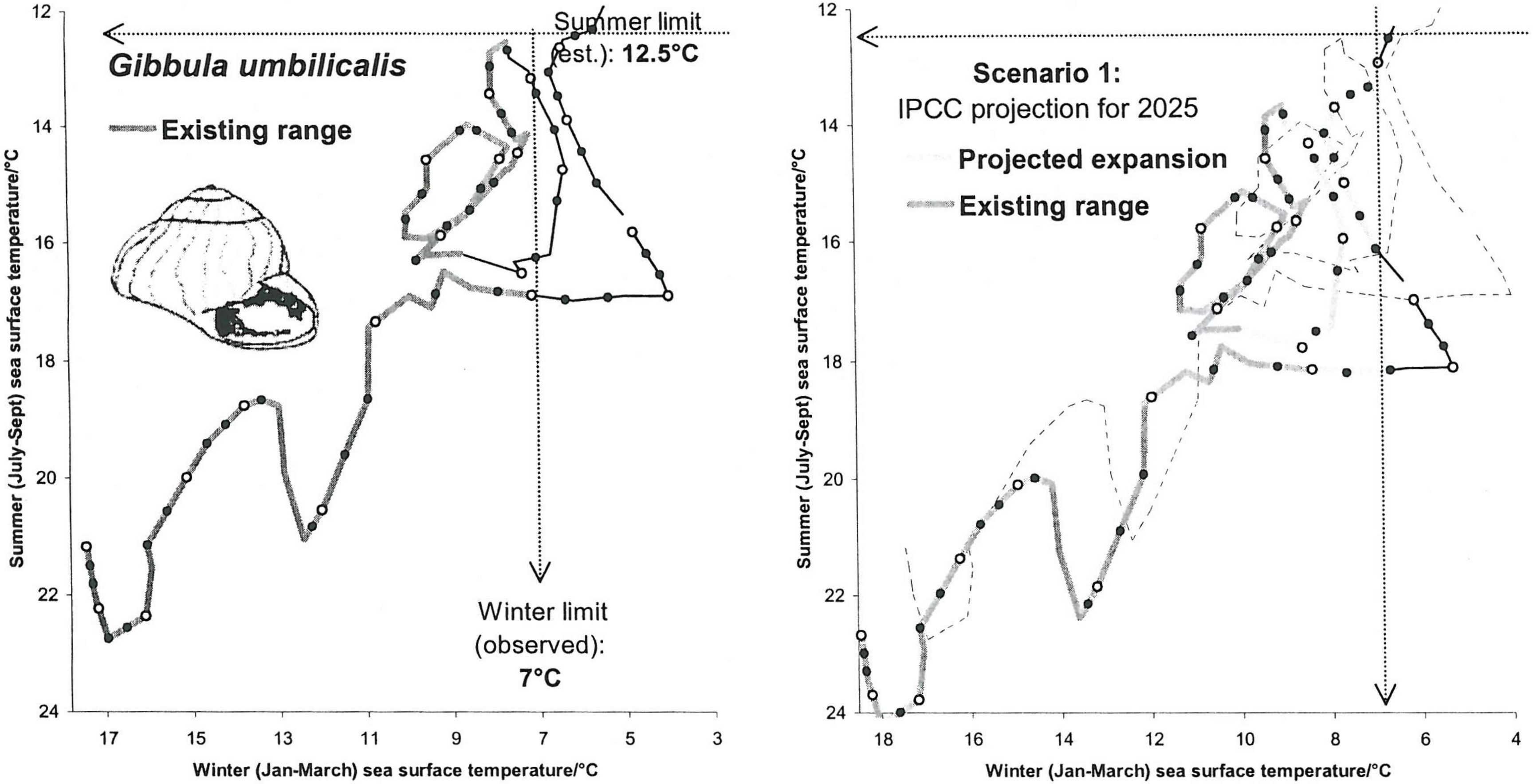


Figure 6.17. Graphical modelling of the temperature limits of *Gibbula umbilicalis* (da Costa) and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

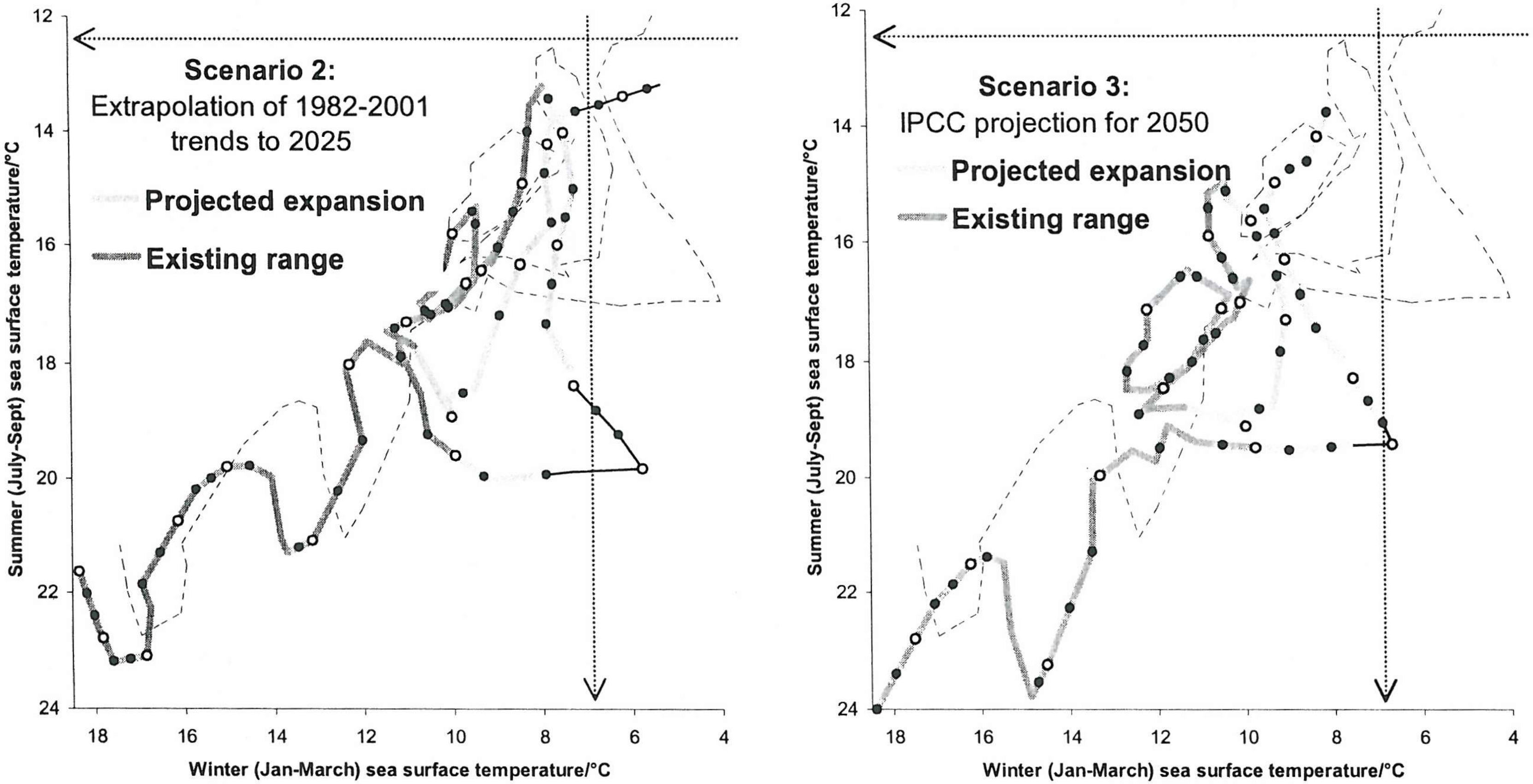


Figure 6.17 (continued). Graphical modelling of the temperature limits of *Gibbula umbilicalis* (da Costa) and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

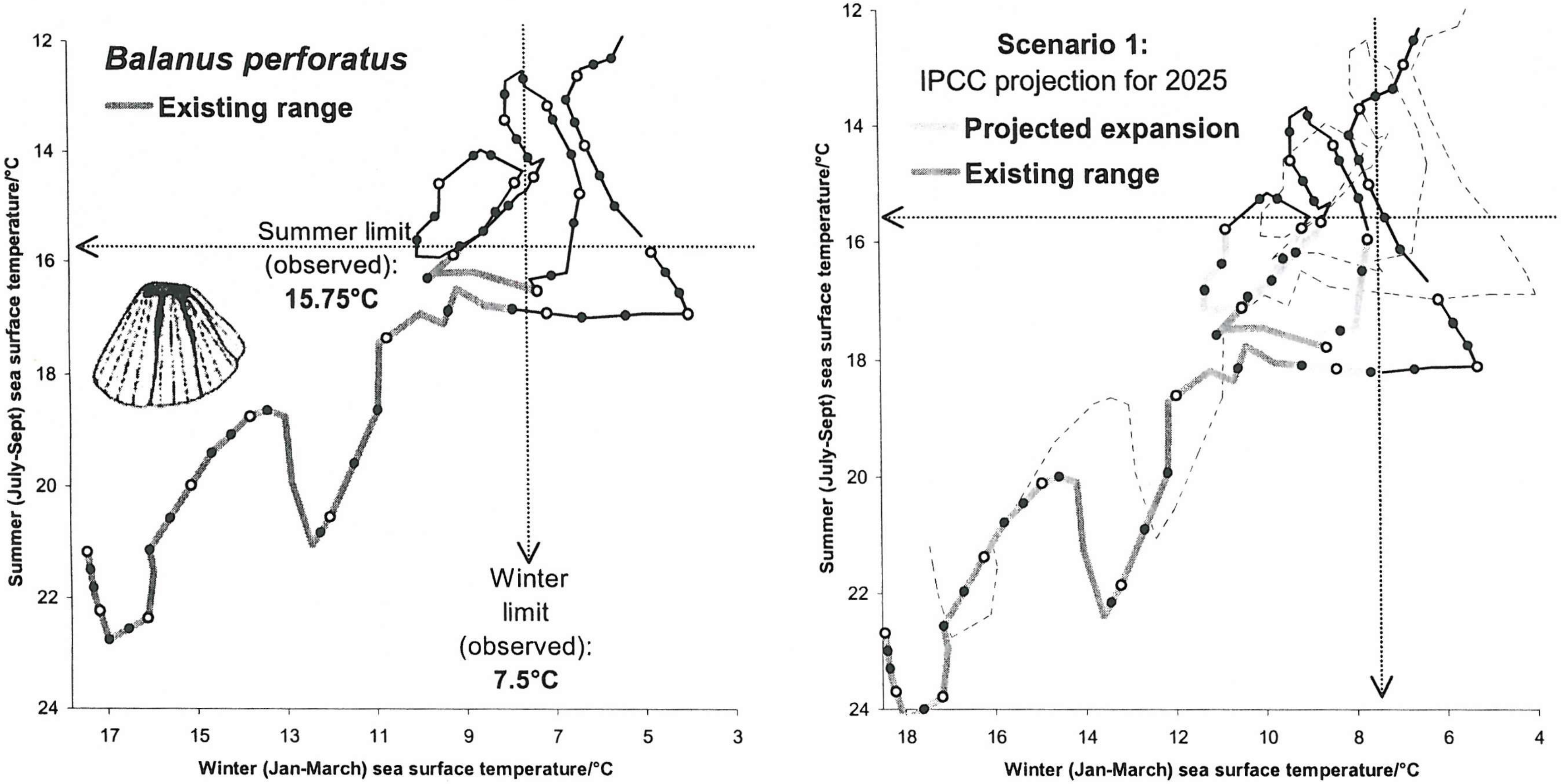


Figure 6.18. Graphical modelling of the temperature limits of *Balanus perforatus* Brugière and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

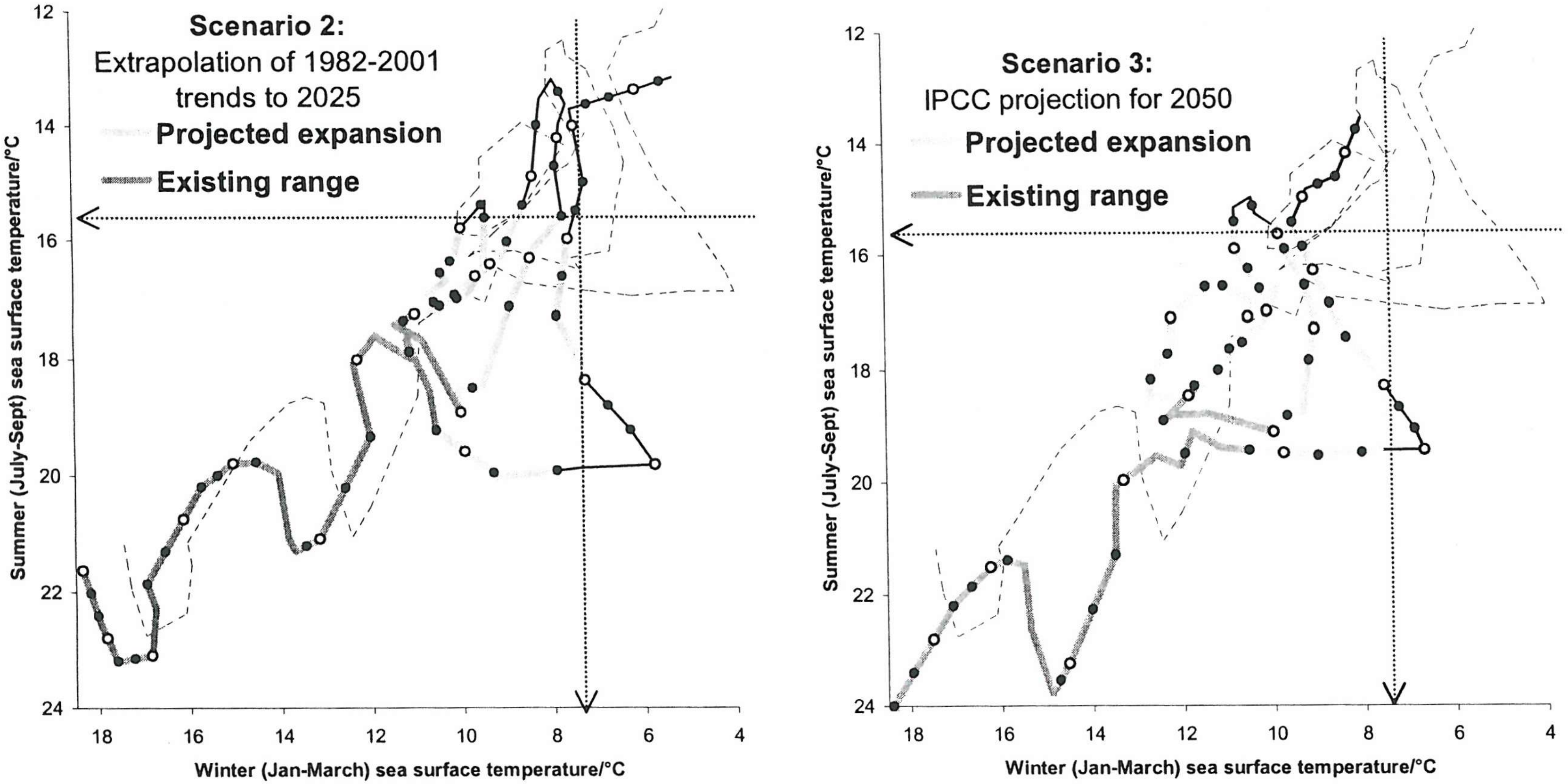


Figure 6.18 (continued). Graphical modelling of the temperature limits of *Balanus perforatus* Brugière and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

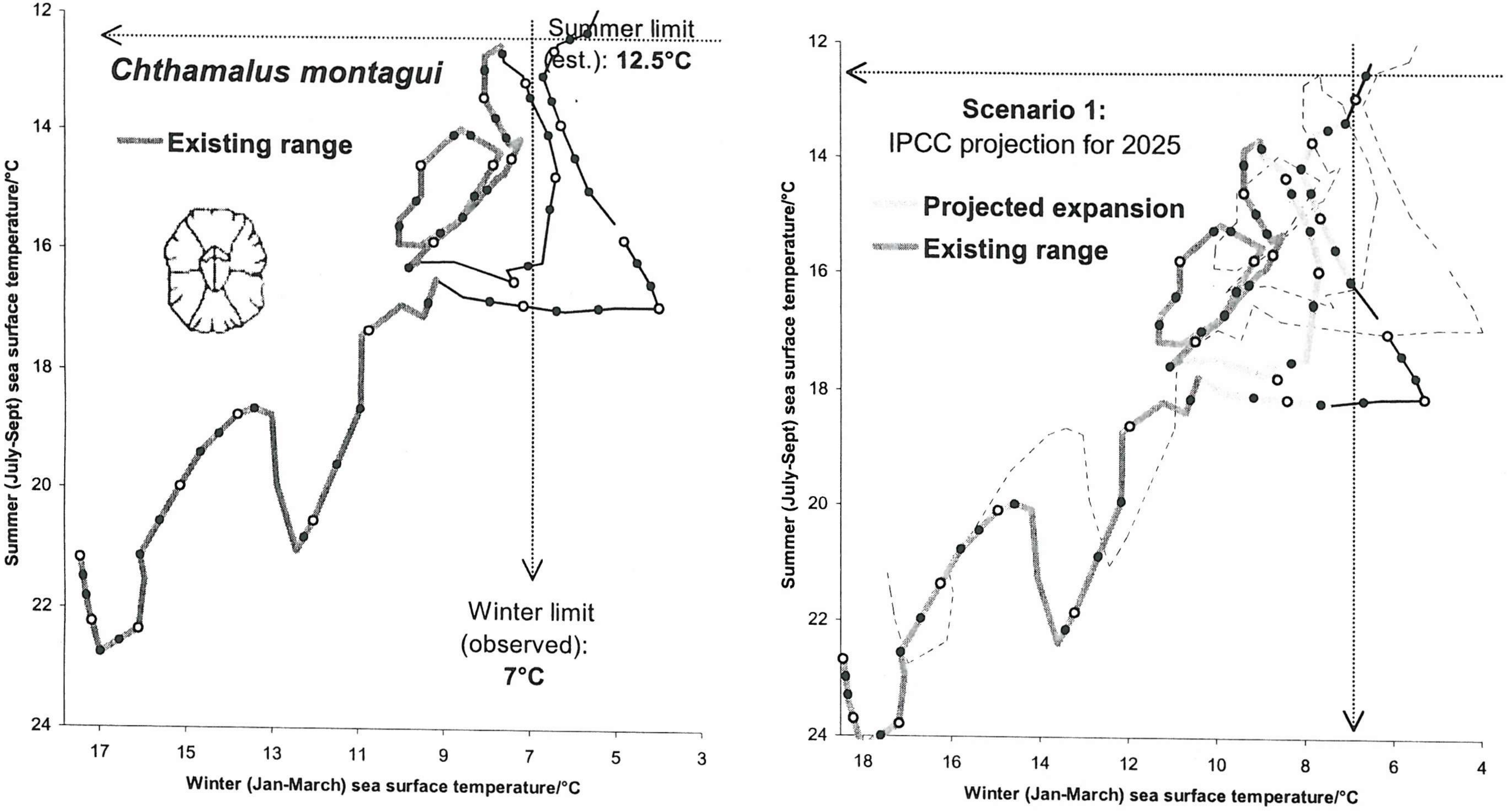


Figure 6.19. Graphical modelling of the temperature limits of *Chthamalus montagui* Southward and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

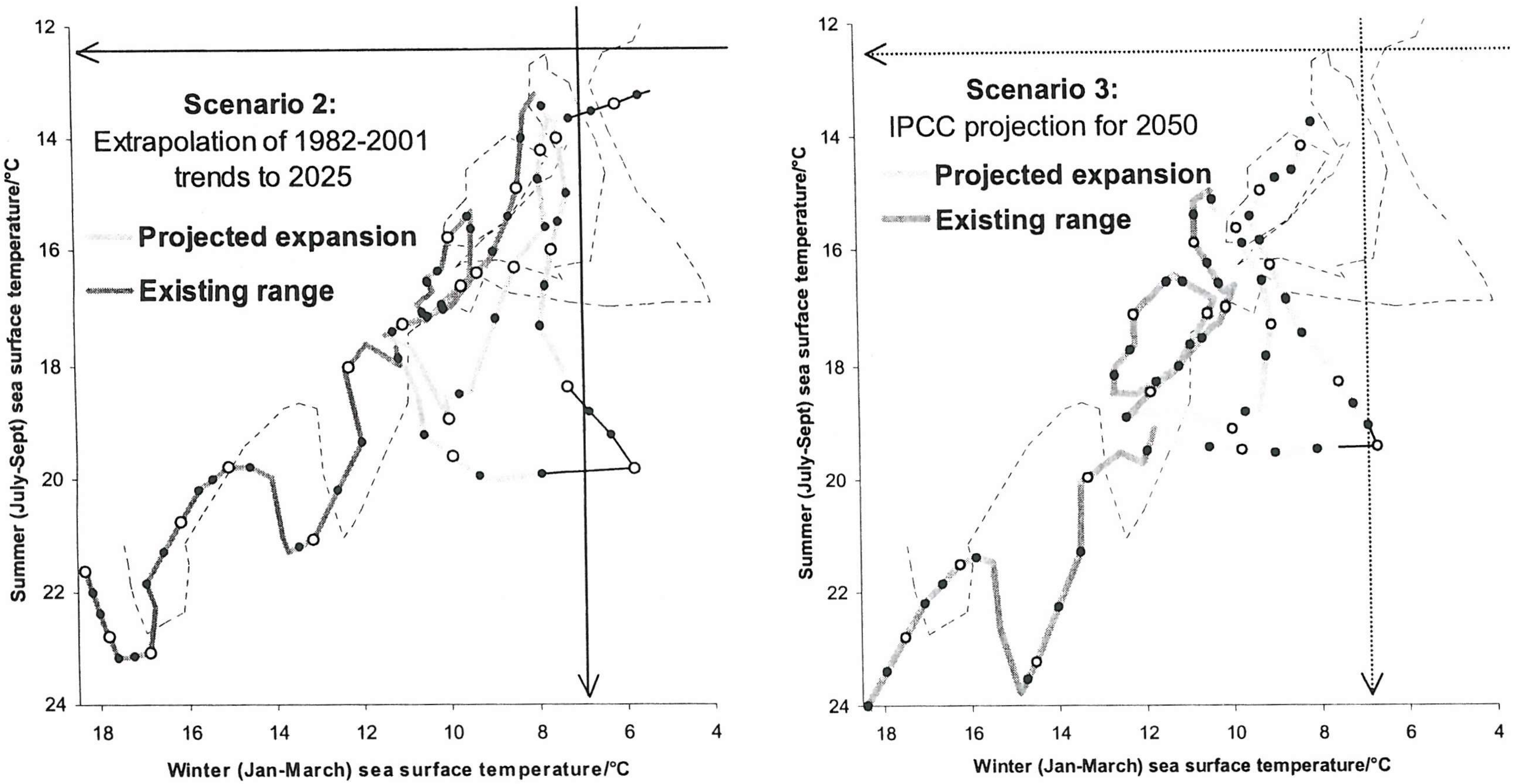


Figure 6.19 (continued). Graphical modelling of the temperature limits of *Chthamalus montagui* Southward and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

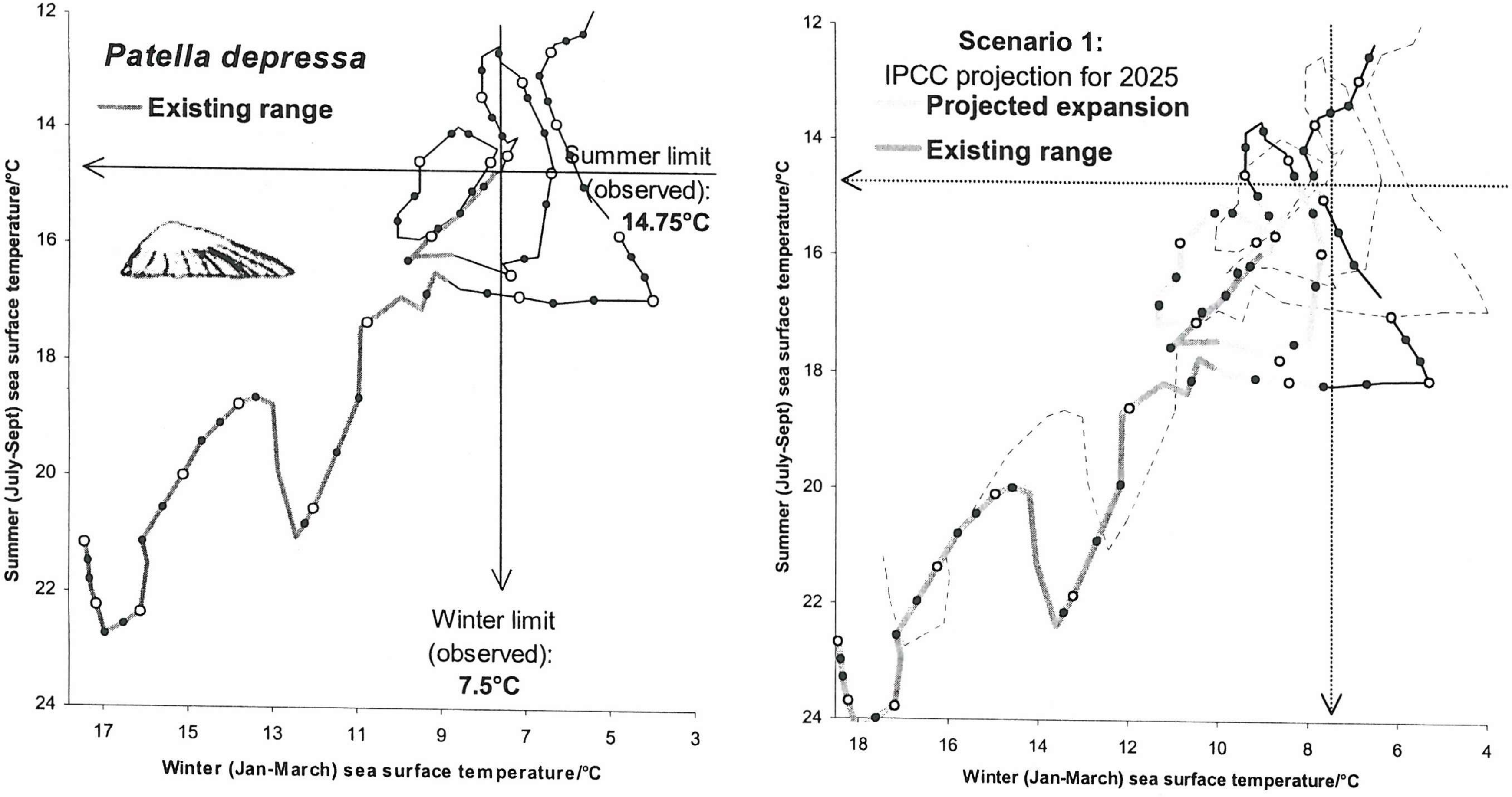


Figure 6.20. Graphical modelling of the temperature limits of *Patella depressa* Pennant and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

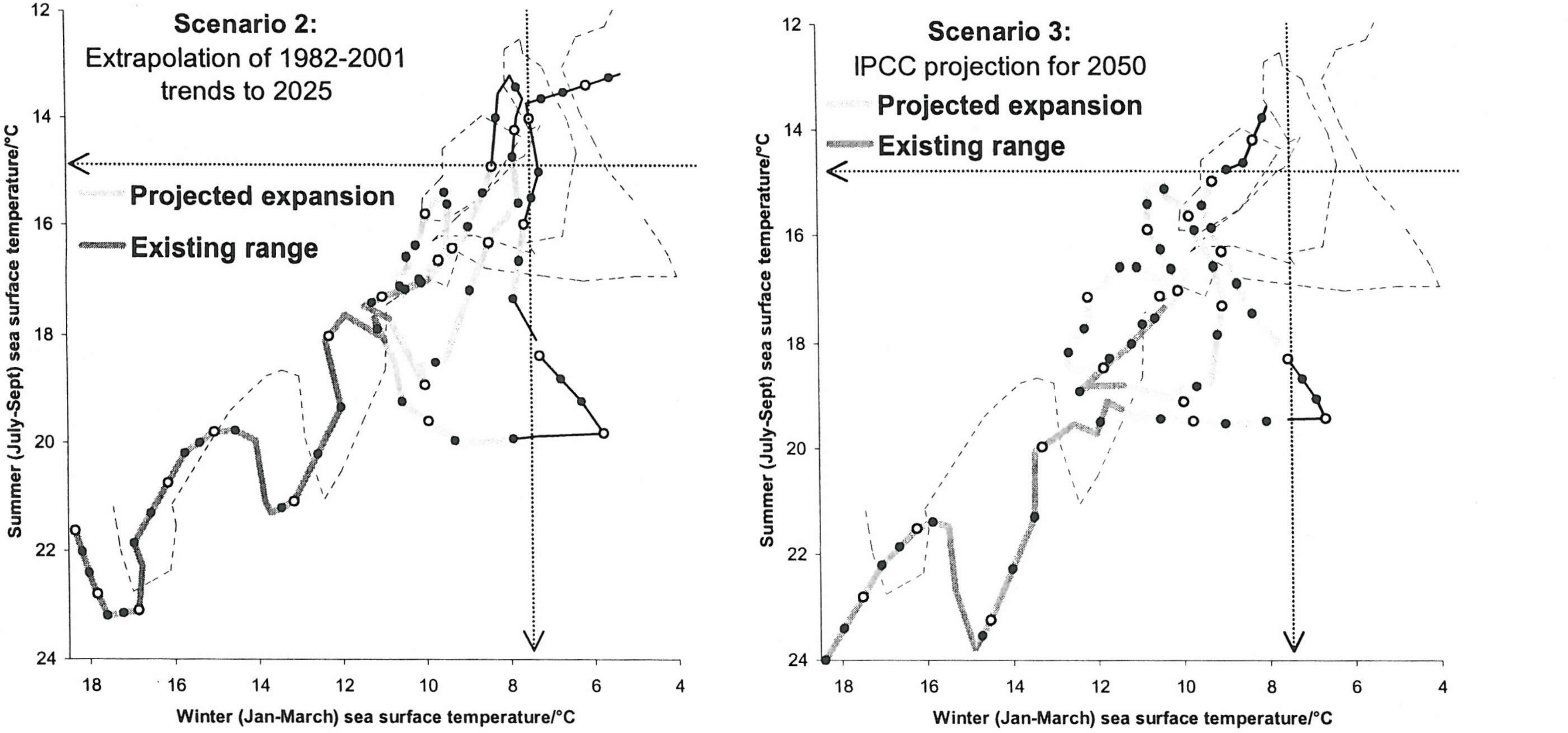


Figure 6.20 (continued). Graphical modelling of the temperature limits of *Patella depressa* Pennant and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

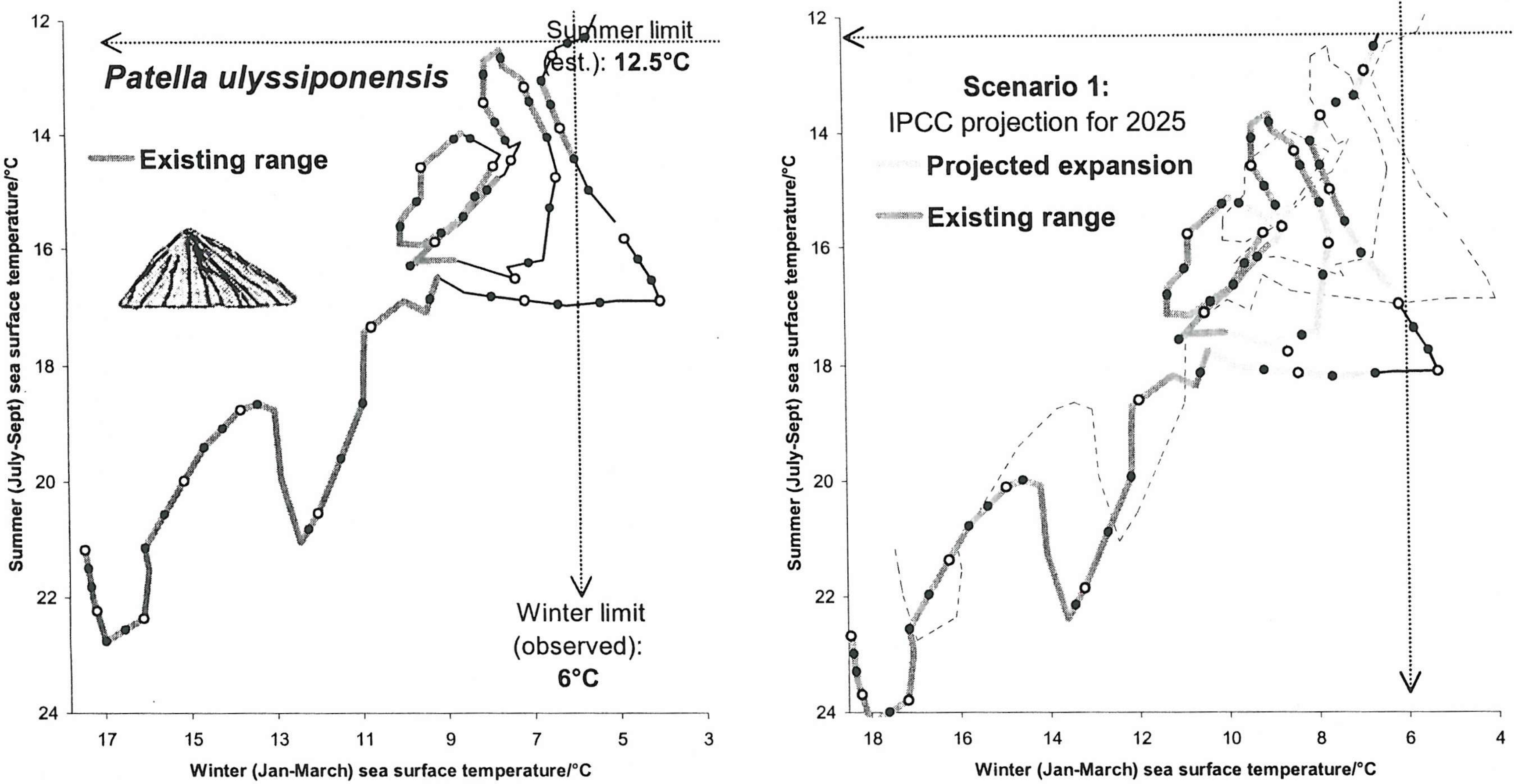


Figure 6.21. Graphical modelling of the temperature limits of *Patella ulyssiponensis* Gmelin and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

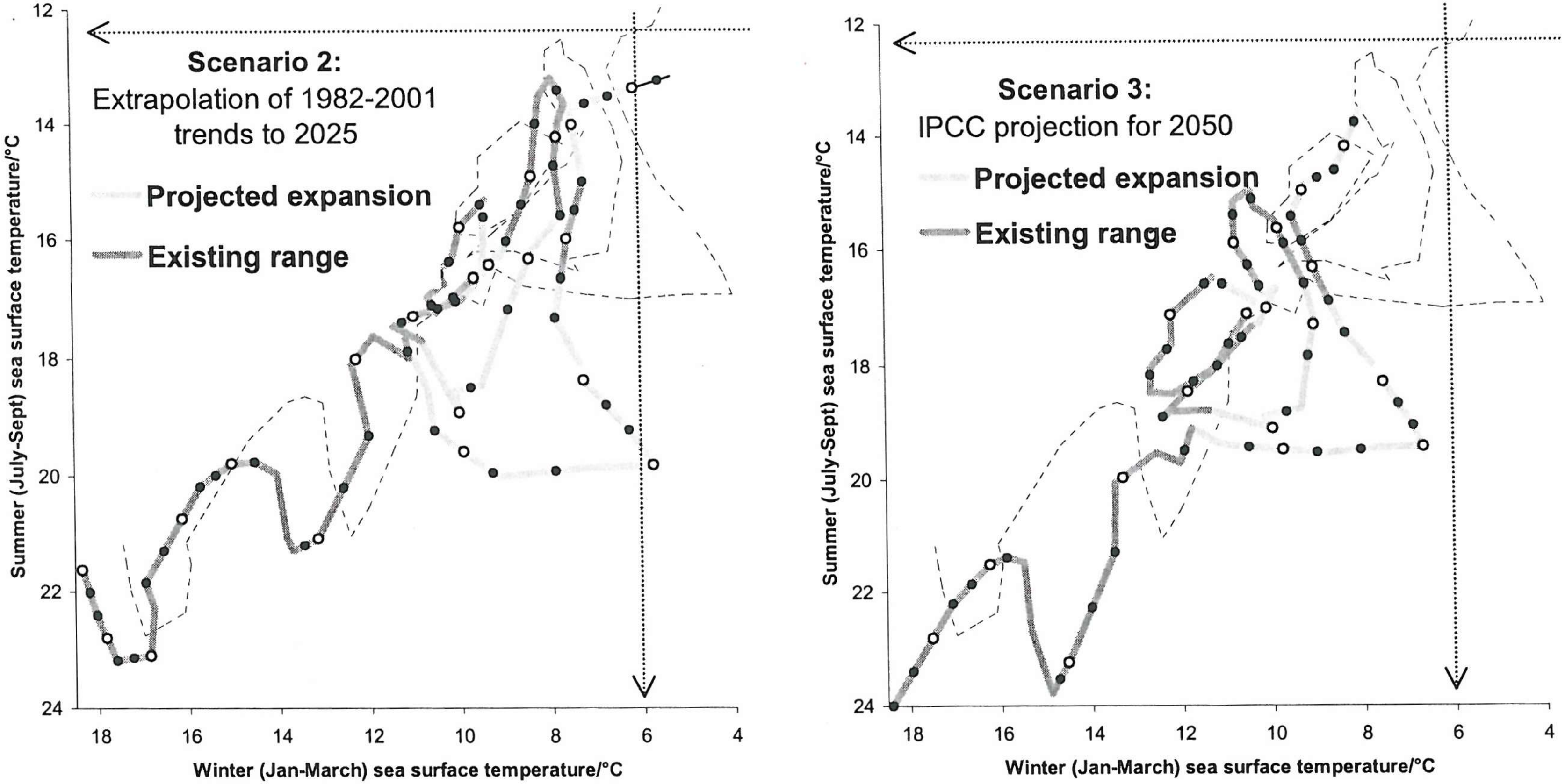


Figure 6.21 (continued). Graphical modelling of the temperature limits of *Patella ulyssiponensis* Gmelin and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

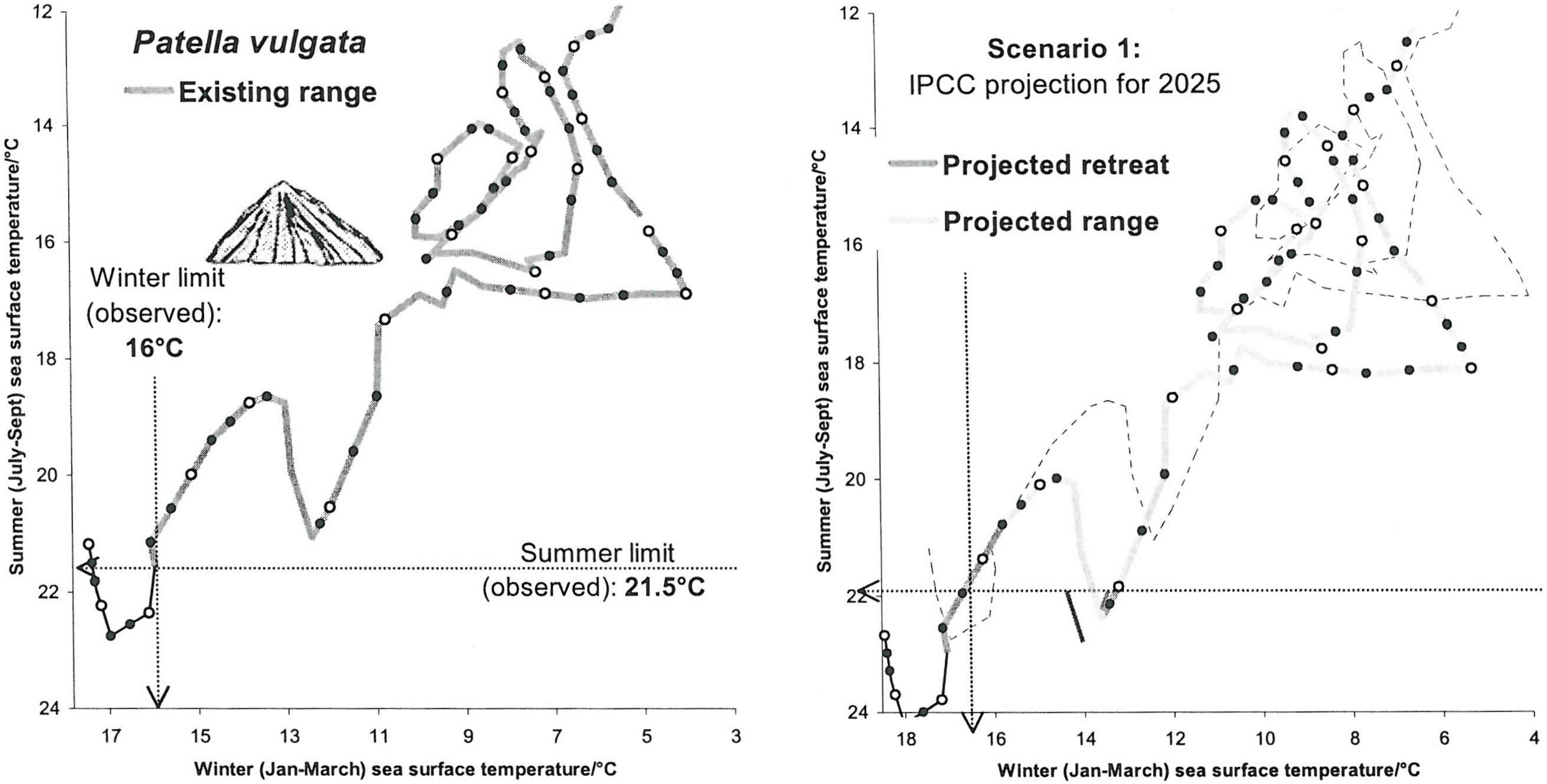


Figure 6.22. Graphical modelling of the temperature limits of *Patella vulgata* L. and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

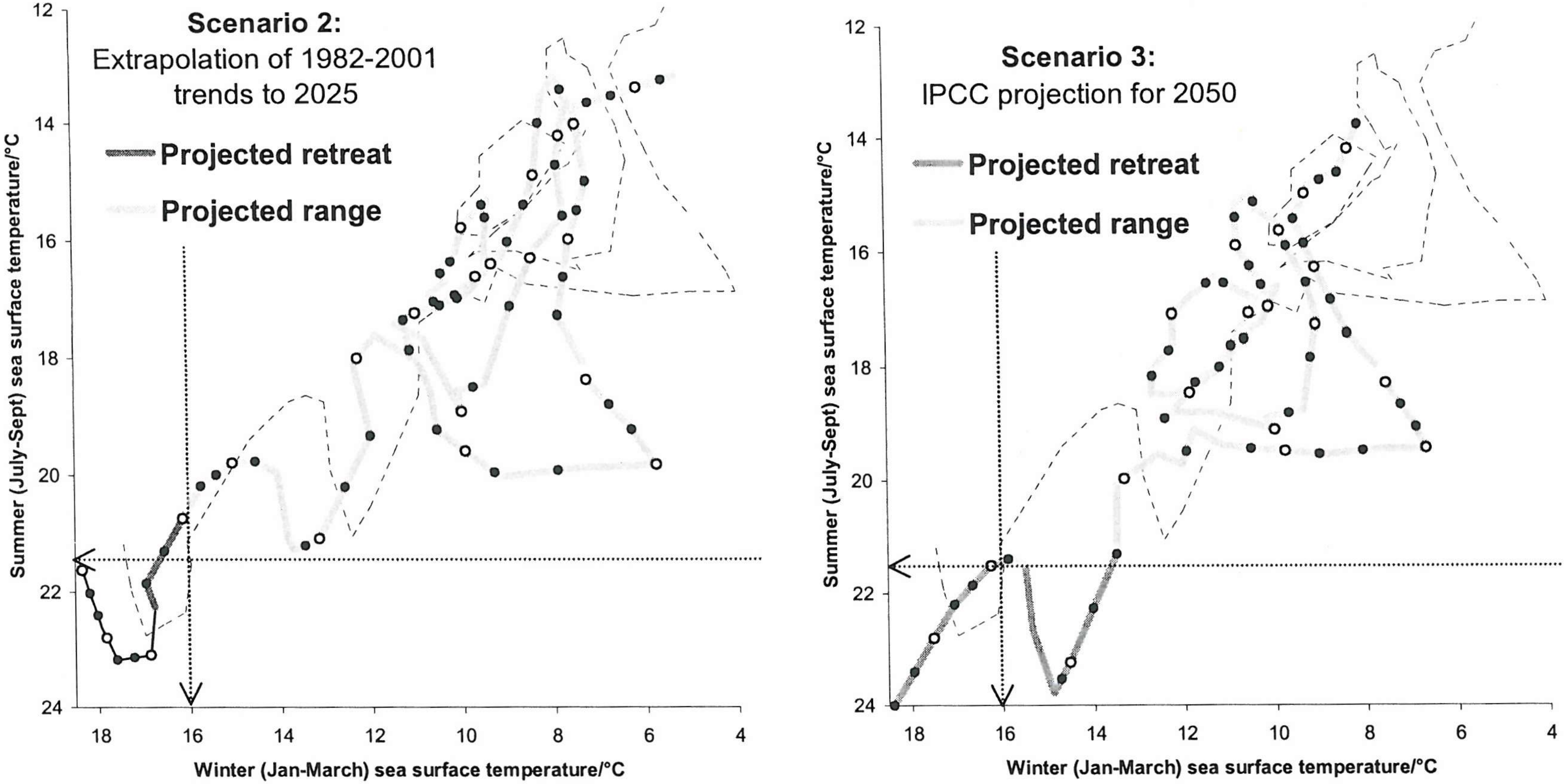


Figure 6.22 (continued). Graphical modelling of the temperature limits of *Patella vulgata* L. and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

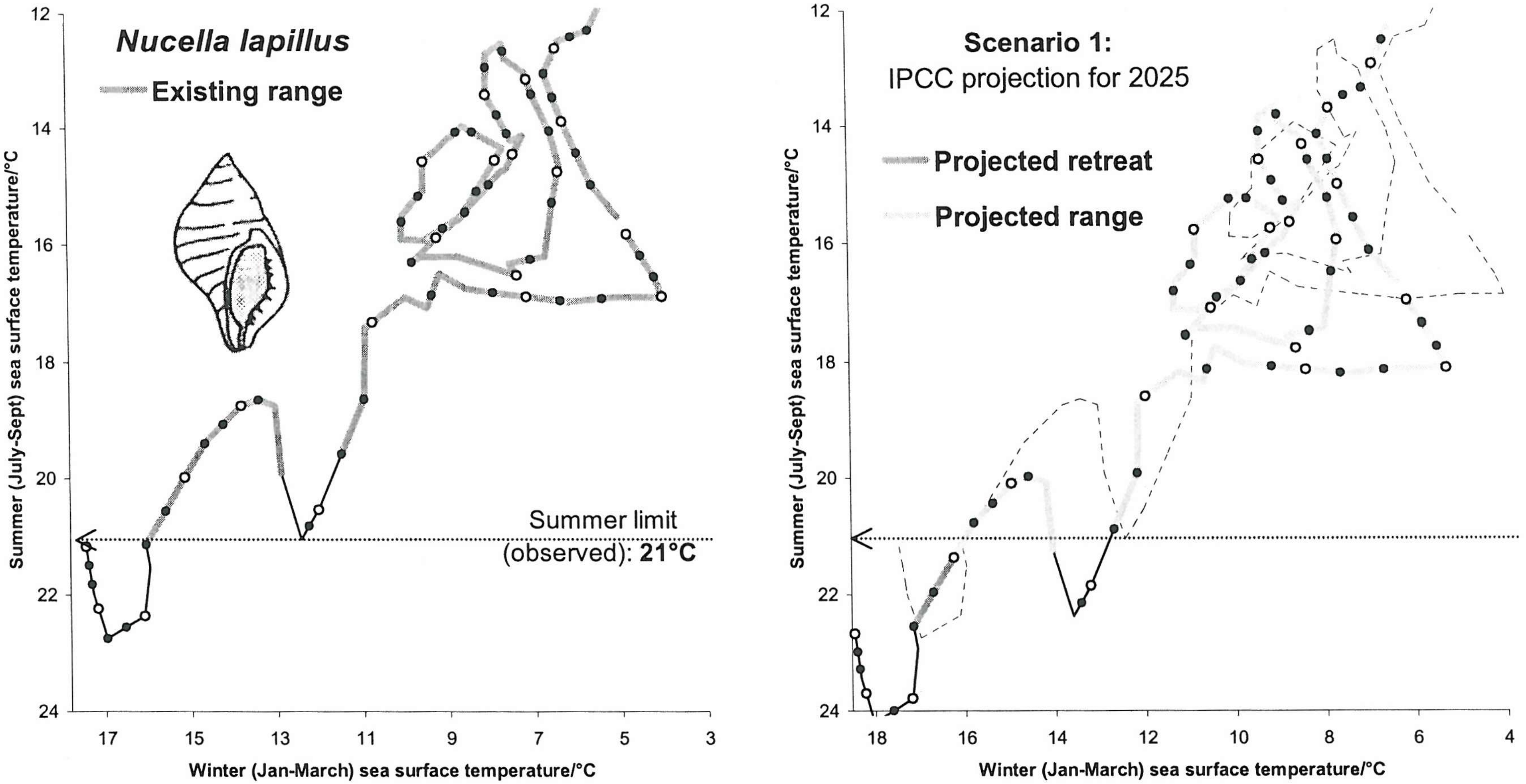


Figure 6.23. Graphical modelling of the temperature limits of *Nucella lapillus* L. and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

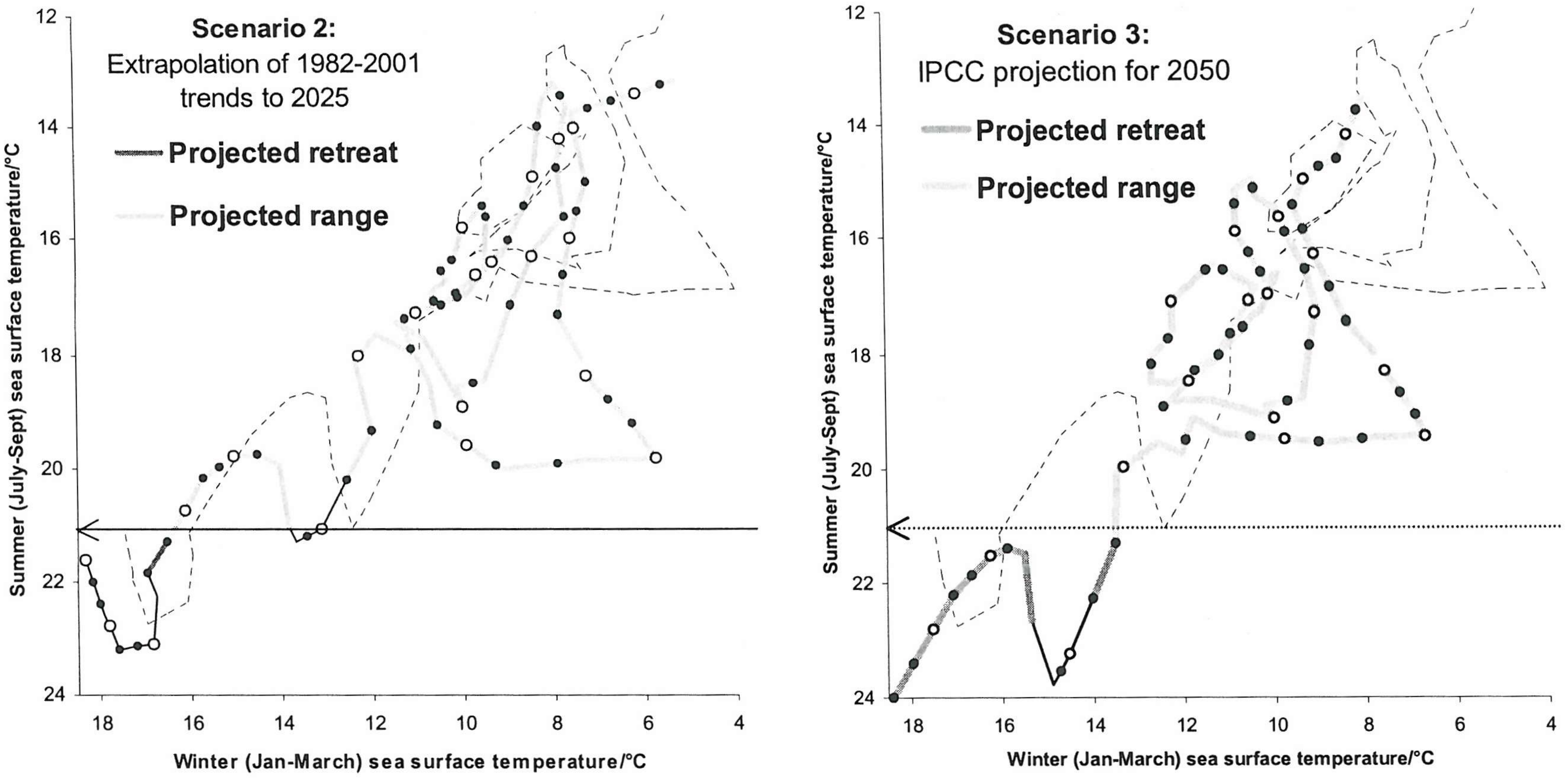


Figure 6.23 (continued). Graphical modelling of the temperature limits of *Nucella lapillus* L. and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

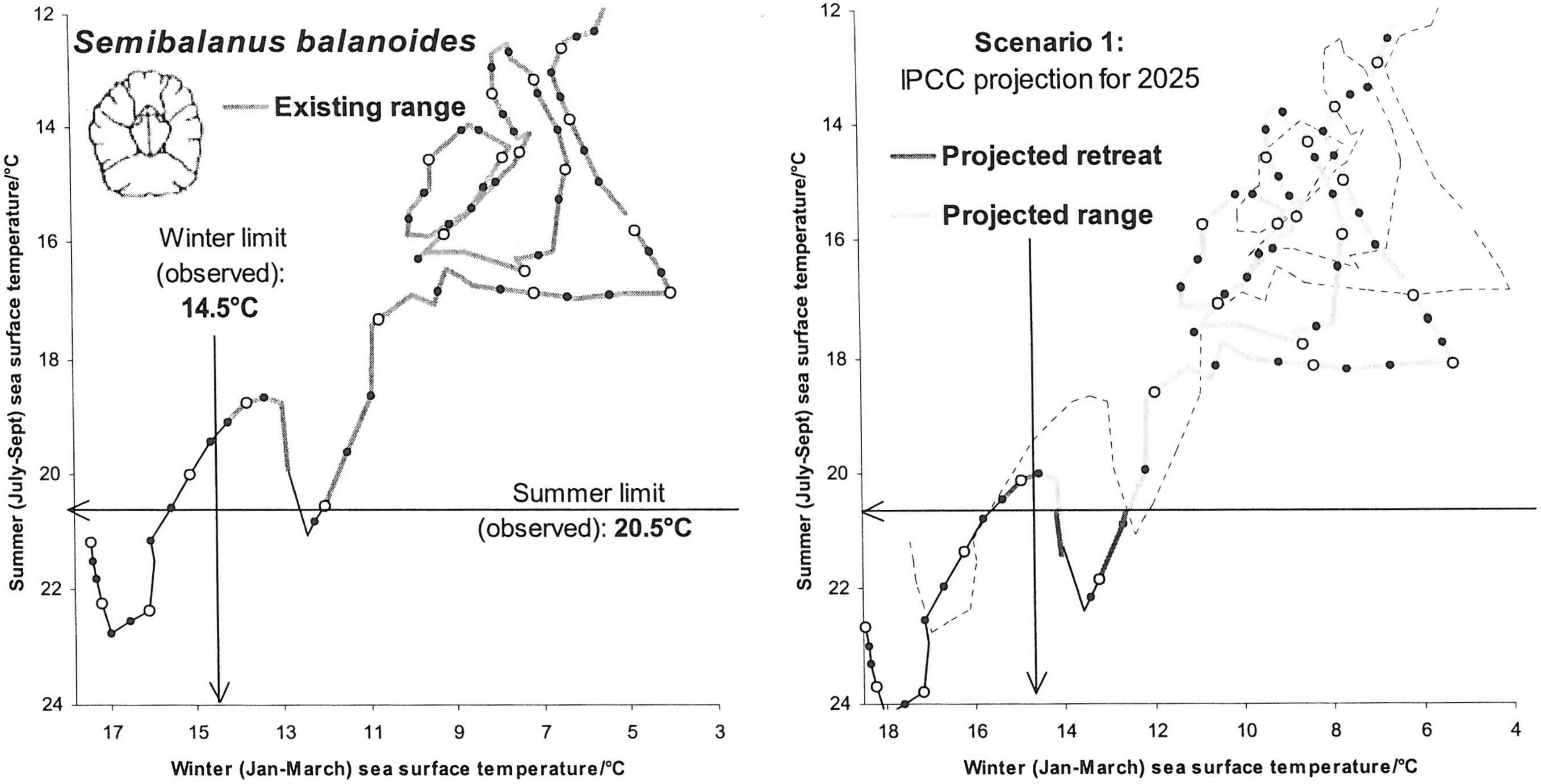


Figure 6.24. Graphical modelling of the temperature limits of *Semibalanus balanoides* (L.) and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

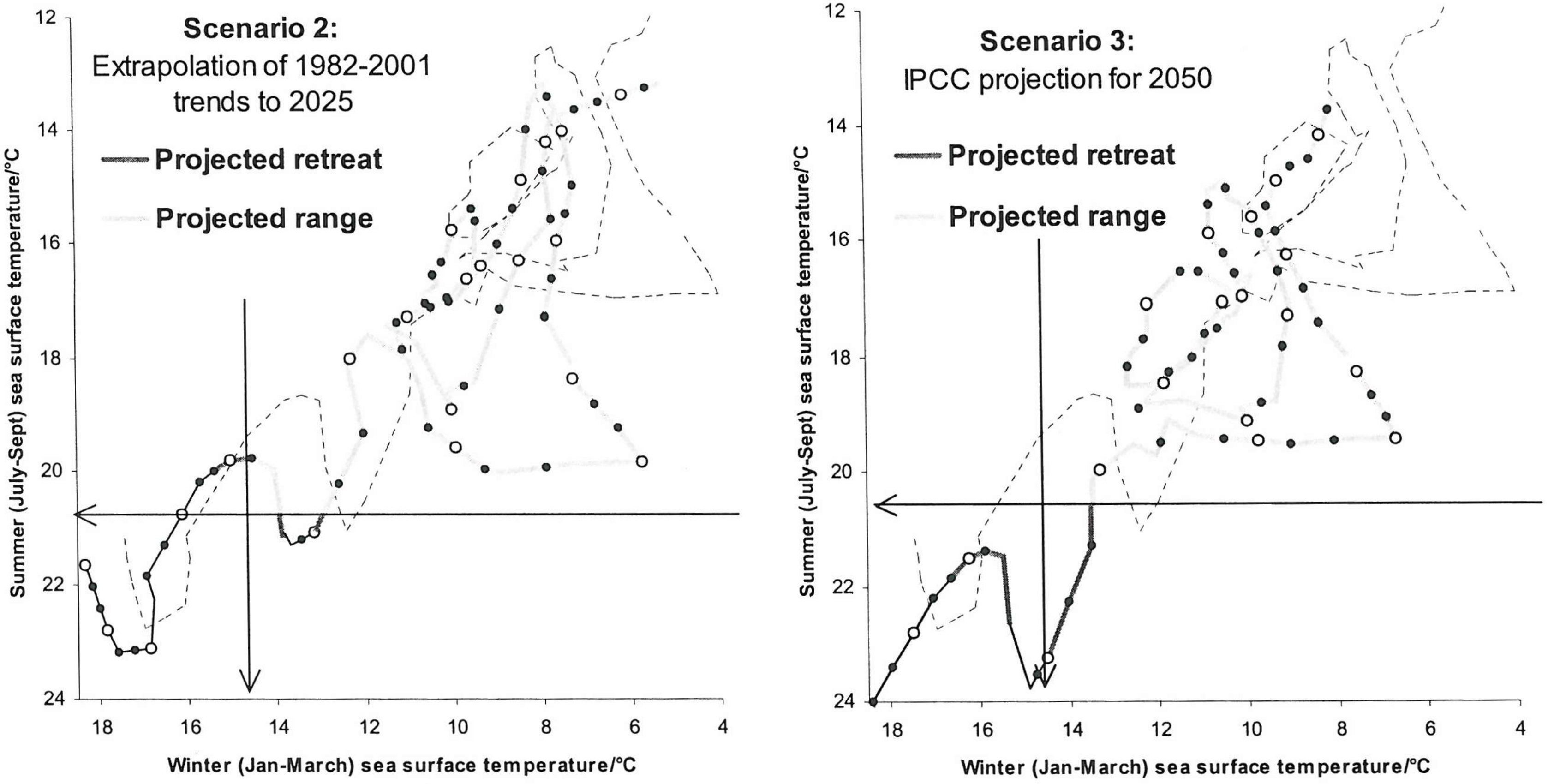


Figure 6.24 (continued). Graphical modelling of the temperature limits of *Semibalanus balanoides* (L.) and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

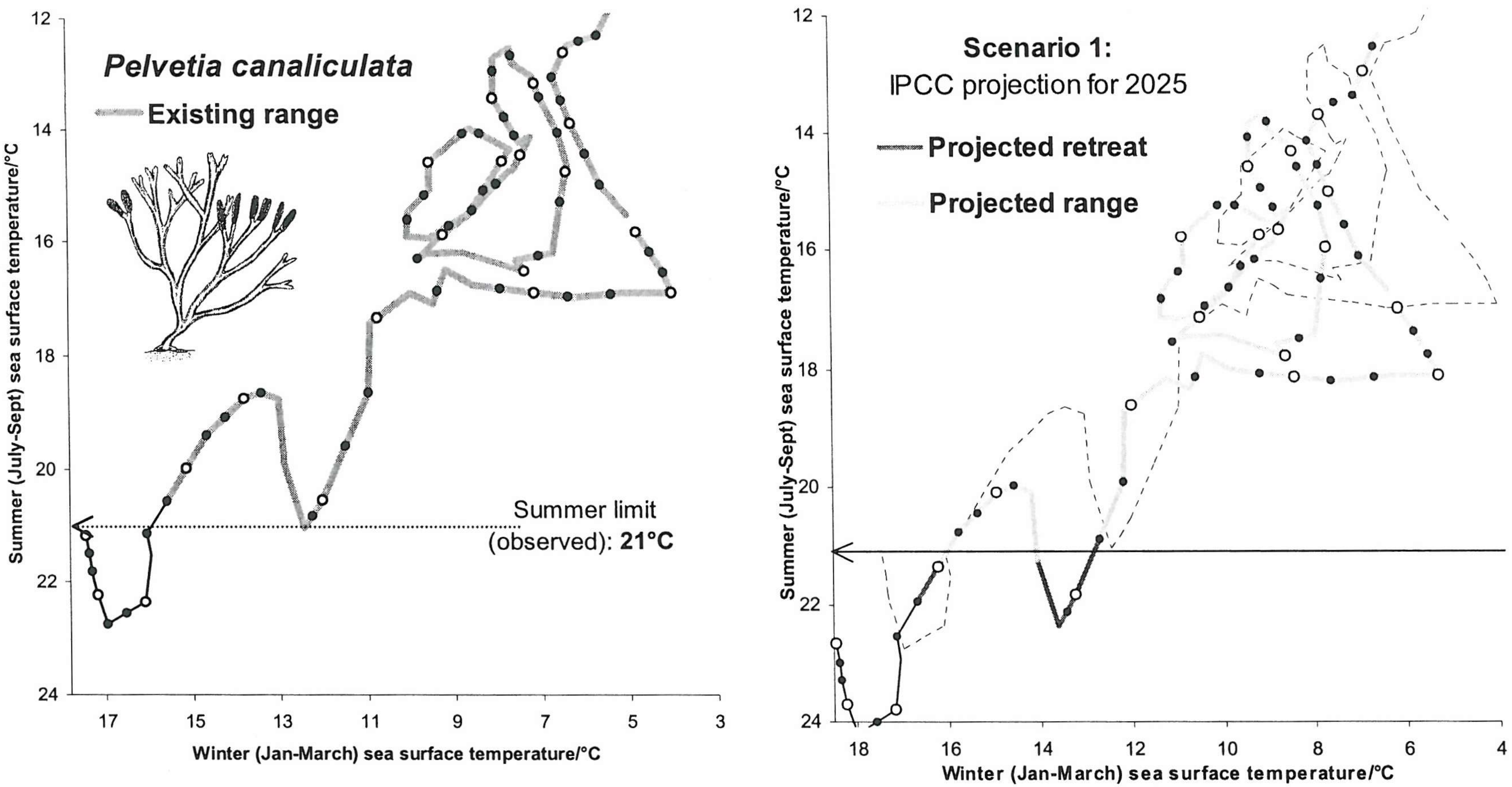


Figure 6.25. Graphical modelling of the temperature limits of *Pelvetia canaliculata* (L.) Decaisnet et Thuret and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

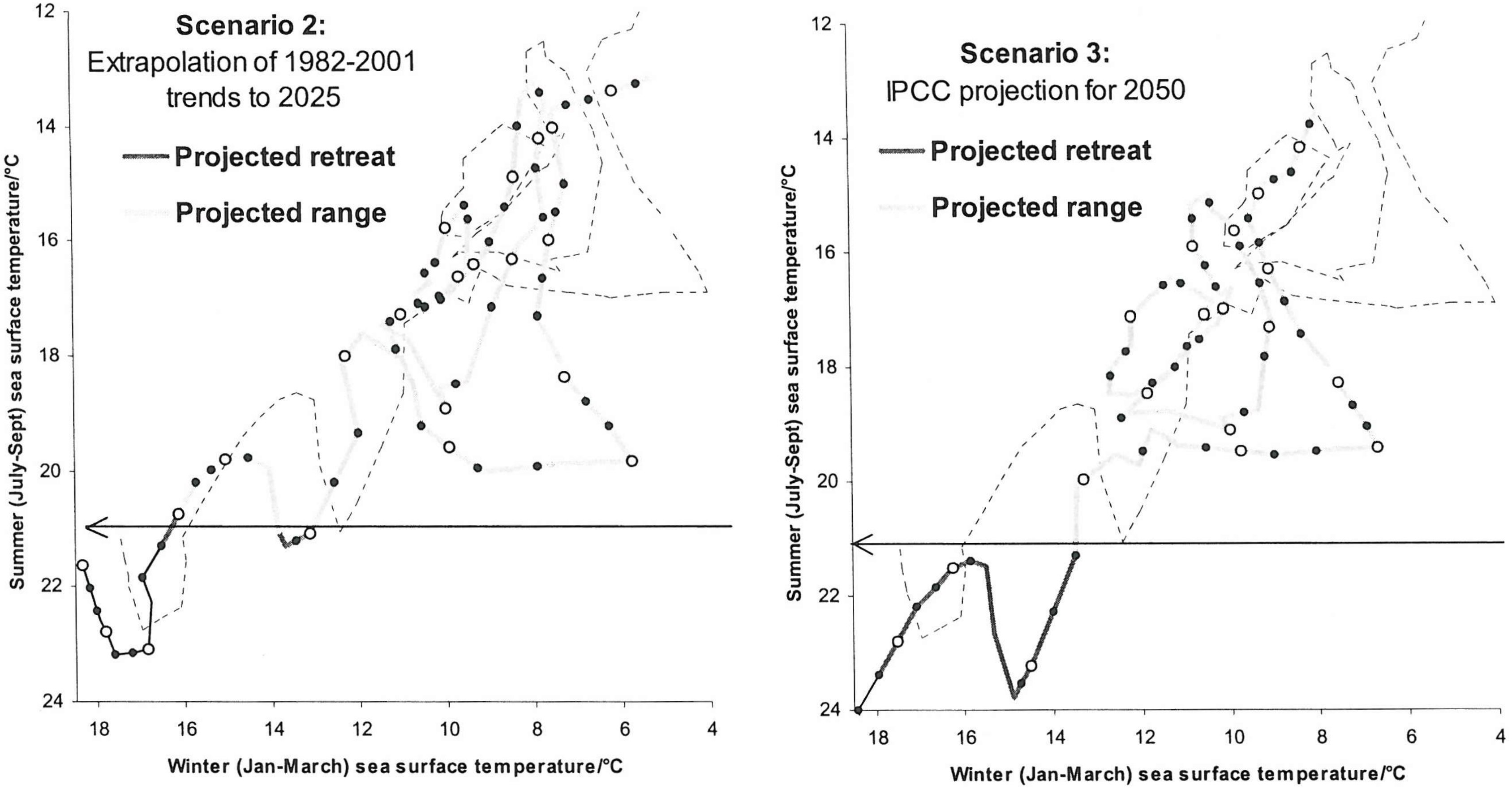


Figure 6.25 (continued). Graphical modelling of the temperature limits of *Pelvetia canaliculata* (L.) Decaisnet et Thuret and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

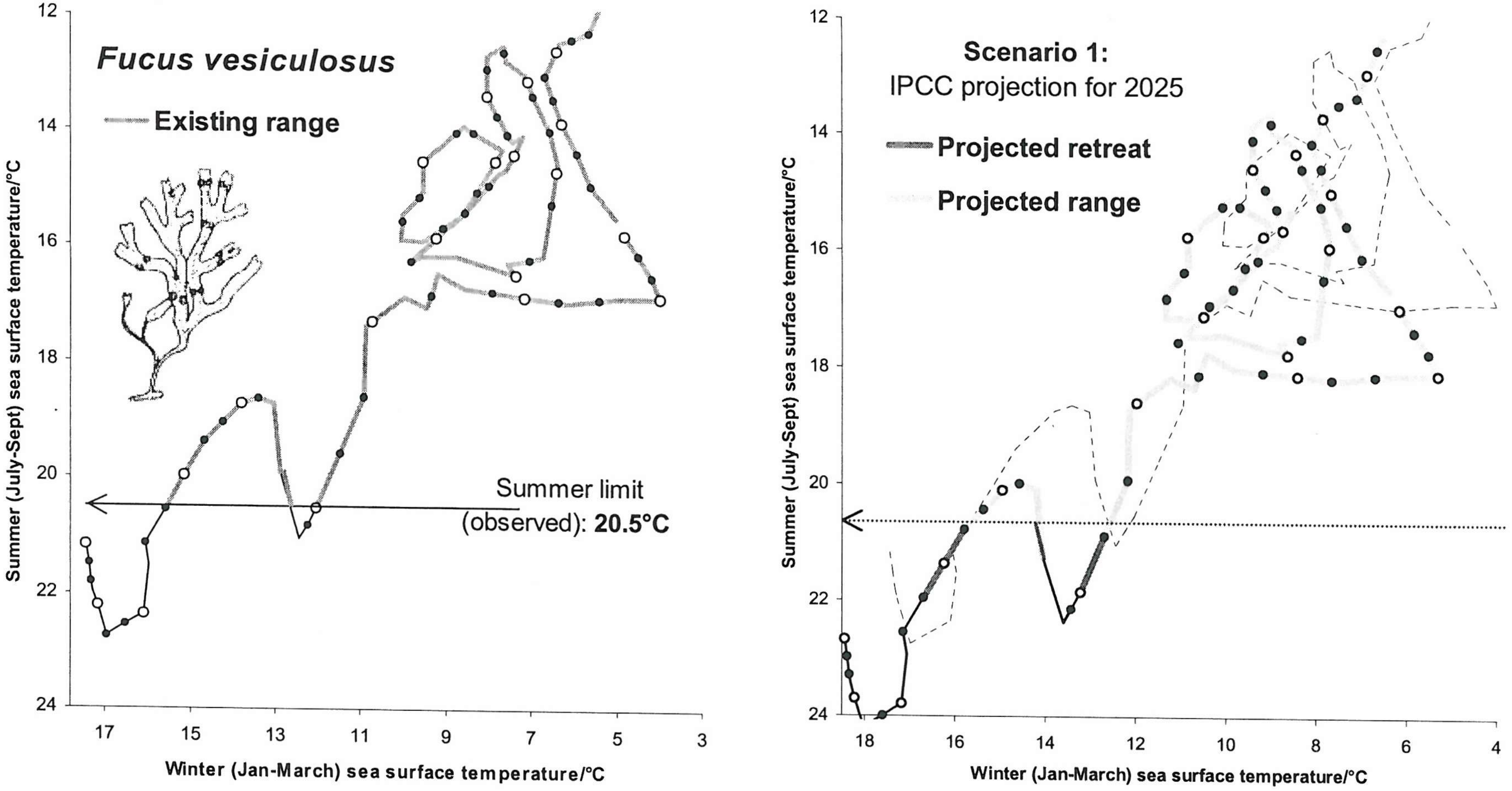


Figure 6.26. Graphical modelling of the temperature limits of *Fucus vesiculosus* L. and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

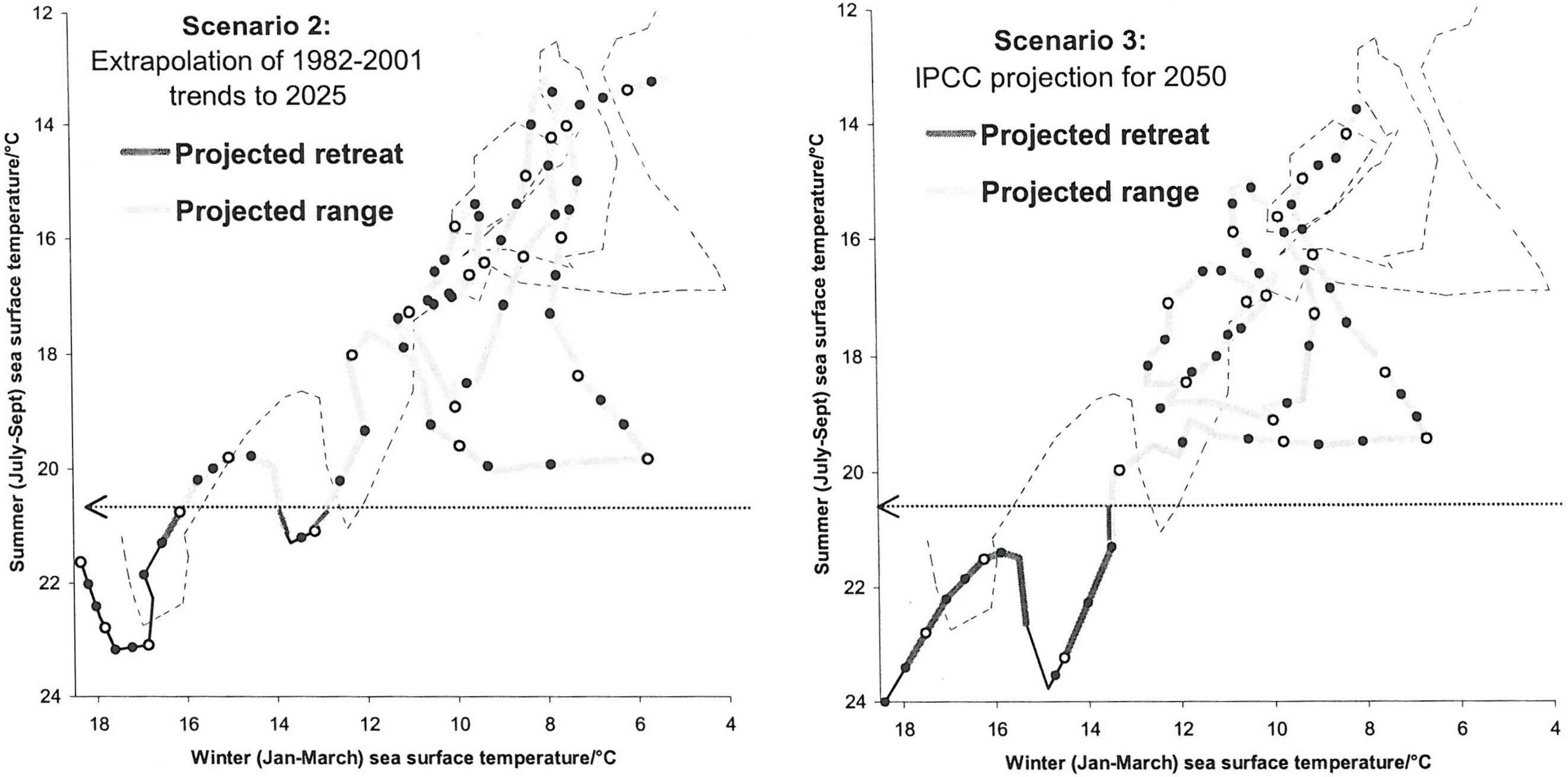


Figure 6.26 (continued). Graphical modelling of the temperature limits of *Fucus vesiculosus* L. and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

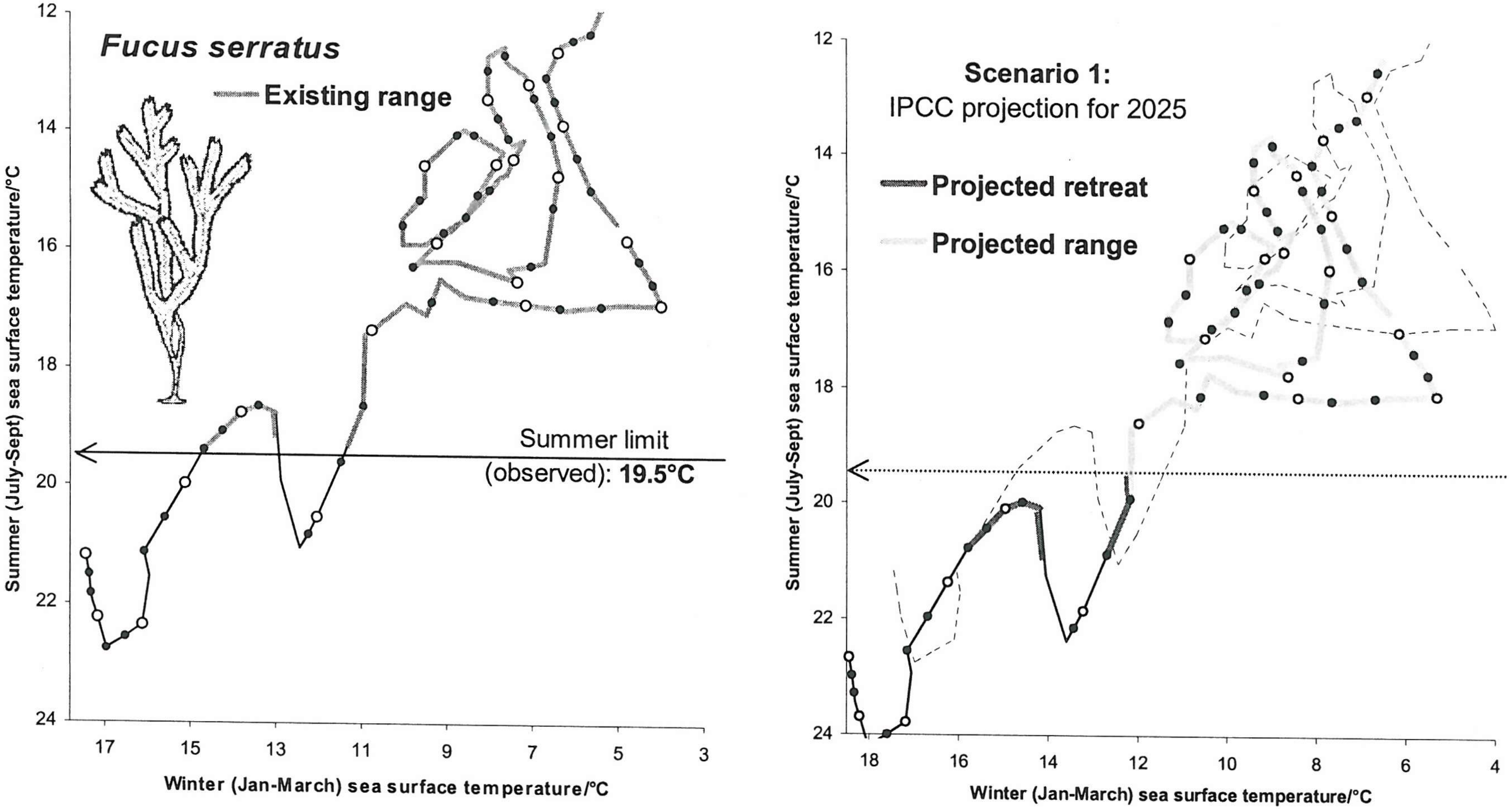


Figure 6.27. Graphical modelling of the temperature limits of *Fucus serratus* L. and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

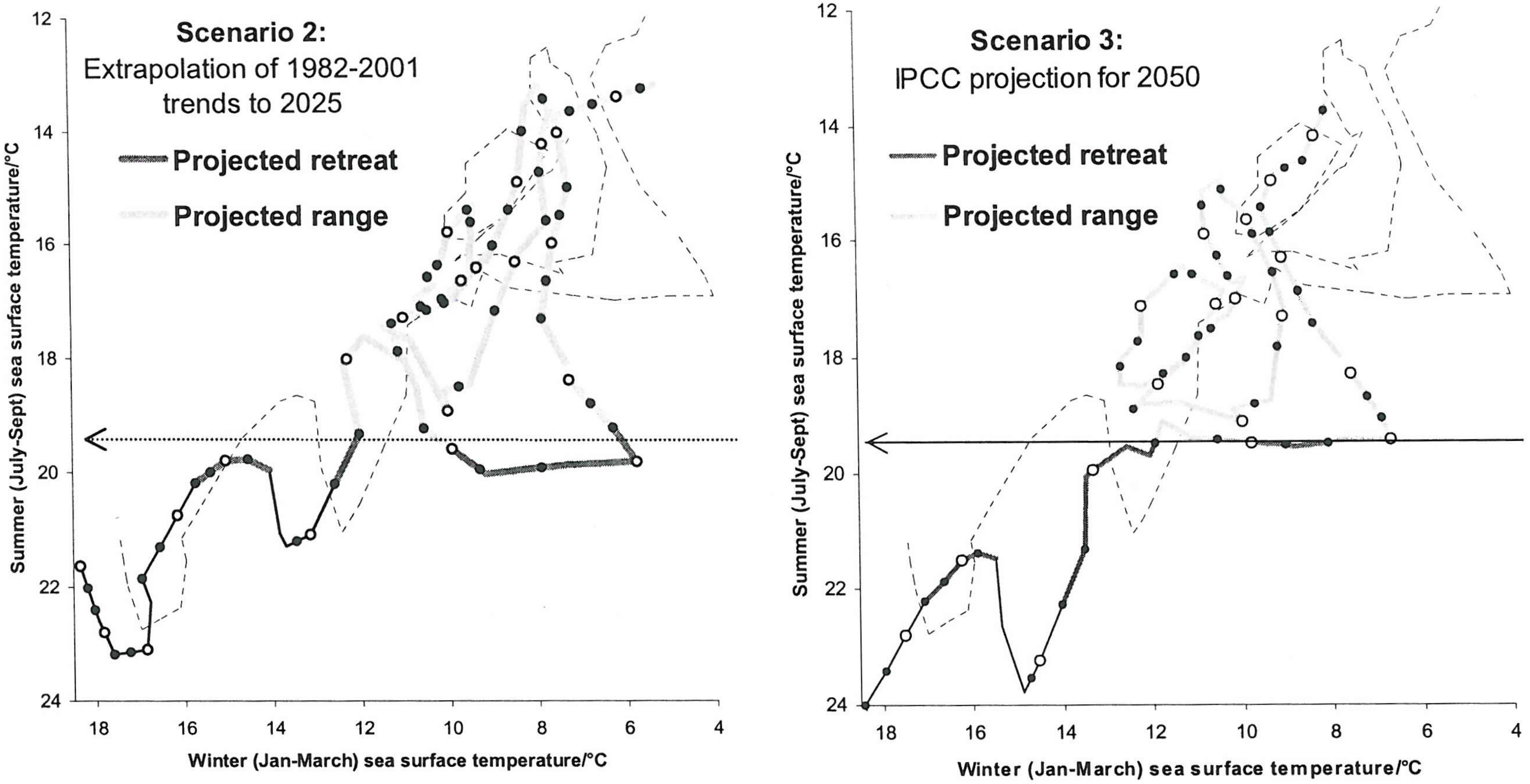


Figure 6.27 (continued). Graphical modelling of the temperature limits of *Fucus serratus* L. and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

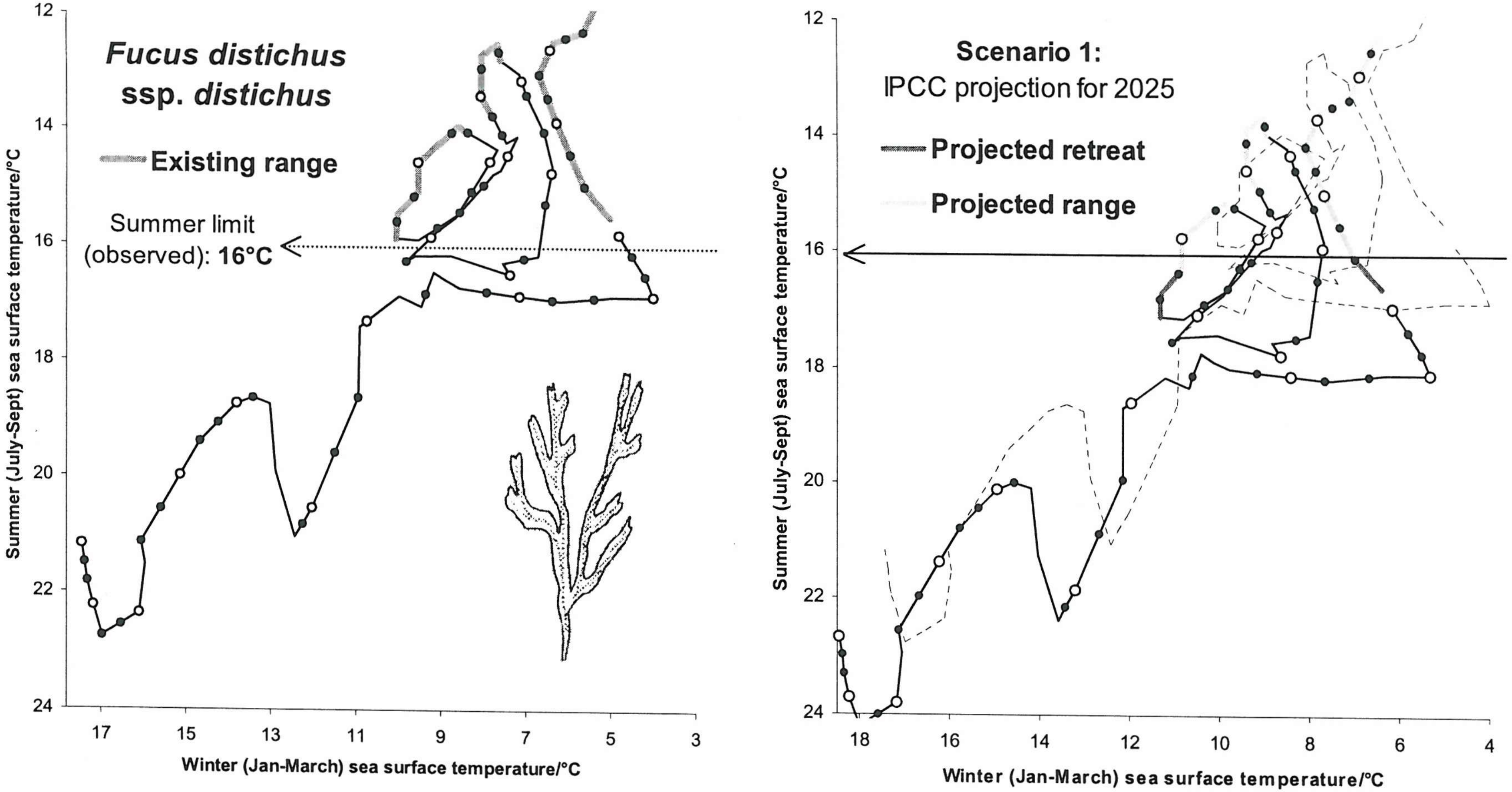


Figure 6.28. Graphical modelling of the temperature limits of *Fucus distichus* L. ssp. *distichus* and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

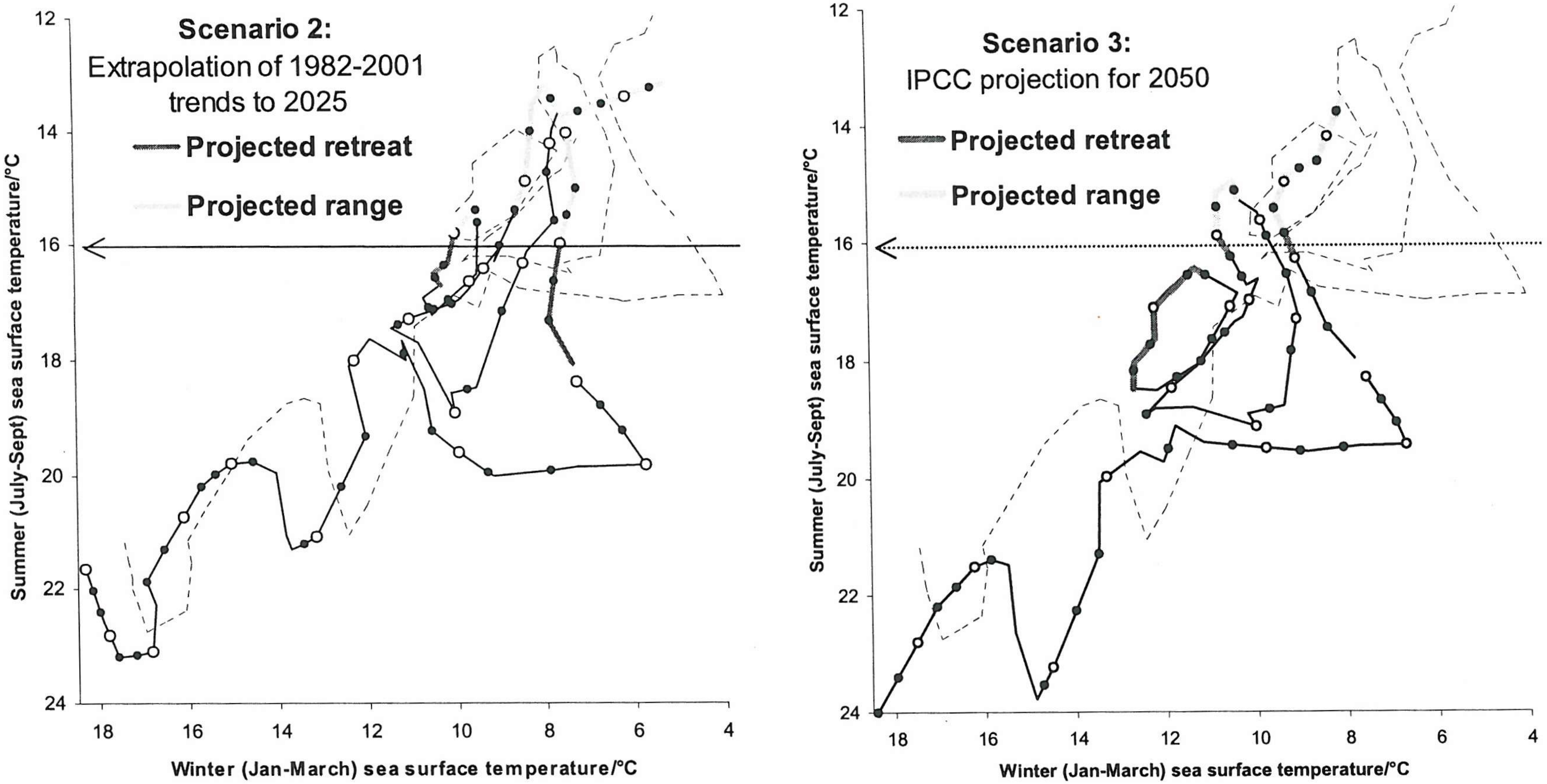


Figure 6.28 (continued). Graphical modelling of the temperature limits of *Fucus distichus* L. ssp. *distichus* and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

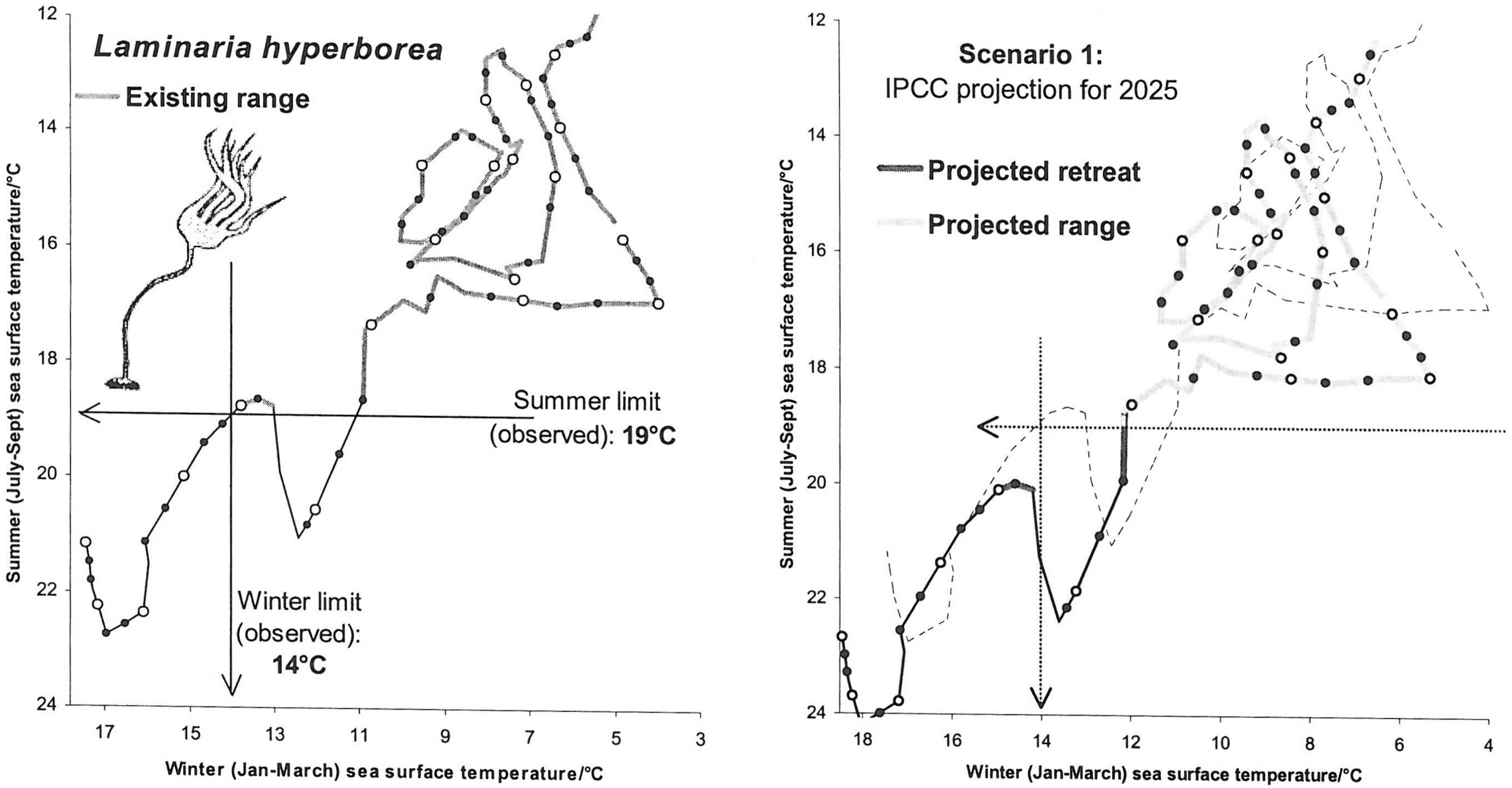


Figure 6.29. Graphical modelling of the temperature limits of *Laminaria hyperborea* (Gunnerus) Foslie and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

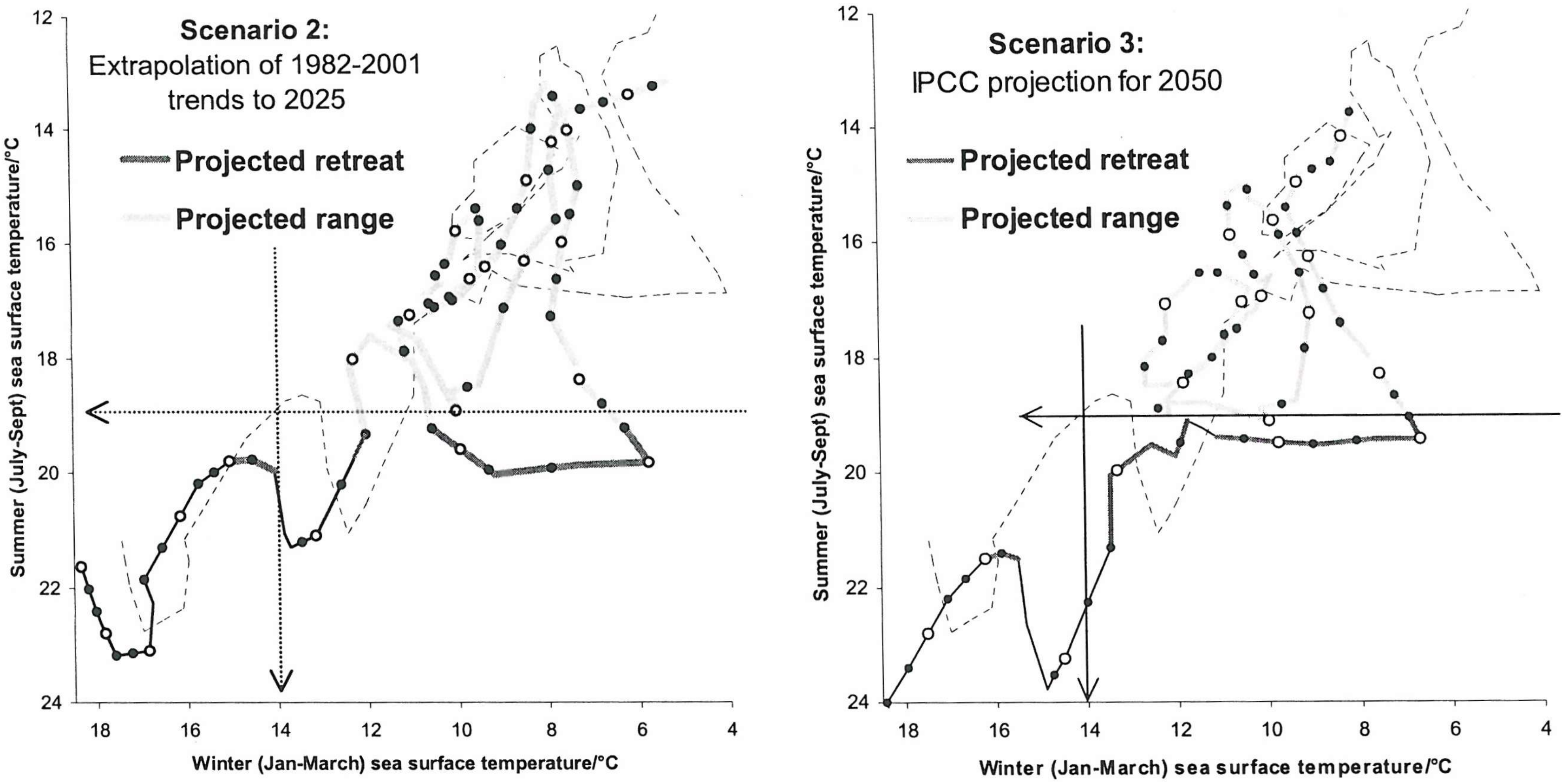


Figure 6.29 (continued). Graphical modelling of the temperature limits of *Laminaria hyperborea* (Gunnerus) Foslie and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

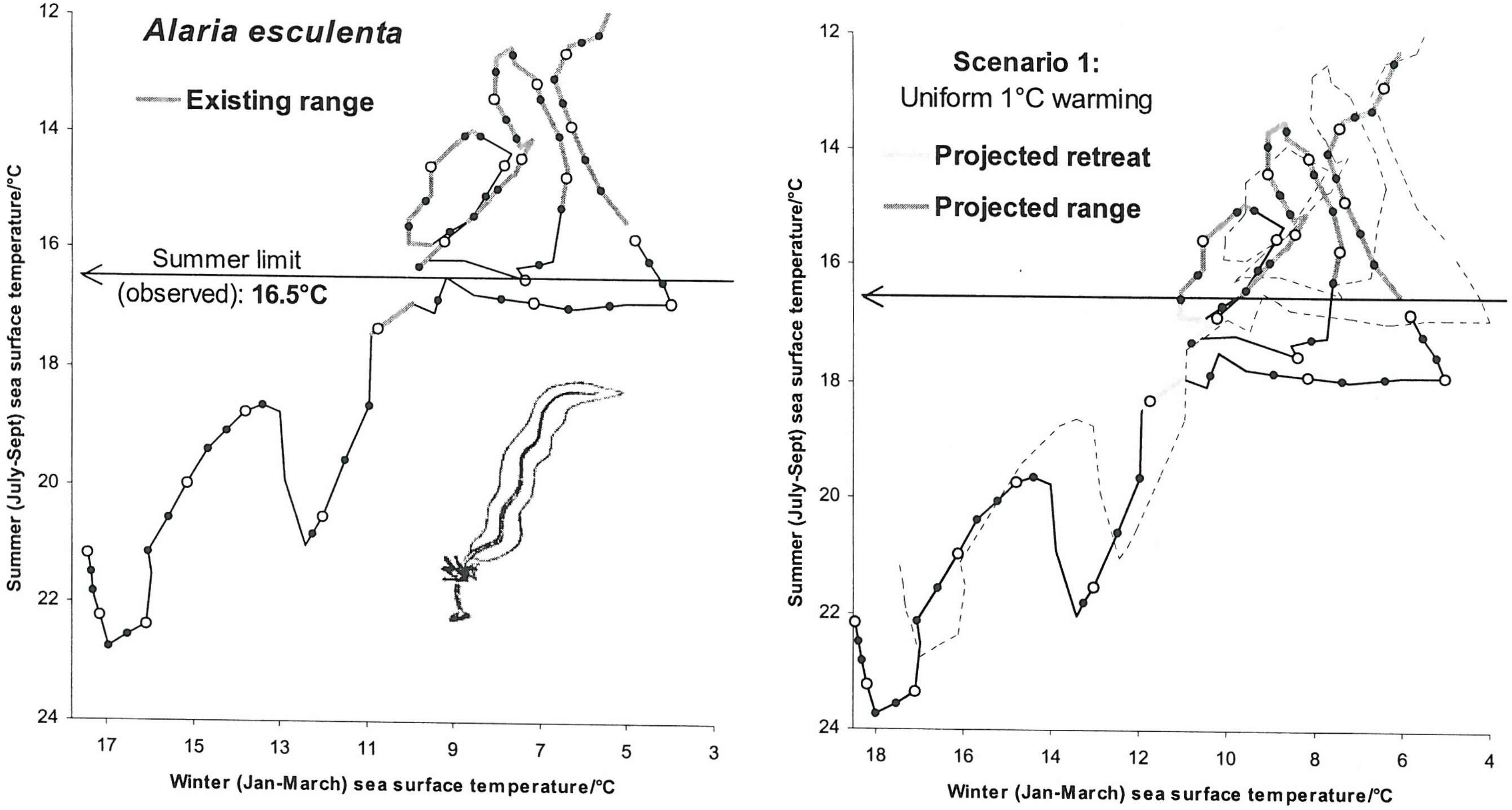


Figure 6.30. Graphical modelling of the temperature limits of *Alaria esculenta* (L.) Greville and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

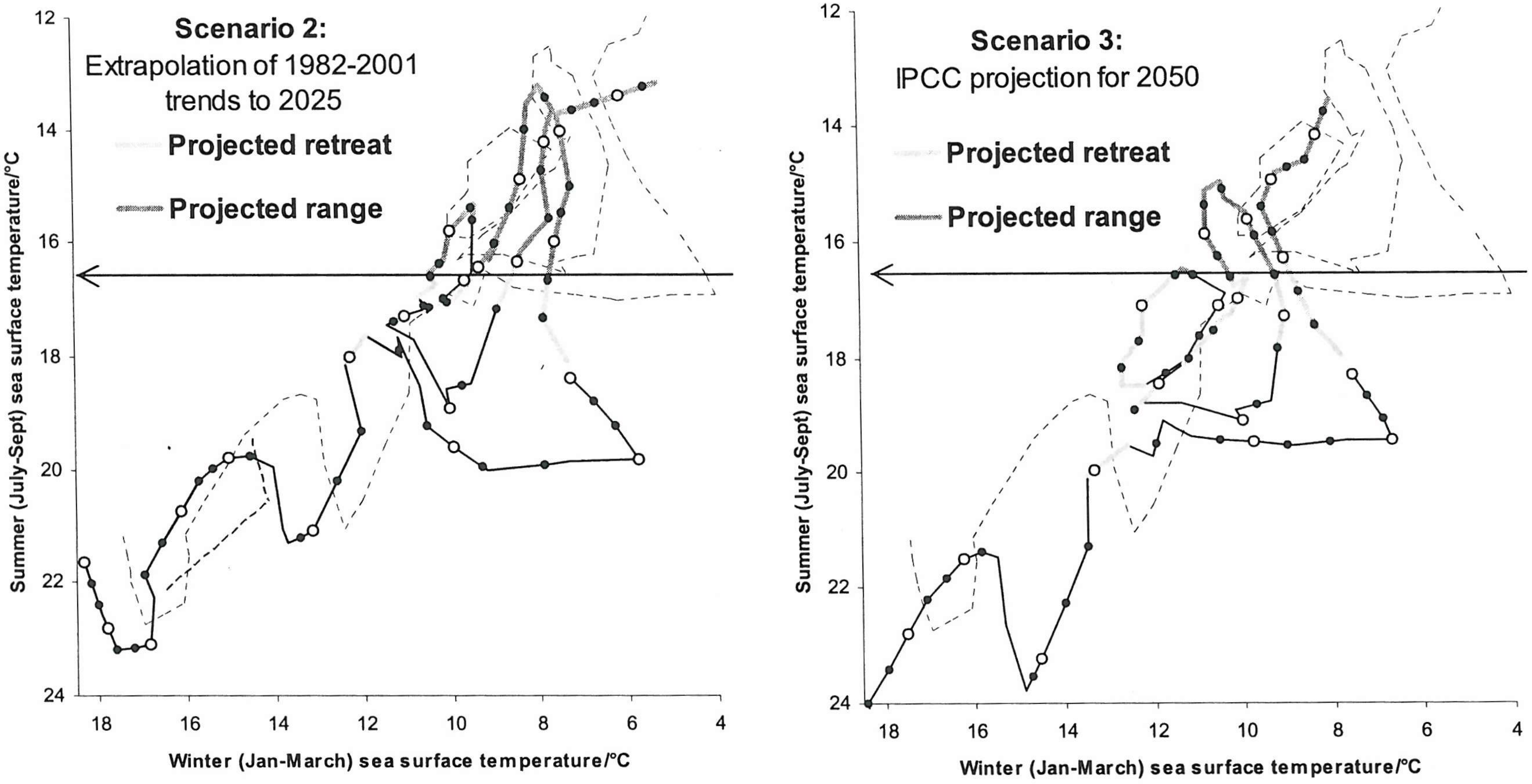


Figure 6.30 (continued). Graphical modelling of the temperature limits of *Alaria esculenta* (L.) Greville and its response to three climate change scenarios. Summer (July-Sept) sea surface temperature is plotted against winter (Jan-March) sea surface temperature for 62 points along the northeast Atlantic coast from 30°N to 67°N. Data are based on the Reynolds SST data set (NOAA-CIRES Climate Diagnostics Centre, 2003). Closed circles represent 1-degree intervals of latitude, open circles represent 3-degree intervals. Arrows represent the estimated summer and winter temperature limits for the species. Dashed curves give 1982-2001 temperatures for comparison with the climate scenarios. See §6.2.2 for explanation of the three scenarios.

Chapter 7: General Discussion

7.1. Overview

My thesis has examined the responses to variations in climate, in both space and time, of a set of rocky shore species within the Bay of Biscay. This is a region of biogeographical transition on rocky shores from northern, cold-temperate assemblages, typically dominated by canopy-forming brown algae, to southern, warm-temperate assemblages, dominated by grazers, filter-feeders and (on the lower shore) red algae, but with few species of brown algae (Sauvageau, 1897; Fischer-Piette, 1935, 1938, 1955a; Crisp and Fischer-Piette, 1959). Species are most sensitive to variations in climate near range edges (Crisp, 1964a; Southward et al., 1995; Lewis, 1984, 1996; Herbert et al., 2003), making this an ideal region in which to study the effects of climate on rocky shore species. I have focussed mainly on the effects of sea surface temperature, and concentrated my study on the north coast of Spain, which has an unusually sharp west-to-east spatial gradient in summer sea temperature (2°C in 500km).

The main aims of my thesis are to detect past effects and to predict future effects of climate change on ecosystems. Chapters 2 to 5 are concerned with detecting the effects of climate change on rocky shore species during the 20th century and understanding the mechanisms underlying these effects, while Chapter 6 makes forecasts of future biological responses.

This discussion chapter places my thesis in a broader context, and reflects on the lessons that can be drawn, both from the process of carrying out the study, and from its results. In §7.2, I discuss how the results presented in Chapters 2 through 5 have contributed to knowledge and understanding of rocky shore ecology. In §7.3, I consider the design and interpretation of studies of ecosystem response to climate change, in the light of my experience in carrying out this study and its limitations. The implications for forecasting the effects of climate change are then discussed. In §7.4, gaps in existing knowledge about rocky shore communities in the context of modelling the effects of climate change are identified. Finally, in §7.5, I propose some key questions for future study.

7.2. Ecological interpretation of the results of the study

Chapters 3, 4 and 5 studied the responses of rocky shore organisms to changes in climate over time, to large-scale spatial gradients of temperature, and to gradients of wave exposure and salinity in estuaries. Figure 7.1 summarises some of the key results, showing patterns that shed light on the ways in which environmental gradients and their interactions affect organisms, the mechanisms involved, and the implications for forecasting the effects of climate change.

The effects of the vertical (land–sea) gradient on rocky shore organisms are perhaps most clearly illustrated by the fucoid algae. In northern Europe, especially on sheltered shores where they are less subject to disturbance by wave action, unbroken fucoid canopies typically dominate the intertidal zone, with belts of different species forming patterns of vertical zonation (Lewis, 1964; Stephenson and Stephenson, 1971). This zonation is maintained by a combination of physical factors and biological interactions. Physical stress during emersion is the main factor preventing mid- and upper-shore species from extending their range upwards; on the upper shore physical stress alone is often sufficient to prevent upward expansion (Schonbeck and Norton, 1978; Hawkins and Hartnoll, 1985). On the lower shore, competition with the species directly above can also contribute to maintaining upper limits (Hawkins and Hartnoll, 1985). Competition is the main factor responsible for establishing the lower limits of fucoid algae on both upper and lower shore (Schonbeck and Norton, 1980). For rocky shore species in general, negative interactions such as competition, grazing (Underwood and Jernakoff, 1984; Jenkins *et al.,* 1999a, b) and predation (Paine, 1974) seem to play a more important role on the lower shore. Recent work has identified the importance of positive interactions such habitat generation and facilitation on the upper shore (Bertness, 1989; Bertness and Leonard, 1997). This follows the general principal in ecology that species in benign environments tend to follow more competitive strategies than those living under more hostile conditions (Grime, 1974).

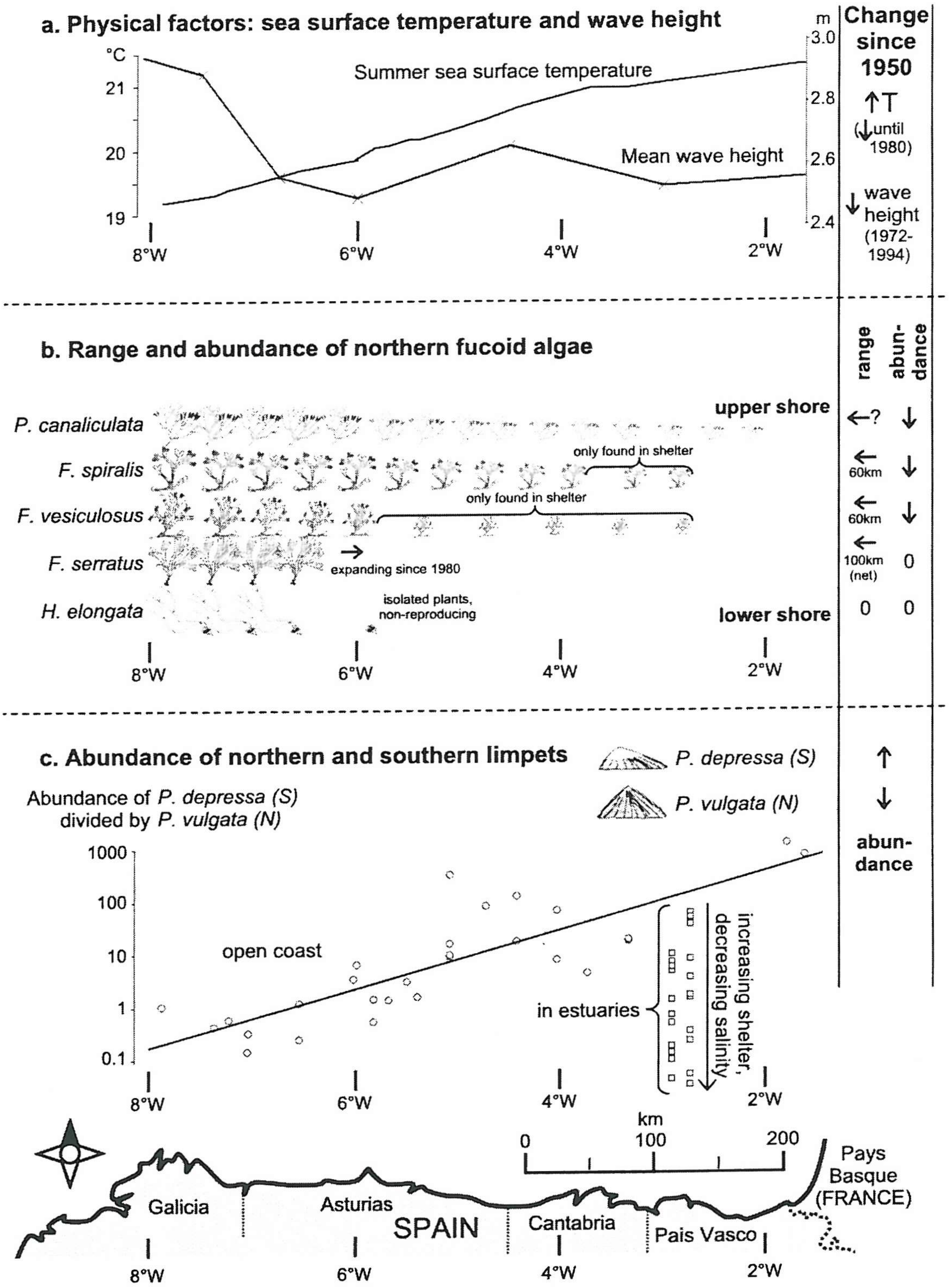


Figure 7.1. Synopsis of key results of thesis. All diagrams share the same x-axis, gradated in degrees longitude along the north coast of Spain. **(a)** Temperatures for 1999–2001 (Reynolds SST: NOAA-CIRES, 2003). Wave heights for 1972–94 (Puertos del Estado, 2003). Changes in T since 1950: see Ch. 2 for refs. **(b)** Species shown in order of vertical zonation. Species range on x-axis; broad-scale abundance patterns represented schematically by plant size. Data from my 2000–01 surveys (see Ch 3 for full distribution maps). Additional *F. serratus* data from Arrontes (2003). Changes since 1950: Fischer-Piette (1955a). **(c)** Ratio in abundance between *P. depressa* (southern) and *P. depressa* (northern). Circles are for sites on the open coast (my 2002 surveys: see Ch. 4). Squares are for the Plentzia and Mundaka Estuaries (my 2001 surveys: see Ch. 5). Changes since 1950 (open coast only): Fischer-Piette (1955a).

In this context, the results of Chapter 3 of my thesis provide further evidence of the differences between the upper and lower shore, as can be seen in Figure 7.1b. This figure shows the range and spatial patterns in the abundance of five species of northern fucoid algae on the north coast of Spain in 2000–01, and how these have changed since 1950. The species are shown in order of their vertical zonation on the shore. These results are seen in the context of the spatial gradient in summer sea temperature along the north coast (Figure 7.1a) and the variations in temperature since 1950: a cooling trend until about 1980, followed by warming, with the 1990s being exceptionally warm in both mean and maximum temperatures. (See Chapter 2 for detailed discussion of temperature and other climatic factors.)

Clear differences can be seen between the response to these variations in temperature of the three upper- and mid-shore species of northern fucoid algae (*Pelvetia canaliculata, Fucus spiralis, F. vesiculosus*) and those of the two lower-shore species (*Fucus serratus* and *Himanthalia elongata*). Another species of northern fucoid, *Ascophyllum nodosum,* is not considered. This species is found in northern Spain only in sheltered locations (Fischer-Piette, 1955a; see also §3.5.1.5); it is very long-lived, grows slowly, and reproduces vegetatively, explaining why it has not responded noticeably to changes in climate during the 20th century (see §3.5.1.5).

The upper- and mid-shore species all diminish progressively in abundance along the north coast from west (cold in summer) to east (warm in summer), with *F. spiralis* and *F. vesiculosus* being progressively restricted to sheltered habitats over the eastern part of their range. All three species were less abundant in 2000–01 compared with 1949 (Fischer-Piette, 1955a). Furthermore, the range limits of both species of *Fucus* have retreated on the open coast, by about 60km in each case, during the period of warming since 1980. The range limit of *Pelvetia canaliculata* may also have retreated, although the location of the limit is difficult to confirm in view of the exceeding rarity of *Pelvetia* in the inner Bay of Biscay. Thus it appears that mid- and especially upper-shore species are susceptible to local extinctions, likely to be caused by extreme high air temperatures.

In contrast, the two lower-shore species remain abundant even as they approach their range limits; neither species has changed noticeably in abundance since 1949; and their range limits do not move in ways that are predictably related to changes in temperature. *F. serratus* retreated substantially from 1949 to 1980 – a period of cooling – and has advanced again since then (Arrontes, 2003). The range limit of *Himanthalia elongata* has not moved since 1949, although it too now shows signs of a possible advance. In 2001 I found a few isolated plants of *Himanthalia* at Gijon, 80km beyond its previous range limit (these plants were not reproductively active, so this cannot be considered as a true range extension.) The lower-shore kelp *Saccorhiza polyschides* (not shown in Figure 7.1b) behaves similarly to the other two lower-shore species: it advanced substantially during the cool period of the late 1970s and early 1980s, but interestingly it has not retreated very much since then, so its range limit is now some 50km further east than it was in 1949.

Patterns of change on the west coast of France are less clear than on the north coast of Spain, because most species are limited not only by temperature but also by lack of rocky shore habitat south of the Gironde. Nonetheless, comparing distribution in 1954–55 (Crisp and Fischer-Piette, 1959) with 2001 (my survey; see Chapter 3), both *P. canaliculata* and *F. spiralis* have diminished in abundance. *F. vesiculosus* has diminished in abundance over much of its range and disappeared from the French Basque coast. *F. serratus* has disappeared from the Arcachon Basin, but otherwise there is little difference in the range or abundance of *F. serratus* or *H. elongata*.

Overall, then, the upper- and mid-shore species *P. canaliculata, F. spiralis* and *F. vesiculosus* have responded fairly predictably to spatial and temporal variations in temperature, showing changes in their abundance and range. The lower-shore species *F. serratus* and *H. elongata* have not. Even though temperature is clearly an important driving factor for these lower-shore species – high summer temperatures are almost certainly ultimately responsible for excluding them from the inner Bay of Biscay – they do not respond in a simple way to changes in temperature.

One explanation is that the direct effects of temperature on lower-shore species are more unpredictable. Widespread mortality of rocky shore organisms can be caused by extreme air temperatures coinciding with low tides (Helmuth *et al.,* 2002). Mortality due to high sea temperatures, on the other hand, is very unlikely to occur in the Bay of Biscay among the species studied; the highest daily sea temperature recorded at San Sebastian Aquarium (43.33°N, 2°W) between 1947 and 2001 was 25.3°C, and the August average was 21.5°C (Borja *et al.*, 2001), whereas *F. serratus* can survive a week in sea water at 25°C, and *F. spiralis* and *F. vesiculosus* at 28°C (Lüning, 1984).

In between episodes of mortality, therefore, lower-shore species are able to grow, reproduce and compete normally, so their abundance is typically high even close to their limits. In contrast, upper-shore species encounter sub-optimal temperatures regularly, and any change in temperature will have a direct impact on their ability to survive and reproduce. A caveat must be made, however: as they approach their southern limits, species tend to move further down the shore relative to tide levels (Fischer-Piette, 1955a; Crisp and Fischer-Piette, 1959; Lewis, 1986), which will modify the conditions they experience. This downward shift, no doubt, is partly a response to the increasing frequency of high temperatures, and partly an indirect effect of reduced competition from other species at lower levels on the shore. However, this tendency is limited; with the disappearance of lower-shore fucoids, lower shore levels do not become occupied by upper-shore fucoids, but by red algae.

Given that mortality due to extremes of temperature is reduced on the lower shore, other physical factors become relatively more important. The expansion of *Fucus serratus* since 1980, for example, may be connected with the downward trend in mean wave height on the north coast of Spain between 1972 and 1994, the period for which data are available (Puertos del Estado, 2003).

Biological interactions also become relatively more important on the lower shore (Connell, 1972; Paine, 1974; Hawkins *et al.*, 1992). Grazers, especially limpets, are the principal agent preventing fucoid algae from becoming established in cleared patches (Southward, 1964a; Hawkins, 1981; Hartnoll and Hawkins, 1985); they also prevent upshore expansion of red algae (in Portugal) and *Fucus serratus* (in the UK) (Boaventura *et al.*, 2002a). They may, therefore, also be important in determining whether lower-shore species are able to extend their range. As warmer temperatures increase the rate of limpet grazing (Thompson *et al.*, 2000; Jenkins *et al.*, 2001), they are also likely to indirectly limit range extension by lower-shore fucoids.

Thus the results of Chapter 3 support the hypothesis that on the upper shore, variations in temperature, particularly extreme temperatures, are directly responsible for changes in fucoid range and abundance; while on the lower shore, the effects of temperature are more indirect and unpredictable, and are modified by other physical factors and by biological interactions.

Chapters 4 and 5 investigated grazers, specifically the limpets *Patella depressa* (a southern species) and *P. vulgata* (a northern species). Some of the key results are summarised in Figure 7.1c, which shows the ratio of abundance between the two species (the abundance of *P. depressa* divided by that of *P. vulgata*) at sites along the north coast of Spain (see Chapter 4) and also in the Mundaka and Plentzia estuaries on the Basque coast (see Chapter 5). Log relative abundance of the two species at different sites on the open coast shows a strong correlation with summer sea surface temperature; fitting a regression line (see §4.3.1) predicts that an increase in summer temperatures of 0.71°C should lead to a tenfold increase in the abundance of *P. depressa* relative to *P. vulgata*. A similar relationship was found between relative abundance of these two species and spatial variations in summer temperature, but not winter temperature, in data collected in the English Channel in the 1950s (Crisp and Southward, 1958). Comparisons with distribution in 1949 (Fischer-Piette, 1955a) indicate that the abundance of *P. vulgata* has declined while that of *P. depressa* has increased.

On the Basque coast, where summer temperatures average over 21°C, *P. depressa* is overwhelmingly more abundant than *P. vulgata,* at least on the open coast. However, mapping the distribution of the two species in the Mundaka and Plentzia Estuaries showed that the relative abundance of *P. vulgata* compared to *P. depressa* increases with increasing distance upstream from the mouth of each estuary, until *P. vulgata* is the dominant species.

Understanding the mechanisms that maintain these similar patterns of species distribution across environmental gradients on very disparate spatial scales could contribute more generally to understanding the responses of species to spatial and temporal variations in climate. The results presented in Chapter 4 and 5 suggest that mortality caused by physical factors may be responsible for the patterns of distribution of the two species, both on the open coast and in estuaries. There are fewer large individuals (>25mm shell length) of both species, but especially *P. vulgata*, in areas with higher summer temperatures, implying higher heat-induced adult mortality in these areas. The translocation study carried out in the Mundaka estuary (Chapter 5), although not conclusive, suggests that increased mortality of *P. depressa* at sites further upstream may be a factor in maintaining the distribution pattern there.

However, mortality caused by environmental factors is unlikely to be the only cause. Competition for food resources is another process that could be involved in the maintenance of the patterns observed. Competition between *P. vulgata* and *P. depressa* is more intense in summer than winter, with effects on the growth of both species (Thompson *et al.*, 2000) and it is therefore to be expected that competition should be more intense in areas with higher temperatures. Studies near the southern limit of *P. vulgata* in Portugal (Boaventura *et al.,* 2002a, b) found that intraspecific competition between the two species was far stronger than interspecific competition, that both types of competition were symmetrical between species, and that *P. vulgata* had higher growth and survival than *P. depressa*. Thus, intraspecific competition, by reducing the effects of variations in recruitment, may help to maintain the balance between the two species and prevent competitive exclusion of one species. It is not likely, however, that interspecific competition limits the range of *P. vulgata* in Portugal nor that it is the principal mechanism maintaining the observed distribution of the two species in northern Spain.

7.3. Design and interpretation of studies of ecosystem response to climate change

This study had its limitations, in common with many ecological studies. Some of these limitations were due to gaps in existing knowledge and the availability of data, such as historical records on species distribution. Others were due to flaws in design or execution, or to time and logistical constraints. Problems, limitations and methodological issues relating to specific parts of the study have already been considered in previous chapters (see discussions in Chapters 3, 4 and 5). This section takes an overall view of the study and its constraints in order to present some general reflections on the design and interpretation of studies of the effects of climate change on ecosystems.

7.3.1. Design of studies: Duration, spatial scale and choice of variables

My thesis has studied the period from 1895 to 2050: from more than 100 years in the past to almost 50 years in the future. It has covered rocky shores from southern Brittany to southern Galicia, encompassing more than 1000 kilometres of coastline. Thus the scale of the study was broad in both space and time. Of course, records of species distribution were only available for certain years in the 20th century, and for a limited number of sites. This was one of the major limitations when trying to detect the effects of climate change, and one that must be considered in the design of future studies.

It has often been argued that extended time-series are essential in order to distinguish broad-scale trends from the natural variation to which all ecosystems, including rocky shores, are subject (Lewis, 1976, 1984, 1996; Southward *et al.*, 1995; Underwood, 1999). The standard 3–4 year funding cycle of ecological studies is far from sufficient to observe the range of natural variations in biological communities, such as those of the rocky shore (Lewis, 1976, 1984; Southward, 1995; Underwood, 1999; Hawkins *et al.*, 2002). This cultural short-termism has perhaps given rise to a sort of temporal myopia, leading some ecologists to describe five-year studies as "long-term" (e.g. Nogueira *et al.*, 1997; Jones *et al.*, 1998). Past long-term data sets that were collected for another purpose can sometimes be applied to the problem of detecting the effects of climate change (e.g. Ball, 1983; Hare and Mantua, 2000). Short-term studies separated by long time intervals (e.g. Barry *et al.*, 1995; Sagarin *et al.*, 1999; Middelboe and Sand-Jensen, 2000; see also Chapter 3) are better than nothing, and can help to make the most of patchy data, but they are not a satisfactory substitute for continuous long-term studies (Underwood, 1999).

For the above reasons, the importance of long-term ecological research has long been recognised by rocky shore ecologists (e.g. Lewis, 1976; Baxter *et al.*, 1985) and the priority given to it has increased in recent years (Southward, 1995; Southward *et al.*, 1995; Dye, 1998; Hawkins *et al.*, 2002) as it has in many other ecosystems (Woodward *et al.*, 1999; Vaughan *et al.*, 2001; Gosz, 2001; Greenland and Kittel, 2002; Hobbie, 2003; Hobbie *et al.*, 2003; Parr *et al.*, 2003). Unfortunately in many cases long-term studies suffer from problems such as insecurity of funding (Bennun, 2001), unclear or changing definition of aims or questions being addressed (Bennun, 2001), or lack of continuity of methods (Thomas, 1996).

The location and spatial scale of studies is another important consideration in the design of ecological studies, especially those that aim to detect ecosystem responses to climate change. Populations near species limits are likely to be more sensitive to climate change (Lewis, 1978, 1996). Therefore biogeographical boundary zones – areas where range limits of many species are found close together – are good places to study the effects of climate change (Allee, 1923; Southward, 1980, 1984; Southward *et al.*, 1995). The Bay of Biscay is such an area (Fischer-Piette, 1955, 1958; Crisp and Fischer-Piette, 1959; see also Chapter 1). Many range limits of rocky shore species are repeated in this region: many species reach limits in western France, northern Spain and western Portugal (the latter area was not covered in this study). The area over which these range limits occur thus influenced the spatial scale of the study.

Of course, the desire to cover a broad area has to be balanced by the need to collect data in sufficient detail so as to observe changes with confidence, as was discussed in Chapter 3. Furthermore, in order to reliably detect shifts in species range in response to climate change, it may not be sufficient to look at abundance at a particular location, even at range edges. Studies throughout the range of a species may be needed to distinguish range shifts from local changes in abundance, range expansions or contractions (Parmesan, 1996, 1999).

7.3.2. Choice and interpretation of biological variables and "indicators"

The choice of variables is equally critical to the successful detection of ecosystem responses to climate change (Lewis, 1976, 1978; Hawkins *et al.*, 1986; Keough and Quinn, 1991; Thomas, 1996; Bennun, 2001). It is important to select variables for study that have a known or suspected mechanistic relation with climate (Lewis, 1978; Keough and Quinn, 1991). If at all possible, these should also be relatively unaffected by other sources of variation (Hartnoll and Hawkins, 1980; Southward, 1991; Southward *et al.*, 1995). The results of the study are likely to have broader value if the variables chosen are of known ecological significance for the ecosystem as whole: for example, the abundance of so-called "keystone" species (Paine, 1974; Tegner and Dayton, 1991) or "ecosystem engineers" (Jones *et al.,* 1994). Monitoring of community-level ecosystem characteristics such as species diversity, which are costly to measure and which may have no clear causal link to climate or other environmental variables of interest, is not generally an effective approach (Keough and Quinn, 1991).

The choice of variables for study is linked with how these variables will be interpreted. My thesis has presented evidence that the fucoid algae *Pelvetia canaliculata, Fucus spiralis* and *F. vesiculosus*, (Chapter 3) and the limpets *Patella vulgata* and *P. depressa* (Chapter 4) respond more-or-less predictably to variations in temperature in both time and space. Many other studies have identified biological variables as being correlated with climatic variables, principally temperature. Often these biological variables have been described as "indicators" of climate change or its effects. Examples from marine systems of biological variables described as climatic indicators include the abundance of different species such as macroalgae (Fernandez *et al.*, 1988), benthic invertebrates (Garrabou *et al.*, 2002), marine mammals (Tynan and DeMaster, 1997), or zooplankton (Southward, 1984), as well as the overall species composition and diversity of assemblages of marine copepods (Beaugrand *et al.*, 2002a, 2002b) or fish (Jury *et al.*, 1997; Holbrook *et al.*, 1997). In terrestrial systems, biological variables that have been described as climatic indicators include the spatial distribution of different species, in particular the vertical distribution and altitude limits of trees (Kullman, 1998, 2001; Didier and Brun, 1998; Meshinev *et al.*, 2000) or insects (Whittaker and Tribe, 1996), as well as phenological variables based on the timing of biological events such as the flowering of locust trees (Walkovszky, 1998), olives (Osborne *et al.*, 2000), eucalypts (Keatley *et al.*, 2002) or herbaceous plants (Taylor and Garbary, 2003).

An indicator, by definition, is something that points to something else. In order for an indicator to be useful, the thing pointed to must be (a) of interest, and (b) more difficult to observe or measure directly. In the context of ecosystem responses to climate change, I would suggest that it is important to draw a distinction between two types of "indicator" variables. On the one hand, a biological variable that responds predictably to changes in a climatic variable (say, temperature) can be described as a "biological indicator of climate": for example, the timing of flowering in olive trees in southern Spain (Osborne *et al.*, 2000) is an indicator of temperature. On the other hand, a biological variable that responds to climate, but which also shows a correlation with other important biological variables (say, the species composition of the community as a whole), may be described as a "indicator of biological responses to climate" of these other variables. For example, the composition of copepod assemblages in the North Atlantic (Beaugrand *et al.*, 2002a, b) has been interpreted as an indicator of changes in the pelagic ecosystem as a whole.

The biological variables in the examples listed above are all indicators of changes in climate. However, not all of these studies have presented evidence to show that the ecological variables in question are also indicators of the effects of climate change on the ecosystem as a whole, which is clearly a stronger result. The use of the generic term "indicator" thus has the potential to create confusion.

In the present study, the range and abundance on the north coast of Spain of the brown algae *Pelvetia canaliculata, Fucus spiralis* and *F. vesiculosus* (Chapter 3), can plausibly be described as an indicator of the effects of climate change on rocky shore communities as a whole. The species studied are among the most important canopy-forming intertidal macroalgae, which play a dominant ecological role in structuring rocky shore communities (Lewis, 1964) affecting processes such as larval settlement (Jenkins *et al.*, 1999b), provision of shelter (Bertness *et al.*, 1999), and grazing (Jenkins *et al.*, 1999a). They are thus partly responsible for differences between cold-temperate and warm-temperate rocky shore communities in overall structure (Ballantine, 1961b) and species composition (Fischer-Piette, 1955, 1958, 1963; Crisp and Southward, 1958; Crisp and Fischer-Piette, 1959; Hoek and Doenze, 1967; Hoek, 1975).

By contrast, spatial variations in the relative abundance of the limpets *Patella vulgata* and *P. depressa* on the north coast of Spain (Chapter 4) may be a better indicator of temperature than the abundance of brown algae, in the sense of being more closely correlated with it – although it is not possible to draw this conclusion with certainty because of a lack of comparable data. However, both species of *Patella* play a similar ecological role as grazers on rocky shores (Hawkins *et al.* 1989a,b), so a shift in dominance from one species to the other is unlikely to have a critical effect on the overall structure of rocky shore communities. Thus it may not necessarily be accurate to describe the relative abundance of limpets as an indicator of the effects of climate change on rocky shore communities as a whole. This does not mean to say that the relative abundance of *Patella vulgata* and *P. depressa* is unimportant as a biological variable. It is an easily measured variable and can be monitored economically over long periods of time (Southward *et al.*, 1995), and may predict the responses of other less easily quantified species (e.g. isopods or amphipods) that are likely to respond in similar ways. Its value as an indicator of climate has been shown in studies of prehistoric shell middens (Ortea, 1986; Southward *et al.*, 1995) and it may also help to elucidate the mechanisms governing the response of these two species to environmental gradients, with broader lessons for rocky shore ecology (see Chapter 4).

7.3.3. Analysis of studies based on the "climate envelope" model

As the result of anthropogenic climate change, biological communities all over the planet, including rocky shores, are being subjected to climatic conditions that are unprecedented in recent history. The question facing ecologists, including those working on rocky shores, is this: to what extent does our understanding of communities allow us to make robust predictions about how they will respond to these new conditions?

Even with the best-designed studies, it will rarely be possible to draw firm conclusions about the effects of climate change on ecosystems. Therefore, in order to build a strong case that climate change is having detectable impacts on natural systems, comparisons have been made (Walther *et al.*, 2002; Parmesan and Yohe, 2003) across studies of large numbers (circa 1700) of species, including rocky shore invertebrates (Southward *et al.*, 1995; Sagarin *et al.*, 1999), butterflies (Parmesan, 1999), birds (Thomas and Lennon, 1999) and plants (Grabherr *et al.*, 1994; Fitter and Fitter, 2002), in many different ecosystems.

Overall, most authors conclude that an overall, globally coherent and highly statistically significant pattern of climate change effects on ecosystems has been observed since about 1960 (Walther *et al.*, 2002; Parmesan and Yohe, 2003). This pattern includes spatial shifts in range of species averaging approximately 6.1 km per decade polewards (95% confidence limits of 1.26–10.87 km) and 6.1 m per decade upwards (in altitude). Advances in the timing of spring events of 2.3 days per decade (95% confidence limits of 1.74–3.23) have also been observed (Parmesan and Yohe, 2003). These figures are headline approximations for expressing the overall global pattern of change in a way that can be easily understood. Without detracting from the importance of these results, however, I would suggest that the same data could be analysed in a way that might enable more rigorous and significant conclusions to be drawn.

The vast majority of the studies included in the meta-analysis by Walther *et al.* (2002) and Parmesan and Yohe (2003) are based on the "climate envelope" model of ecosystem response to climate change (Davis *et al.*, 1998b; Walther *et al.*, 2002). A few studies cited by Walther *et al.* (2002) that are based on analysis of species interactions, are excluded from the present discussion, and do not contribute to the global averages given above.

The "climate envelope" model (Davis *et al.* 1988a,b) assumes, in effect, that ecological phenomena (such as species range limits or phenological events) occur at a position in time and space that is essentially determined by the climatic conditions, primarily temperature, at that point. Thus, for example, a plant might flower when the maximum daily temperature reached 20°C, say, no matter whether this occurred on 1 March or 30 April.

Implicitly, the meta-analysis carried out by Walther *et al.* (2002) and Parmesan and Yohe (2003) tests the validity of this "climate envelope" model against the null hypothesis that climate change has had no observable effect on ecosystems. In effect, the null hypothesis is rejected. There is, clearly, a detectable effect of climate, which, moreover, is in the direction that would be expected due to climate change. This meta-analysis was made by comparing the rate of movement along a physical axis in space or time (latitude, altitude, or date) of particular phenomena, with the average global rate of isotherm movement along the same axis. Thus, for example, the average global upward (altitudinal) shift in isotherms is cited as 8–10 m per decade (Walther *et al.*, 2002), and the rate of change in phenomena such as the altitude limits of mountain plants (Grabherr *et al.*, 1994) has been compared with this average.

The implicit assumption is that relationships of temperature (the main climatic variable considered) with latitude, altitude, date within the year, and year (within the four-decade time period studied), are all straight lines with globally homogeneous gradients. This assumption is far from being true, as can clearly be seen by looking, for example, at spatial variations in temperature on rocky shores. Sea surface temperatures along the west coast of Europe do not by any means conform to a simple temperature-latitude relationship (see Chapter 6). A 0.5°C increase in mean seasonal temperatures, in different areas, can be equivalent to moving along the coast some 100km south (e.g. west coast of Norway in summer) or 200km north (e.g. west coast of Norway in winter), 100km east (e.g. north coast of Spain in summer) or 250km west (e.g. north coast of Spain in winter). In another region, the west coast of North America, the extremes of temperature likely to be experienced by rocky shore organisms are determined by the interaction between seasonal, diurnal and tidal cycles, and over a large area are in practice almost independent of latitude (Helmuth *et al.*, 2002). Equally, while long-term variations in temperature may be correlated more-or-less closely to the global average rate of warming, they include considerable year-to-year and regional variations (see Chapter 2 for data from the Bay of Biscay area) that introduce another source of extraneous variation.

In Chapter 6, I argued that the climate envelope model is one whose essential axes are of climatic variables, not space or time. Therefore, the best approach to testing the climate envelope model is to compare the temperatures (or other relevant climatic variables) at which given phenomena occur, not the positions or dates. By transforming data from axes of space and time to axes of temperature, the main climatic variable, it should be possible to test the validity of the "climate envelope" model. This also allows identification of time lags and spatial correlations for particular phenomena. Estimates can be made of the extent to which changes in phenomena diverge from the predictions of the model, giving an idea of the extent to which other factors should be taken into consideration to modify this simplistic model.

For example, the relative abundance of warm- and cold-water barnacle species on rocky shores in southwest Britain over the past fifty years (Southward and Crisp, 1954, 1956; Southward, 1967, 1980, 1983, 1991; Southward *et al.*, 1975, 1995) can be shown to be correlated with sea surface temperature. The best correlations are found with offshore (Bay of Biscay) temperatures with a time lag of two years (corresponding to the time lag between the onset of reproduction in successive generations). This implies that the main influence of climate on these species is on reproductive output, survival of planktonic larval stages, and subsequent recruitment.

Seasonally lagged correlations also show that abundance of *Semibalanus balanoides* is negatively correlated with warm spring temperatures, while abundance of *Chthamalus* spp. is positively, but less strongly correlated. This is currently being interpreted as an indirect effect of temperature on the interactions between the species (Hawkins, pers. comm., based on unpublished data of Southward, Burrows and Hawkins).

The climate envelope model is both widely used in detecting and predicting ecosystem responses to climate change (see reviews by Walther *et al.*, 2002; Gitay *et al.*, 2002; Parmesan and Yohe, 2003), and widely criticised as being limited and simplistic (Davis *et al.*, 1998a, 1998b; see also Chapter 1). The model as it stands does not take into account the effects of factors such as dispersal (Gaylord and Gaines, 2000), species interactions (Davis *et al.*, 1998a, 1998b; Sanford, 1999; Fox and Morin, 2001), loss and fragmentation of habitat (Warren *et al.*, 2001) or climate-related disturbances, for example fire (Flannigan *et al.*, 2000). However, rather than being accepted or rejected as such, the climate envelope model should perhaps be seen as a basic model that can be tested and refined, and then extended and adapted to particular situations by introducing ecosystem-specific elements such as extreme events, habitat availability, disturbance, dispersal and species interactions. In order to model such elements, detailed knowledge of the mechanisms governing ecosystem responses to climate is necessary. However, this is difficult to achieve, given the complexity of ecosystems, the amount that there is to be known about them, and the limited resources available. Ecologists are, as it were, standing on the rocky shore of knowledge, looking out across an ocean of ignorance. Nonetheless, while precise prediction may not be possible, approximate forecasts can be made, tested and refined, and key gaps in knowledge can be identified and filled.

The next section looks at gaps in existing knowledge and understanding of the responses of rocky shore communities to climate, and about climate itself, that are likely to limit the accuracy of models.

7.4. Gaps in knowledge and understanding of ecosystem responses to climate

Rocky shore communities, particularly those of temperate zones, have been studied extensively for a long time (Baker, 1909; Lewis, 1964; Stephenson and Stephenson, 1971; Newell, 1979; Ricketts *et al.,* 1985; Little and Kitching, 1996; Raffaelli and Hawkins, 1999). They have often been used as a tractable model system for experimental studies contributing to general ecological theory (Connell, 1972; Paine, 1977; Underwood, 2000). Their biology and ecology are therefore probably as well understood as any marine ecosystem. Nonetheless, I would argue that there are significant gaps in knowledge that need to be addressed in order to successfully model the response of these communities to climate change.

Detailed studies have been made of the effects of temperature on some common species, including its effects at the individual level such as reproduction (Orton, 1920; Barnes, 1963; Barnes and Barnes, 1975), photosynthesis (Davison, 1987; Pfetzing *et al.*, 2000), respiration (Sandison, 1967), feeding (Southward, 1964b), growth (Lough and Gonor, 1973; Moss and Sheader, 1975; Bolton and Lüning, 1982; Stromgren, 1983; Davison, 1987; Sjotun *et al.*, 1996; Pfetzing *et al.*, 2000; Sanford, 2002a), morphology (Kalvas and Kautsky, 1998), and physiological tolerances (Evans, 1948; Sandison, 1967; Foster, 1969; Newell *et al.*, 1971; Cornelius, 1972; Bolton and Lüning, 1982; Todd and Lewis, 1984; Yarish *et al.*, 1987; Gerard and Du Bois, 1988; Wiencke *et al.*, 1994; Gaston and Spicer, 1995; Pakker and Breeman, 1996). In other cases, the relationship between biological processes and temperature has been inferred from studies of geographical variation (Allee, 1923; Hutchins, 1947; Lewis *et al.*, 1982; Bowman and Lewis, 1986; Lewis, 1986; Kendall and Lewis, 1987; see also Chapters 4 and 5 of this thesis). However, there are still major gaps in knowledge. The thermal biology of many common species has not been studied for important parts of their life cycles.

Also, the actual temperatures experienced by rocky shore organisms can differ widely from those recorded at nearby weather stations. Ambient temperatures on the rocky shore are affected by local factors as well as the interaction of tidal, diurnal and seasonal cycles (Denny and Paine, 1998; Helmuth *et al.*, 2002). Height on the shore (Broekhuysen, 1940; Schonbeck and Norton, 1978, 1980; Helmuth, 2002) and probably also local topography can have profound effects on the temperature regime. In addition, body temperatures of intertidal organisms can differ widely from local ambient temperatures, especially during emersion (Southward, 1958; Davies, 1970; Helmuth, 1999, 2002). Thus knowledge of the thermal requirements of life processes may be difficult to translate into robust predictions of the responses of intertidal species to climate change.

Another important source of uncertainty is the effect of temperature on interactions within rocky shore communities. Processes that have been shown to be significantly affected by temperature include predation of mussels by sea stars (Sanford, 1999, 2002a,b), grazing of algae by limpets (Thompson *et al.*, 2000; Jenkins *et al.*, 2001; Boaventura *et al.*, 2002a,b), and protective shading of barnacles by algal canopies (Hawkins, 1983; Jenkins *et al.*, 1999c; Bertness *et al.*, 1999). In the first two cases the interaction is crucial to structuring the community in question (Sanford, 1999; Jenkins *et al.*, 1999a). Doubtless many other examples exist of interactions that are affected by temperature but which have not yet been studied.

Thus there are major uncertainties and gaps in knowledge about the effects of temperature on rocky shore species and their interactions. Other important variables whose effects on rocky shore communities are not comprehensively understood include wave action (Ballantine, 1961a; Denny, 1995), coastal upwelling (Sverdrup, 1938; Richards, 1981; McQuaid and Branch, 1984; Sakko, 1998), ocean currents (Connolly and Roughgarden, 1998) and tidal fronts (Crisp, 1989). All of these variables are likely to be affected by climate change.

Certain other aspects of the biology of rocky shore species also need further investigation. In particular, there is little knowledge of the dispersal rates or maximum dispersal distances of different species. Studies of the spread of the Australian barnacle *Elminius modestus* (Crisp, 1958; Barnes and Barnes, 1965), which arrived in Europe in the 1940s, indicate that its dispersal is based on two mechanisms: dispersal along the coast at a rate of some 20–30 km per year, and remote dispersal via ships. Macroalgae are known to be able to disperse by floating hundreds or thousands of kilometres in their adult stage (Hoek, 1987; Santelices, 1990; Norton, 1992). Dispersal of macroalgae by micropropagules is much less well understood (Santelices, 1990) although in some species it is believed to take place only across relatively small distances (Johnson and Brawley, 1998).

The maximum distance of dispersal of most invertebrate species is unknown, although it can sometimes be inferred. For example the absence of *Patella depressa* and *Balanus perforatus* from Ireland (although present in southwest Wales), and *Gibbula pennanti* from Britain (although present in Normandy) (Southward *et al.*, 1995), suggest upper bounds of about 80–100km for the maximum dispersal distances of these species. Factors such as currents (Gaines and Roughgarden, 1985; Astraldi *et al.*, 1995) and larval supply (Gaines and Roughgarden, 1985; Lewin, 1986; Underwood and Fairweather, 1989; Gaines and Bertness, 1992) may also be crucial in determining dispersal rates and, ultimately, the limits of species (see review in Hiscock *et al.*, 2004).

The rate of dispersal can have considerable relevance to predicting the expansion of warm-water rocky shore species under conditions of climate change. In some areas, where large areas of the coast have similar temperature regimes (e.g. the north coast of Spain in winter, or the southern North Sea in summer), the theoretical range limits of species are likely to shift very rapidly under climate change, and dispersal may then temporarily become the limiting factor to species expansion. More generally, the ability of species to overcome barriers to dispersal (seas and channels, and areas with little rocky shore habitat) is likely to depend on their ability to disperse.

Thus there are many important gaps in knowledge about the mechanisms governing the effects of climate on rocky shore communities and the likely response of these communities to climate change. In addition to this, knowledge about the present-day distribution of rocky shore species in many areas is still patchy and is often based on studies that may be decades old (e.g. for western Europe, Fischer-Piette, 1955, 1958, 1963; Crisp and Southward, 1958; Crisp and Fischer-Piette, 1959; Ardre, 1971, cited in, for example, Lüning, 1990; Southward *et al.*, 1995; see also Chapter 3). Accurate information about present-day and past species distribution is clearly a prerequisite for successful detection and prediction of the effects of climate change on communities.

Clearly, it is unlikely that all these gaps in knowledge will be filled in the near future. To address the urgent problems of detecting and predicting ecosystem response to climate change, the most important gaps in knowledge must be prioritised. Updating knowledge about species distribution is perhaps the most crucial. The MARCLIM project in Britain and Ireland (http://www.mba.ac.uk/marclim) is carrying out detailed surveys of rocky shore communities all around the coast in order to update knowledge about distribution (from classic studies mostly carried out in the mid-20th century, e.g. Southward and Crisp, 1954b; Crisp and Southward, 1958) and to study the past and future effects of climate change. Comparable projects in other countries would be very valuable, especially if data were shared on a European or global scale. Dispersal is another key theme that should probably be addressed with high priority.

However, modelling of ecosystem responses to climate change will inevitably have to be done on the basis of knowledge that is far from complete. Quantitative testing of the climate envelope model against observations of past changes in ecosystems is a priority. Only after this is done can elements such as variations in the temperatures experienced by organisms on the shore, habitat availability and dispersal, and species interactions be incorporated into the model. Projections of future climate change themselves include high levels of uncertainty (Weaver and Zwiers, 2000; Allen *et al.*, 2000; Schneider, 2001; Allen *et al.*, 2001; Reilly *et al.*, 2001; Forest *et al.*, 2002), and it is important for ecologists to understand these uncertainties when forecasting the responses of ecosystems to climate change. IPCC projections of global mean warming by 2100 (from a 1990 base) range from 1.4 to 5.8°C (Houghton *et al.*, 2001), under "business as usual" scenarios which exclude major reductions in anthropogenic fossil fuel emissions. Different authors have estimated the 5–95% probability limits of warming by 2100 at 1.1–4.5°C (Reilly *et al.*, 2001) and 1.7–4.9°C (Wigley and Raper, 2001). Trends in climate on a local scale can differ significantly from regional and global averages (compare Scenarios 1 and 2 in Chapter 6). Furthermore, IPCC climate scenarios do not take into account possible non-linear responses to warming in the carbon cycle or thermohaline ocean circulation (Broecker, 1997; Allen *et al.*, 2001; Clark *et al.*, 2002) which could bring about a rapid shift in the global climate regime (Smith *et al.*, 1997; Stauffer, 1999) comparable to those that have occurred several times in the past (Lorius *et al.*, 1990; Smith *et al.*, 1997; Stauffer, 1999), most recently in the Younger Dryas event, which ended 11,500 years ago (Mayewski *et al.*, 1993; Taylor *et al.*, 1997; Lea *et al.*, 2003). If such a shift occurs again it could lead to catastrophic global warming or rapid cooling in Europe (Broecker, 1997; Clark *et al.*, 2002).

Clearly, then, predictions of the effects of climate change on ecosystems will inevitably be subject to at least equally wide uncertainties. Projections based on climate scenarios for, say, 2050, should carry a warning to the effect that this climate scenario could take place as early as 2025 or as late as 2095 (see Chapter 6). Furthermore, all projections should at least mention the possibility of rapid non-linear change in climate.

7.5. Key questions for future studies

In the course of my research on the topic of climate change, by far the most common questions people have asked me have been along the lines of "Is climate change really happening?" and "Is it man-made?"

It is now clear that the answer to both is "yes, very probably". The world has indeed been warming very rapidly during the 20th century (Cane *et al.*, 1997), although regional variations, such as the cool period of the 1970s and 1980s in the Bay of Biscay, may have obscured this trend. The 1990s were probably the warmest decade in the last two thousand years (Mann *et al.*, 1999, 2003; Pearce, 2003). It is widely believed that most of the warming since 1950 can be attributed to emissions of greenhouse gases by agriculture and industry (Mann *et al.*, 1998; Zwiers and Weaver, 2000; Kerr, 2001), which are now continuing unabated, indeed accelerating (Keeling *et al.*, 1995). These questions are discussed in greater detail in Chapter 1.

Given the level of consensus on these two fundamental points, I would suggest focussing on two further questions. The first: "What are likely to be the effects of climate change?" is the subject of my thesis. I have addressed this question as it applies to ecosystems, in particular, to rocky shores in the Bay of Biscay, and to both past and future effects of climate change between 1895 and 2050. A future strategy for approaching this question, I believe, would consist of three main strands.

The first is refining and modifying the climate envelope approach, along the lines described above, especially taking into account disturbances, dispersal, recruitment and biological interactions. At present this is the main approach that has been applied to detecting the effects of climate change (Walther *et al.*, 2002; Parmesan and Yohe, 2003).

The second is a programme of long-term monitoring and study of ecosystems to detect the effects of climate change in detail and improve predictions. This programme should make a combined use of all appropriate methods. These include surveys by professional biologists and ecologists, such as the MARCLIM project for rocky shores in Britain and Ireland (http://www.mba.ac.uk/marclim), backed up by volunteers, whose effectiveness has been proved in conservation and monitoring projects (Mumby *et al.*, 1995; Newman *et al.*, 2003; Foster-Smith and Evans, 2003; Pattengill-Semmens and Semmens, 2003). Remote sensing can also provide broad-scale ecological data in many ecosystems (Skole and Tucker, 1993; Jury *et al.*, 1997; Eastwood *et al.*, 1998), including rocky shores (Guillamont *et al.*, 1993; Deysher, 1993; Deysher *et al.*, 1995; Ducrotoy and Simpson, 2001). Analysis of past natural and manmade records of ecosystems ("data mining") is also invaluable to detecting past effects of climate change and testing models.

The third strand of the proposed strategy consists of continued experimental and theoretical investigation of the mechanisms underlying ecosystem responses to climate change, feeding back into modelling efforts. Studies of the extent and limits to dispersal in rocky shore species, using molecular genetic methods to identify the extent of mixing between nearby populations (e.g. Coyer *et al.*, 2003), are a possible avenue for research.

Despite the best efforts to detect and predict the effects of climate change on ecosystems, the uncertainties involved are likely to remain large. This does not imply uncertainty about whether ecosystems are, in fact, responding to climate change: they almost certainly are (Walther *et al.*, 2002; Parmesan and Yohe, 2003). Nor does uncertainty offer an excuse for inaction. If anything, the threat of possible sudden, non-linear change in climate, or in ecosystem responses to it, should be a spur to society to answer another key question as soon as possible: "What is to be done about climate change?"

Appendix A: Data from the author's surveys of rocky shore communities in the Bay of Biscay, 2000–2001

Table A.1. The SACFOR semi-quantitative scale for estimating the abundance of rocky shore organisms. Based on Hawkins and Jones (1992), adapted from Crisp and Southward (1958).

Abundance	Algae	Limpets	Small barnacles	Large barnacles	Mussels, oysters
Super-abundant	>60% cover	>100 m^{-2}	>3 cm^{-2}	>100 dm^{-2}	>50% cover
Abundant	30–60%	50–100 m^{-2}	>1 cm^{-2} rocks well covered	10–100 dm^{-2}	20–50%
Common	5–30%	10–50 m^{-2}	0.1–1 cm^{-2} rocks up to $^{1}/_{3}$ covered	1–10 dm^{-2}	large patches
Frequent	<5%, distinct zone	1–10 m^{-2}	100–1000 m^{-2}	10–100 m^{-2}	scattered, sm patches
Occasional	scattered, no zone	<1 m^{-2}	1–100 m^{-2}	1–9 m^{-2}	scattered, no patches
Rare	few found in 30 min.	few found in 30 min.	few found in 30 min.	few found in 30 min.	few found in 30 min.

Abundance	Lichen, crustose algae	Anemones, worms, small gastropods	*Pomatoceros*	*Spirorbis*
Superabundant	>50%	>50 m^{-2}		
Abundant	20–50%	10–50 m^{-2}	> 500 m^{-2}	5 cm^{-2}, >50% cover
Common	1–20%, zone well defined	1-10 m^{-2}	100–500 m^{-2}	5 cm^{-2}, <50% cover
Frequent	large scattered patches, zone ill-defined	~1 m^{-2}	10–100 m^{-2}	1–5 cm^{-2}
Occasional	small patches	< 1 m^{-2}	1–9 m^{-2}	< 1 cm^{-2}
Rare	few (30 min.)	few (30 min.)	<1 m^{-2}	few (30 min.)

Table A.2. Results of survey phase 1, spring 2000. **Lower, mid** and **upper shore** indicate all the species which were found and identified in that section of the intertidal zone, defined by dividing the shore into three sections of roughly equal height. Letters after the species name indicate abundance on the SACFOR scale (see Table A.1).

Location **Exposure** **Lat & Lon, Date**	**Species found**		
	Lower shore	**Mid shore**	**Upper shore**
San Sebastian: Monte Igeldo Moderate 43.33N 1.97W 06/06/00	*Cladophora rupestris* **F** *Codium tomentosum* **O** *Codium adhaerens* **F** *Ulva lactuca* **O** *Colpomenia peregrina* **R** *Cystoseira tamariscifolia* **F** *Corallina officionalis* **A** *Gelidium sesquipedalium* **C** *Mesophyllum lichenoides* **F** Red weed (unidentified) **F** *Patella* sp. **C** *Chthamalus* sp. **F** Hermit crab **O**	*Codium tomentosum* **F** *Codium adhaerens* **O** *Enteromorpha* sp. **C** *Ulva lactuca* **O** *Colpomenia peregrina* **O** *Corallina officionalis* **C** *Gelidium sesquipedalium* **O** *Hildenbrandia rubra* **F** *Gibbula umbilicalis* **F** *Patella* sp. **C** *Chthamalus* sp. **C** Hermit crab **F** *Paracentrotus lividus* **F**	*Pelvetia canaliculata* **O** *Lithophyllum lichenoides* **O** *Verrucaria maura* **C** *Mytilus edulis* **R** *Patella* sp. **C** *Chthamalus* sp. **A**
San Sebastian: Rio Urumea Sheltered (Estuary) 43.33N 2.00W 06/06/00	*Ralfsia* sp. **O** *Catenella caespitosa* **A** *Corallina officionalis* **C** *Ostrea edulis* **R** *Patella* sp. **C** *Pachygrapsus marmoratus* **C** *Chthamalus* sp. **A**	*Enteromorpha* sp. **F** *Patella* sp. **C** *Chthamalus* sp. **A**	*Enteromorpha* sp. **O** *Littorina neglecta* **O** *Patella* sp. **F** *Chthamalus* sp. **F**
Zumaia: Rocks E of beach Moderate 43.30N 2.25W 20/05/00	*Ulva lactuca* **O** *Bifurcaria bifurcata* **F** *Halydris siliquosa* **C** *Ceramium* sp. **F** *Corallina officionalis* **S** *Actinia equina* **O** *Patella* sp. **F** *Chthamalus* sp. **C** *Manthasterias glacialis* **R** *Paracentrotus lividus* **C**	*Enteromorpha* sp. **O** *Ceramium* sp. **C** *Corallina officionalis* **C** *Lithophyllum lichenoides* **F** *Verrucaria mucosa* **F** *Actinia equina* **R** *Patella* sp. **C** *Pachygrapsus marmoratus* **O** *Chthamalus* sp. **C**	*Lichina pygmaea* **C** *Patella* sp. **C** *Chthamalus* sp. **S**
Bermeo: Cobbled beach W of port Moderate 43.43N 2.72W 16/05/00	*Codium adhaerens* **O** *Enteromorpha* sp. **C** *Ulva lactuca* **C** *Bifurcaria bifurcata* **O** *Colpomenia peregrina* **O** *Ceramium* sp. **O** *Chondrus crispus* **O** Red weed (unidentified) **F** *Eulalia viridis* **R** Hermit crab **F**	*Enteromorpha* sp. **A** *Ulva lactuca* **O** *Colpomenia peregrina* **R** *Ceramium* sp. **A** *Corallina officionalis* **O** *Anemonia sulcata* **C** *Patella* sp. **O** Hermit crab **C**	*Enteromorpha* sp. **C** *Ulva lactuca* **O** *Ceramium* sp. **O** *Anemonia sulcata* **R** *Gibbula umbilicalis* **A** *Patella* sp. **C** *Chthamalus* sp. **O**
Bermeo: Inside mole (1st steps from end) Moderate 43.43N 2.72W 16/05/00	*Codium adhaerens* **C** *Corallina officionalis* **A** *Patella* sp. **C**	*Patella* sp. **C** *Pachygrapsus marmoratus* **C** *Chthamalus* sp. **A**	*Enteromorpha* sp. **C** *Mytilus edulis* **C** *Patella* sp. **C** *Pachygrapsus marmoratus* **A** *Chthamalus sp.* **S**

Location **Exposure** **Lat & Lon, Date**	**Species found**		
	Lower shore	**Mid shore**	**Upper shore**
Bermeo Inside mole (4th steps from end) Sheltered 43.43N 2.72W 16/05/00	*Corallina officionalis* **A** *Eulalia viridis* **O** *Patella* sp. **A** *Pachygrapsus marmoratus* **C** *Pilimnus hirtellus* **R** *Balanus perforatus* **A** *Carcinus maenas* **C** Crab (unident.) **R** *Chthamalus* sp. **F**	*Enteromorpha* sp. **O** *Mytilus edulis* **C** *Ostrea edulis* **F** *Patella* sp. **C** *Chthamalus* sp. **S** *Balanus perforatus* **A**	*Enteromorpha* sp. **A** *Littorina neritoides* **R** *Patella* sp. **R** *Chthamalus* sp. **S**
Sukarrieta-Pedernales: E side of island Sheltered (Estuary) 43.40N 2.70W 16/05/00	*Ceramium* sp. **C** *Mytilus edulis* **A** *Ostrea edulis* **A** Hermit crab **C**	*Enteromorpha* sp. **C** *Ceramium* sp. **A** *Osilinus lineatus* **C** *Mytilus edulis* **C** *Ostrea edulis* **S** *Pachygrapsus marmoratus* **O**	*Enteromorpha* sp. **C** *Chthamalus* sp. **S**
Sukarrieta-Pedernales: S side of island V. Sheltered (Estuary) 43.40N 2.70W 16/05/00	*Enteromorpha* sp. **C** *Ulva lactuca* **O** *Anemonia sulcata* **R** *Ostrea edulis* **S**	*Ascophyllum nodulosum* **F** *Fucus vesiculosus* **O** *Ostrea edulis* **S**	*Lichina pygmaea* **F** *Pachygrapsus marmoratus* **C** *Chthamalus* sp. **A**
Plentzia: Footbridge - E side V. Sheltered (Estuary) 43.42N 2.93W 22/04/00	*Littorina* sp. **R** *Mytilus edulis* **R** *Ostrea edulis* **A** *Patella* sp. **C** *Pachygrapsus marmoratus* **C**	*Enteromorpha* sp. **C** *Ostrea edulis* **C** *Pachygrapsus marmoratus* **C** *Semibalanus balanoides* **A**	
Plentzia: Footbridge - W side V. Sheltered (Estuary) 43.42N 2.93W 22/04/00	*Enteromorpha* sp. **A** *Fucus spiralis* **A**	*Enteromorpha* sp. **C**	
Plentzia: Sea wall, by beach Moderate 43.42N 2.93W 22/04/00	*Mytilus edulis* **A** *Ostrea edulis* **A** *Patella* sp. **C** *Pachygrapsus marmoratus* **C**	*Mytilus edulis* **C** *Ostrea edulis* **C** *Patella* sp. **C** *Chthamalus* sp. **S**	*Enteromorpha* sp. **F** *Patella* sp. **F** *Chthamalus* sp. **F**

Location **Exposure** **Lat & Lon, Date**	**Species found**		
	Lower shore	**Mid shore**	**Upper shore**
Santoña: Barria beach Moderate 43.47N 3.47W 03/06/00	*Enteromorpha* sp. **S** *Ulva lactuca* **C** *Fucus spiralis* **A** *Ceramium* sp. **F** *Gibbula umbilicalis* **O** *Patella* sp. **F** *Chthamalus* sp. **C**	*Enteromorpha* sp. **C** *Ulva lactuca* **C** *Fucus spiralis* **A** *Ceramium* sp. **C** *Hildenbrandia rubra* **R** *Lichina pygmaea* **R** *Verrucaria mucosa* **O** *Actinia equina* **F** *Gibbula umbilicalis* **O** *Ostrea edulis* **R** *Patella* sp. **F** *Pachygrapsus marmoratus* **C** *Chthamalus* sp. **A**	*Lichina pygmaea* **A** *Verrucaria mucosa* **O** *Patella* sp. **F** *Chthamalus* sp. **C**
Santander: El Sardinero beach (Magdalena peninsula) Moderate 43.47N 3.78W 03/06/00	*Cladophora rupestris* **O** *Codium tomentosum* **C** *Ulva lactuca* **O** *Bifurcaria bifurcata* **C** *Colpomenia peregrina* **O** *Sargassum muticum* **C** *Chondrus crispus* **O** *Corallina officionalis* **C** *Gelidium sesquipedalium* **O** *Gracilaria* sp. **O** *Halurus equisetifolius* **F** *Lithophyllum incrustans* **F** Red weed (unidentified) **O** *Gibbula umbilicalis* **O** *Mytilus edulis* **R** *Patella* sp. **R** *Electra pilosa* **R**	*Cladophora rupestris* **R** *Codium tomentosum* **R** *Ulva lactuca* **F** *Bifurcaria bifurcata* **O** *Ectocarpus* sp. **O** *Nemalion helminthoides* **O** *Ceramium* sp. **C** *Corallina officionalis* **A** *Lithophyllum incrustans* **O** *Lithophyllum lichenoides* **O** *Verrucaria mucosa* **C** *Actinia equina* **O** *Mytilus edulis* **F** *Patella* sp. **C** *Pollicipes pollicipes* **R** *Paracentrotus lividus* **A**	*Ceramium* sp. **O** *Lithophyllum incrustans* **R** *Lithophyllum lichenoides* **O** Red weed (unidentified) **F** *Lichina pygmaea* **O** *Verrucaria mucosa* **C** *Anemonia sulcata* **O** *Patella* sp. **C** *Chthamalus* sp. **C**
Ubiarco: San Juan beach Moderate 43.43N 4.10W 03/06/00	*Codium tomentosum* **C** *Ulva lactuca* **C** *Alaria esculenta* **O** *Corallina officionalis* **A** *Lawrencia pinnatifida* **R** *Lithophyllum incrustans* **C** Red weed (unidentified) **F** *Gibbula umbilicalis* **O**	*Codium tomentosum* **R** *Enteromorpha* sp. **A** *Ulva lactuca* **C** *Ectocarpus* sp. **F** *Nemalion helminthoides* **R** *Corallina officionalis* **O** *Lithophyllum lichenoides* **F** *Plocamium cartilagineum* **O** *Verrucaria mucosa* **F** *Gibbula umbilicalis* **C** *Mytilus edulis* **F** *Patella* sp. **C** *Pachygrapsus marmoratus* **C** *Chthamalus* sp. **C**	*Corallina officionalis* **O** *Lithophyllum incrustans* **O** *Mastocarpus stellatus* **F** *Lichina pygmaea* **F** *Verrucaria maura* **F** *Actinia equina* **O** *Gibbula umbilicalis* **O** *Mytilus edulis* **O** *Patella* sp. **C** *Chthamalus* sp. **A**

Location Exposure Lat & Lon, Date	Species found		
	Lower shore	Mid shore	Upper shore
San Vicente de la Barquera: Punta Liñera Exposed 43.40N 4.40W 07/05/00	*Cladophora rupestris* **A** *Codium adhaerens* **O** *Ulva lactuca* **C** *Bifurcaria bifurcata* **A** *Colpomenia peregrina* **C** *Ectocarpus* sp. **O** *Chondrus crispus* **O** *Corallina officionalis* **A** *Lithophyllum incrustans* **F** *Verrucaria mucosa* **O** *Anemonia sulcata* **C** *Chthamalus* sp. **F** Hermit crab **C** *Paracentrotus lividus* **S**	*Enteromorpha* sp. **O** *Ulva lactuca* **O** *Colpomenia peregrina* **C** *Fucus* sp. **C** *Corallina officionalis* **A** *Gelidium latifolium* **O** *Lithophyllum lichenoides* **C** *Verrucaria mucosa* **C** *Actinia equina* **F** *Anemonia sulcata* **F** *Gibbula umbilicalis* **C** *Patella* sp. **C** *Chthamalus* sp. **C**	*Ectocarpus* sp. **O** *Fucus* sp. **C** *Ceramium* sp. **O** *Corallina officionalis* **O** *Gelidium latifolium* **O** *Lawrencia pinnatifida* **O** *Lithophyllum lichenoides* **F** *Lichina pygmaea* **C** *Actinia equina* **F** *Patella* sp. **C** *Chthamalus* sp. **C**
San Vicente de la Barquera: Liñera cove, near small beach Moderate 43.40N 4.40W 07/05/00	*Cladophora rupestris* **C** *Ulva lactuca* **C** *Bifurcaria bifurcata* **C** *Corallina officionalis* **A** *Gelidium latifolium* **O** *Verrucaria mucosa* **F** Hermit crab **S**	*Enteromorpha* sp. **A** *Ulva lactuca* **C** *Colpomenia peregrina* **F** *Verrucaria mucosa* **C** *Gibbula umbilicalis* **C** Hermit crab **C**	*Enteromorpha* sp. **C** *Lithophyllum incrustans* **F** *Lithophyllum lichenoides* **O** *Verrucaria mucosa* **C** Anemone (unidentified) **O** *Gibbula umbilicalis* **A** *Patella* sp. **A** *Chthamalus* sp. **A**
San Vicente de la Barquera: Rocks below lighthouse Exposed 43.40N 4.40W 07/05/00	*Enteromorpha* sp. **F** *Ulva lactuca* **F** *Bifurcaria bifurcata* **A** *Colpomenia peregrina* **O** *Ectocarpus* sp. **F** *Corallina officionalis* **A** *Gelidium latifolium* **C** *Chthamalus* sp. **O**	*Enteromorpha* sp. **C** *Ectocarpus* sp. **O** *Fucus* sp. **F** *Nemalion helminthoides* **O** *Corallina officionalis* **F** *Gelidium latifolium* **A** *Lithophyllum lichenoides* **C** *Verrucaria mucosa* **C** *Actinia equina* **C** *Gibbula umbilicalis* **C** *Patella* sp. **A** *Chthamalus* sp. **A** *Paracentrotus lividus* **C**	*Corallina officionalis* **F** *Lithophyllum lichenoides* **C** *Lichina pygmaea* **C** *Verrucaria mucosa* **O** *Gibbula umbilicalis* **F** *Osilinus lineatus* **F** *Patella* sp. **A** *Chthamalus* sp. **A**
Ribadesella: Atalaya beach Moderate 43.47N 5.05W 06/05/00	*Cladophora rupestris* **S** *Codium tomentosum* **C** *Ulva lactuca* **F** *Bifurcaria bifurcata* **C** *Cystoseira tamariscifolia* **F** *Chondrus crispus* **O** *Corallina officionalis* **C** *Lawrencia* sp. **F** *Lithophyllum incrustans* **O** *Verrucaria mucosa* **C**	*Codium tomentosum* **A** *Enteromorpha* sp. **A** *Ulva lactuca* **C** *Bifurcaria bifurcata* **C** *Colpomenia peregrina* **O** *Fucus spiralis* **C** *Sargassum muticum* **O** *Chondrus crispus* **C** *Corallina officionalis* **F** *Lithophyllum lichenoides* **R** Red weed (unidentified) **F** *Anemonia sulcata* **A** *Gibbula umbilicalis* **F** *Patella* sp. **O** *Chthamalus* sp. **A** Hermit crab **A** *Holothuria forskali* **R** *Manthasterias glacialis* **R**	*Enteromorpha* sp. **C** *Fucus* sp. **O** *Lithophyllum lichenoides* **F** *Littorina neritoides* **R** *Osilinus lineatus* **R** *Mytilus edulis* **F** *Patella* sp. **C** *Chthamalus* sp. **S**

Location Exposure Lat & Lon, Date	**Species found**		
	Lower shore	**Mid shore**	**Upper shore**
Gijon Arbeyal beach Moderate 43.55N 5.67W 05/05/00	*Cladophora rupestris* **O** *Codium tomentosum* **O** *Ulva lactuca* **F** *Colpomenia peregrina* **O** *Himanthalia elongata* **R** *Pelvetia canaliculata* **O** *Sargassum muticum* **C** *Ceramium* sp. **A** *Chondrus crispus* **F** *Corallina officionalis* **O** *Gelidium latifolium* **C** *Hildenbrandia rubra* **O** *Palmaria palmata* **O** Red weed (unidentified) **O** *Verrucaria mucosa* **R** *Anemonia sulcata* **O** *Pomatoceros triqueter* **O** *Gibbula umbilicalis* **C** *Patella* sp. **C** Hermit crab **C** *Carcinus maenas* **R**	*Ectocarpus* sp. **O** *Gibbula umbilicalis* **A** *Patella* sp. **F** Barnacles (large) **F** *Chthamalus* sp. **C**	*Gibbula umbilicalis* **A** *Patella* sp. **C** *Chthamalus* sp. **S**
Gijon: Marina Sheltered 43.55N 5.68W 05/05/00	*Enteromorpha* sp. **F** *Sargassum muticum* **S** *Hildenbrandia rubra* **O** *Lithophyllum incrustans* **C** Red weed (unidentified) **R** *Gibbula umbilicalis* **R** *Pachygrapsus marmoratus* **O**	*Enteromorpha* sp. **C** *Patella* sp. **A** *Pachygrapsus marmoratus* **O** Barnacles (large) **O** *Chthamalus* sp. **F** Hermit crab **O** *Semibalanus balanoides* **O**	*Enteromorpha* sp. **S** *Gibbula umbilicalis* **C** *Patella* sp. **C** *Pachygrapsus marmoratus* **C** *Chthamalus* sp. **C**
Salinas: Rocks W of town beach Moderate 43.58N 5.97W 04/05/00	*Ulva lactuca* **O** *Fucus vesiculosus* **C** *Pelvetia canaliculata* **C** *Chondrus crispus* **F** *Corallina officionalis* **C** *Lomentaria articulata* **F** *Membranoptera alata* **F** *Hymeniacidon perleve* **F** *Anemonia sulcata* **F** *Eulalia viridis* **R** *Gibbula umbilicalis* **R** *Patella* sp. **C** *Pachygrapsus marmoratus* **C** *Electra pilosa* **O**	*Pelvetia canaliculata* **O** *Verrucaria mucosa* **C** *Mytilus edulis* **F** *Patella* sp. **A** *Pachygrapsus marmoratus* **C** *Chthamalus* sp. **A**	*Hildenbrandia rubra* **C** *Patella* sp. **C**
Luarca: River, below footbridge V. Sheltered (Estuary) 43.55N 6.53W 03/05/00	*Enteromorpha* sp. **O** *Fucus spiralis* **S**	*Enteromorpha* sp. **O** *Fucus spiralis* **S**	*Enteromorpha* sp. **S** *Verrucaria maura* **F**

Location **Exposure** **Lat & Lon, Date**	**Species found**		
	Lower shore	**Mid shore**	**Upper shore**
Luarca: Rocks W of beach Moderate 43.55N 6.53W 03/05/00	*Enteromorpha* sp. **O** *Ulva lactuca* **O** *Bifurcaria bifurcata* **F** *Fucus* sp. **O** *Himanthalia elongata* **A** *Pelvetia canaliculata* **A** *Corallina officionalis* **A** *Lithophyllum incrustans* **O**	*Fucus* sp. **O** *Pelvetia canaliculata* **O** *Corallina officionalis* **O** *Hildenbrandia rubra* **O** *Lithophyllum lichenoides* **O** *Actinia equina* **O** *Mytilus edulis* **C** *Patella* sp. **C** *Chthamalus* sp. **A** *Paracentrotus lividus* **F**	*Lithophyllum lichenoides* **F** *Lichina pygmaea* **C** *Actinia equina* **F** *Littorina* sp. **O** *Mytilus edulis* **C** *Patella* sp. **C** *Chthamalus* sp. **A** *Manthasterias glacialis* **R**
Ribadeo: Port Sheltered 43.53N 7.03W 02/05/00	*Enteromorpha* sp. **O** *Colpomenia peregrina* **O** *Fucus serratus* **O** Red weed (unidentified) **A** *Hymeniacidon perleve* **R** *Pachygrapsus marmoratus* **O**	*Enteromorpha* sp. **O** *Fucus vesiculosus* **S** *Hildenbrandia rubra* **O** Red weed (unidentified) **O** *Gibbula umbilicalis* **C** *Littorina neglecta* **O** *Mytilus edulis* **R** *Patella* sp. **O** Barnacles (large) **C** *Chthamalus* sp. **C** *Manthasterias glacialis* **R**	*Enteromorpha* sp. **O** *Gibbula umbilicalis* **C** *Osilinus lineatus* **O** *Patella* sp. **C** *Chthamalus* sp. **S**
Ribadeo: Rocks E of lighthouse Exposed 43.57N 7.03W 02/05/00	*Codium tomentosum* **O** *Ulva lactuca* **O** *Bifurcaria bifurcata* **F** *Cystoseira tamariscifolia* **O** *Fucus serratus* **O** *Himanthalia elongata* **A** *Pelvetia canaliculata* **O** *Corallina officionalis* **A** *Gelidium latifolium* **F** *Lithophyllum lichenoides* **F** *Paracentrotus lividus* **C**	*Codium tomentosum* **R** *Ulva lactuca* **R** *Ectocarpus* sp. **O** *Himanthalia elongata* **F** *Pelvetia canaliculata* **O** *Corallina officionalis* **C** *Lithophyllum lichenoides* **O** *Verrucaria maura* **O** *Actinia equina* **R** *Mytilus edulis* **F** *Patella* sp. **C** *Chthamalus* sp. **A** *Paracentrotus lividus* **C**	*Ectocarpus* sp. **O** *Lithophyllum incrustans* **C** *Lithophyllum lichenoides* **O** *Verrucaria maura* **F** *Actinia equina* **R** *Osilinus lineatus* **O** *Mytilus edulis* **F** *Patella* sp. **C** *Chthamalus* sp. **S** *Paracentrotus lividus* **C**

Table A.3. Results of survey phase 2, spring 2001. Exp: wave exposure (X = exposed, M = moderate, S = sheltered, VS = very sheltered; E = estuarine conditions, i.e. significant input of fresh water.) Column headings in *italics* indicate the species studied, as follows: *Fsp: Fucus spiralis. Fv: F. vesiculosus. Fsr: F. serratus. Fc: F. ceranoides. An: Ascophyllum nodosum. Pc: Pelvetia canaliculata. He: Himanthalia elongata. Bb: Bifurcaria bifurcata. Sp: Sccorhiza polyschides. P: Patella* sp. (combined). *Pv: P. vulgata. Pd: P. depressa. Pa: P. aspera Pr: P. rustica. O: Osilinus* sp. (formerly *Monodonta). Gu: Gibbula umbilicalis. Gc: G. cinerarea. Nl: Nucella lapillus..* Letters indicate abundance on the SACFOR scale (see Table A.1). Numbers under algal species indicate maximum percentage cover, based on a minimum area of 10 m^2. Blank means the species was not found.

Location	**Lat & Lon**	**Exp.**	**Date**	*Fsp*	*Fv*	*Fsr*	*Fc*	*An*	*Pc*	*He*	*Bb*	*Sp*	*P*	*Pv*	*Pd*	*Pa*	*Pr*	*O*	*Gu*	*Gc*	*Nl*
Ribadeo: Port	43.53N 7.03W	S(E)	10/03/01		S 75			F 5					F	F	F						
Ribadeo: Rocks E of lighthouse	43.57N 7.03W	X	10/03/01							C 15	A 50	R <1	C	F	F	F	F				R
Luarca: River, below footbridge	43.55N 6.53W	VS(E)	10/03/01	S 100																	
Luarca: Rocks in centre of beach	43.55N 6.53W	M	10/03/01	C 10						C 30	A 40		C	C	F	F		A	F	F	
San Esteban de Pravia: Guardada beach	43.50N 6.00W	M	10/03/01	C 20									C	F	C	F		A	O		R
S. Esteban: Port	43.50N 6.00W	S(E)	10/03/01	A 50									C	C							
Ribadesella: Atalaya beach	43.47N 5.05W	M	11/03/01	R <1							C 25		C	C	C			A	A	C	
Ribadesella: Port	43.47N 5.05W	VS(E)	10/03/01	S 75																	
San Vicente: Port	43.40N 4.40W	S	11/03/01	R <1	S 75			S 75					C	C	O						
San Vicente: W of pier	43.40N 4.40W	M	11/03/01	R <1							S 75		C			C		A			
Suances: Locos beach	43.45N 4.00W	X	12/03/01	R <1							S 75		C		C	C			C	F	
Suances: Port	43.45N 4.00W	S(E)	12/03/01										C	C	C			A	A		
Suances: Ribera beach	43.45N 4.00W	S	12/03/01	A 50									C		C						
Loredo: E end of beach	43.45N 3.70W	M	11/03/01	A 40							A 50	R <1	C	F	F	F					
Somo: Bridge	43.45N 3.70W	VS(E)	11/03/01		C 30			S 75					R	R					O		
Sonabia: Peninsula, E side	43.41N 3.30W	M	12/03/01								A 50		C		C			A	A		

Location	**Lat & Lon**	**Exp.**	**Date**	*Fsp*	*Fv*	*Fsr*	*Fc*	*An*	*Pc*	*He*	*Bb*	*Sp*	*P*	*Pv*	*Pd*	*Pa*	*Pr*	*O*	*Gu*	*Gc*	*Nl*
Sonabia: River mouth	43.41N 3.30W	S(E)	14/03/01				A 50														
Plentzia: Barrika beach	43.42N 2.97W	M	08/03/01								A 50		C		C	F			S		
Plentzia: Footbridge	43.42N 2.93W	VS(E)	08/03/01	C 15									F	F				O	R		
Plentzia: Gorliz beach, N end	43.42N 2.93W	M	23/03/01										C		C			A	C		
Sukarrieta-Pedernales: Island	43.40N 2.70W	VS(E)	09/03/01	C 10				C 10					C	C				R	S		
Mundaka: Santa Catalina	43.45N 2.70W	M	09/03/01										C		C	C		F	A	F	
Zumaia: R Narondo	43.30N 2.25W	VS(E)	13/03/01	O 5																	
Zumaia: Rocks E of Atalaya beach	43.30N 2.25W	M	13/03/01								O		C		C	C			A		
San Sebastian: Rio Urumea	43.33N 2.00W	S(E)	25/03/01																		
San Sebastian: Monte Igeldo	43.33N 1.97W	M	25/03/01										C	O	C			R	A		
Hondarribia: International bridge	43.34N 1.75W	VS(E)	25/03/01				S 80														
Hondarribia: Cabo Higuer	43.40N 1.75W	X	25/03/01										C	O	C				C	F	
Hondarribia: Fishing port	43.40N 1.75W	S	25/03/01										C	O	C				C		
Biarritz: Rochers de la Vierge	43.48N 1.58W	M	24/03/01										A	O	A	F			A		
Bayonne: R Adour	43.49N 1.48W	VS(E)	24/03/01				S 75														

Table A.4. Results of survey phase 3, summer 2001. Key as for Table A.3 except: *G: Gibbula* sp. (combined). *Ll: Littorina littorea. Lm: L. maraea* or *L. obtusata.*

Location	**Lat & Lon**	**Exp.**	**Date**	*Fsp*	*Fv*	*Fsr*	*Fc*	*An*	*Pc*	*He*	*Bb*	*Sp*	*P*	*Pv*	*Pd*	*O*	*G*	*Nl*	*Ll*	*Lm*
Capbreton: Marina, below bridge	43.65N 1.45W	VS(E)	18/07/01				S 95													
Capbreton: Old port	43.65N 1.45W	M	18/07/01	O 5									C		C					
Mimizan: Mouth of river	44.21N 1.31W	M	19/07/01																	
Arcachon: Marina	44.66N 1.14W	S	20/07/01	C 25	S 75								F		F					
Lacanau: Breakwater	45.00N 1.19W	M	21/07/01										R		R					
le Verdon: Embarcadero	45.57N 1.06W	VS(E)	22/07/01		S 90								A							
Royan: NW side of beach	45.62N 1.03W	M	22/07/01		A 50	C 25							C	O	C				R	
Royan: Palais de Mer	45.62N 1.03W	M	23/07/01			C 25							C	R	C					
Le Palmyre: Port	45.68N 1.16W	M	23/07/01	O <5	S 90								S		S					
Boyardville: Channel	45.97N 1.25W	VS	24/07/01		A 50			C 10												
St Denis d'Oleron: Beach	46.03N 1.38W	M	24/07/01		A	A 50							C	R	C	A	C	O		
Jard-sur-Mer: Beach	46.41N 1.58W	M	26/07/01			C 10							C		C	C	C			
Jard-sur-Mer: Marina	46.41N 1.58W	VS	26/07/01	S 65																O
les Sables d'Olonne: Channel	46.49N 1.62W	S(E)	26/07/01	S 95		C 25		S 95								C				O
les Sables d'Olonne: Fort St Nicolas	46.49N 1.62W	M	26/07/01			O						O	C	R	C		C			
Bretignolles-sur-Mer: Beach	46.62N 1.88W	M	26/07/01	A 50		A 50		C 10	A 50				C	C	C	C			C	
St Gilles: Beach	46.69N 1.96W	M	26/07/01	S 95				A 50	C 25				C	C	C				F	
St Gilles: Channel	46.69N 1.96W	S(E)	26/07/01	S 90				A 50					O	O						
la Bernerie en Retz: Main beach	47.07N 2.04W	M	27/07/01		C 20	S 75		S 75					F		F		A	O	C	

Appendix B: Estimating species range based on observed distribution

The following original method was developed to calculate the expected position of a species' distributional limit and the confidence limits of this expected position, based on its observed presence or absence at a series of sites.

The following assumptions were made:

1. There are N sites numbered 1 through N at which an observation of a species' presence or absence was made.
2. The limit of the species' range lies between sites X and X+1, i.e. it is absent from sites X+1 through N, and may or may not be present at sites 1 through X.
3. The species is equally likely to be observed at each site, 1 through X, within its range, with probability $1-f$. (Using $1-f$ instead of f simplifies calculations later.)

Assumption (3) is a first approximation; in reality most species are probably less common towards the edge of their range. Note that f, the probability of a Type I error or "false negative" (i.e. recording the species as absent at a site within its true range) depends both on the species' real distribution and on the effectiveness of the survey.

Suppose the last site at which the species was found (the observed limit) was site x. We want to estimate the position of the true limit, X. This can be done based on the probability distribution of $(X-x)$, the error in the observed limit. Note that this error can only be zero or positive, never negative, assuming the possibility of a "false positive" observation of the species at a site outside its true range to be neglegible.

Figure B.1 shows a graphical derivation of the formula for the probability distribution of $(X-x)$, the number of sites by which the observed limit is in error:

$$\mathrm{p}(X-x=n) = (1\text{-}f)f^n \qquad [\mathrm{B.1}]$$

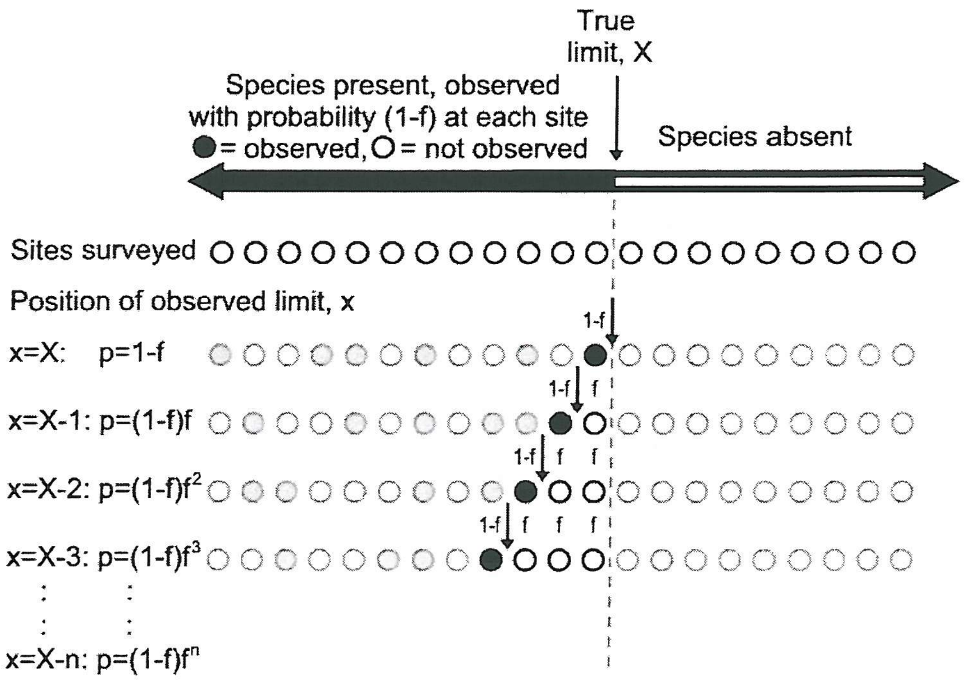


Figure B.1. Graphical derivation of the probability distribution for the error in the observed position of a species' distributional limit. Closed circles (●) indicate sites at which the species was observed; open circles (○) indicate sites at which it was not observed. Greyed circles (○●) indicate that presence or absence at that site does not affect the position of the observed limit.

The expected value of $(X-x)$, then, is

$$\sum_{n=0}^{\infty} [n\, \mathrm{p}(n)] \, / \sum_{n=0}^{\infty} [\mathrm{p}(n)]$$

$$= \sum_{n=0}^{\infty} [n\,(1-f)\,f^n] \qquad *$$

$$= f(1-f)\,[\sum_{n=0}^{\infty} f^n]^2 \qquad **$$

$$= f(1-f)\,[1/(1-f)]^2 \qquad ***$$

$$\overline{X} = x \;+\; f\,/\,(1-f) \qquad [\mathrm{B}.2]$$

---

[*] Based on equation 3.1, and using the fact that $\sum_{r=0}^{\infty} [\mathrm{p}(r)] = 1$.

[**] Rearranging the infinite series, $\sum_{r=0}^{\infty} r f^r = f[\sum_{r=0}^{\infty} f^r]^2$.

[***] Using the partial sum $\sum_{r=0}^{n} f^r = (1-f^{r+1})/(1-f)$, with 0 <= f < 1 and n set to infinity.

This equation may be interpreted verbally by noting that $f / (1 - f)$ is the average number of false negative observations per positive observation, within the species' true range, which corresponds to the expected error in the observed position of the limit.

Based on equation B.1, confidence limits for X can also be calculated. These are values of X that are exceeded in no more than a given proportion (say c) of surveys. This proportion c could be 5% or whatever level of confidence is desired. The value of X at the confidence limit (call this X_c) should satisfy the following inequation:

$$p(X <= X_c - 1) \quad <= \quad (1 - c)$$

Thus X_c is a conservative upper confidence limit of X, equalled or exceeded in less than a proportion c of surveys.

Calculating partial sums based on equation B.1 (see footnote *** on previous page), this inequation becomes

$$(1 - f^{X_c}) \quad <= \quad (1 - c)$$

$$f^{X_c} \quad >= \quad c$$

$$X_c \log f \quad >= \quad \log c$$

$$X_c \quad <= \quad \log c / \log f$$

or, for an upper bound for X_c,

$$X_c \quad = \quad \log c / \log f \qquad [B.3]$$

Note that the probability of getting X consecutive false negatives (at the edge of the species' true range) is f^X which when set to equal c gives the above equation.

Figure 3.11 and Table 3.7 give expected values and 95% and 99% upper and lower confidence limits for the error in the observed limit in number of sites for different values of f, the frequency of absences within the species' range (false negatives), ranging from 0 to 1.

Estimating the value of f based on the observed frequency of the species within its observed range gives a value of $f = N_A / (x - 1)$, where x is the observed range and N_A is the number of sites within that range at which the species was not found. The denominator is $(x - 1)$ and not x because of the fact that the species must necessarily be observed at the last site in its observed range. Since $x = N_A + N_P$, where N_P is the number of sites at which the species was found, from equation B.2

$$\overline{X} = x + N_A / (N_P - 1) \qquad [B.4]$$

Note that the calculations made so far are based on integer values of X., i.e. they are only able to calculate the position of the limit to the nearest site. As the species' true limit may, however, lie between two sites, the true expected value of X (call it X') is greater than the value for X given by equations 3.2 and 3.4. Based on the assumption that the true limit could be at any point between two adjacent sites with equal probability, the expected value of X' is

$$\overline{X'} = x + 0.5 + [f / (1 - f)] = x + 0.5 + [N_A / (N_P - 1)] \qquad [B.5]$$

The confidence limits for X' are likewise different from those for X. The calculation of their precise value involves summing two probability distributions and is beyond the scope of this chapter. A conservative upper bound can be obtained by adding the upper confidence limits of the two distributions together. This means adding $(1 - c)$ to the value of X_c given by equation B.3, so that

$$X'_c = x + \log c / \log f + (1 - c) \qquad [B.6]$$

As regards lower confidence limits, the lower confidence limit given by equation B.3 is very close to the observed position x for all but large values of f. Therefore the observed limit can be used as a lower confidence value.

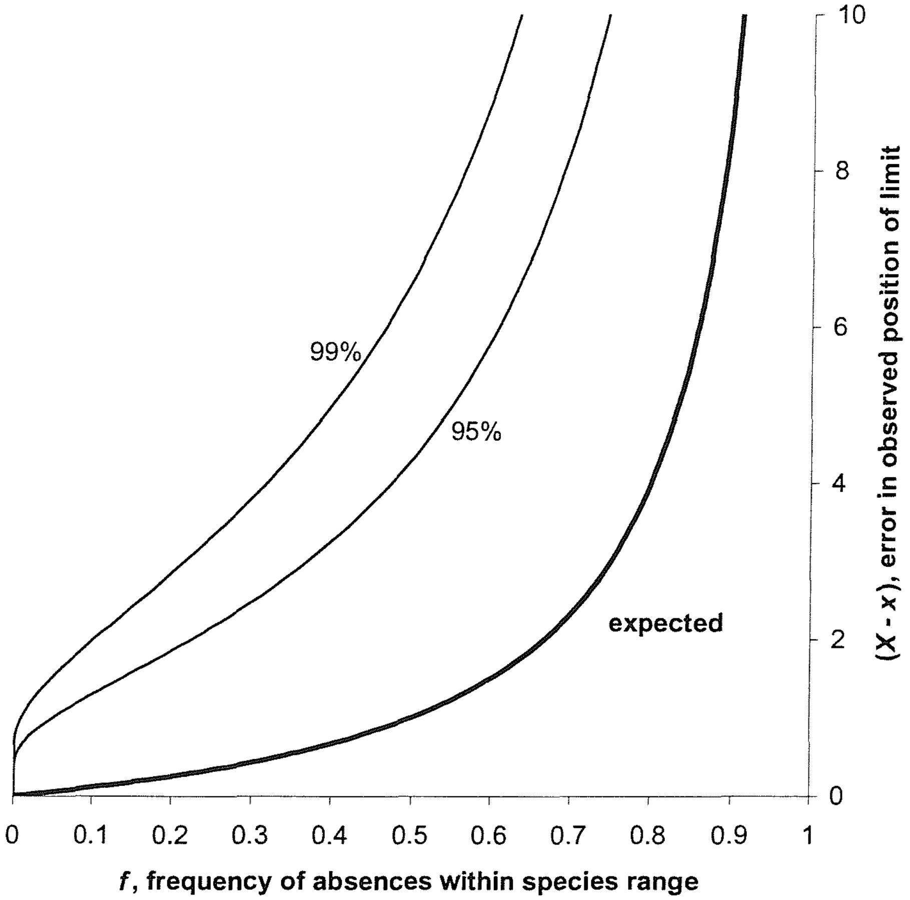


Figure B.2. Expected values and 95% and 99% upper confidence limits for error in observed position of species limits (in number of sites) for different values of *f*, the frequency of absences within the range, based on equations 3.2 and 3.3.

Table B.1. Tabulated values of expected value (mean) and upper confidence limits for error in observed position of species limit, for different values of *f*, frequency of false negatives, based on equations B.2 and B.3.

f	mean	95%	99%
0.00	0.00	0.00	0.00
0.05	0.05	1.00	1.54
0.10	0.11	1.30	2.00
0.15	0.18	1.58	2.43
0.20	0.25	1.86	2.86
0.25	0.33	2.16	3.32
0.30	0.43	2.49	3.82
0.35	0.54	2.85	4.39
0.40	0.67	3.27	5.03
0.45	0.82	3.75	5.77

f	Mean	95%	99%
0.50	1.00	4.32	6.64
0.55	1.22	5.01	7.70
0.60	1.50	5.86	9.02
0.65	1.86	6.95	10.69
0.70	2.33	8.40	12.91
0.75	3.00	10.41	16.01
0.80	4.00	13.43	20.64
0.85	5.67	18.43	28.34
0.90	9.00	28.43	43.71
0.95	19.00	58.40	89.78

Probability of Type I and Type II errors

It is possible to calculate the probability of getting a Type I or Type II error when comparing the observed range of a species at two different times, assuming that (i) The probability of a false negative observation, f, remains constant between the two surveys, and (ii) The difference between the position of the species' true limit at time 1 and time 2 is D sites, where D can be positive, zero (the null hypothesis), or negative.

The probability that the observed difference, O, is equal to the true difference, D, is:

$$p_{(O=D)} = (1-f)^2 + f^2(1-f)^2 + f^4(1-f)^2 + f^6(1-f)^2 + \ldots$$

based on cross-multiplying the terms in figure B.1 (the probability that both observed limits are equal to the true limit is $(1-f)$ times $(1-f)$; the probability that both underestimate the true limit by 1 is $f(1-f)$ times $f(1-f)$; and so on.)

The probability that O is equal to $D+1$ (or $D-1$) is:

$$p_{(O=D\pm 1)} = f(1-f)^2 + f^3(1-f)^2 + f^5(1-f)^2 + f^7(1-f)^2 + \ldots = f p_{(r=D)}$$

In general:

$$p_{(O=D\pm N)} = f^N p_{(O=D)}$$

$p_{(r=D)}$ can therefore be found by using the fact that summing over all values of N,

$$\sum_{N=-\infty}^{\infty} p_{(O=D+N)} = 1$$

$$\sum_{N=-\infty}^{\infty} p_{(O=D)} f^{|N|} = 1$$

$$p_{(O=D)} = 1 / (2[\sum_{N=0}^{\infty} f^N] - 1)$$

$$= 1 / (2[1/(1-f)] - 1)$$

$$= (1-f)/(1+f)$$

$$p_{(O=D+N)} = f^{|N|}(1-f)/(1+f) \qquad [B.7]$$

This equation makes it possible to calculate the probability of a Type I or Type II error, as follows:

Type I error: Given that the null hypothesis is correct (the difference between the position of true range limits, D, equals zero), what is the probability of rejecting it falsely? Or, equivalently, what is the smallest difference between observed range limits that is necessary to reject the null hypothesis with a certain level of confidence?

Given that true range limits are the same, the probability of getting a difference between observed range limits of at least ±N sites is equal to:

$$p_{(|O|>=\mathrm{N})} = 2\,[{}_{r=N}\Sigma^{\infty} f^{r}\,(1-f)\,/\,(1+f)]$$

$$= 2f^{N}\,({}_{r=0}\Sigma^{\infty} f^{r})\,(1-f)\,/\,(1+f)$$

$$p_{(|O|>=\mathrm{N})} = 2f^{N}\,/\,(1+f) \qquad [\mathrm{B.8}]$$

Therefore to reject the null hypothesis (that true range limits are equal) with confidence level c, the difference in the observed range limits must be at least:

$$N = [\log c + \log(1+f) - \log 2]\,/\,\log f \qquad [\mathrm{B.9}]$$

For example, if $f = 0.5$ and $c = 0.05$, then $N = 4.7$, so a difference in the observed limit of 5 sites is sufficient to reject the null hypothesis at a 5% level of significance. If $f = 0.5$ and $c = 0.01$ then $N = 7.06$, so a difference of 8 sites is required to reject the null hypothesis at 1% level of significance. Clearly, different values of f lead to very different critical values of N at a given level of significance: at the 5% level, for example, $f = 0.25$ given $N = 3.66$ while $f = 0.75$ gives $N = 10.9$.

Type II error: The probability of a Type II error depends on the choice of alternative hypothesis. Consider the hypothesis H_1 that the true range in survey 1 is greater than that in survey 2 by D_1 sites. Given that this is true, the probability of rejecting the null hypothesis equals the probability of falling into the lower rejection zone (i.e. the observed range for survey 2 is at least N sites greater than for survey 1): that is, from equation B.8,

$$p_{lower} = f^{(N+D1)}\,/\,(1+f),$$

plus the probability of falling into the upper rejection zone (i.e. the observed range for survey 1 is at least N sites greater than for survey 2). This probability depends on the value of D_1 which could be less than, equal to, or greater than N. If D_1 is less than or equal to N then the probability is, again from equation B.8:

$$p_{upper} = f^{(N-D1)}\,/\,(1+f)$$

whereas if D_l is greater than or equal to N it is:

$$p_{upper} = 1 - [f^{(1 + Dl - N)} / (1 + f)]$$

The probability of a Type II error is then $1 - (p_{upper} + p_{lower})$. However, in most cases p_{lower} will be very small, so to a close approximation the probability will be $1 - p_{upper}$.

If $f = 0.5$, for example, then the case $D_l = N$ leads to a probability of a Type II error of 0.333, which certainly does not allow confidence in correctly rejecting the null hypothesis. In order to have confidence in rejecting the null hypothesis at a probability level of c, then the value of D_l would have to be considerably larger. In fact it would need to be at least equal to a critical value D_c, defined by

$$c = f^{(1 + Dc - N)} / (1 + f)$$

$$D_c = N - 1 + [\log c + \log (1 + f)] / f$$

which from equation B.9, assuming that the critical value c is constant, is equal to

$$D_c = 2N - 1 - \log 2 / \log f \qquad [B.10]$$

or, to calculate D_c independently of N,

$$D_c = -1 + [2 \log c + 2 \log (1 + f) - \log 2] / \log f \qquad [B.11]$$

Thus for a significance level of $c = 0.05$, when $f = 0.5$ the value of D_c is 9.5, when $f = 0.25$ then $D_c = 6.8$, and when $f = 0.75$ then $D_c = 23.2$.

The size of effect (true range shift) that it is possible to detect with confidence, then, is again very dependent on the value of f, the probability of a false negative observation.

Worked example

Table B.2 (overleaf) sets out a worked example of how this method can be used to estimate the range of *Fucus vesiculosus* on the north coast of Spain in 2000–01, based on observations by the author (see Figure 3.3e). The species' distributions on the open coast and in sheltered habitats are treated separately. It can be seen that the expected and 95% confidence estimates for the true position of the range limits differ considerably from the observed limits, indicating that the number of sites surveyed was not sufficient to accurately establish the position of the limits.

Table B.2. Worked example of estimating the range of *Fucus vesiculosus* on the north coast of Spain in 2000–01, using the method described in this appendix, based on the species distribution as observed by the author and plotted in Figure 3.3.

Fucus veisculosus	**Open coast**	**Sheltered**
Observed position of eastern limit	Gijon (5.68°W)	Mundaka (2.70°W)
No. of sites where sp. present (N_P)	2	4
No. of sites within observed range where sp. absent (N_A)	3	8
Estimated probability of false negatives: $f = N_A / (N_A + N_P - 1)$	0.750	0.727
Estimated error in position of limit: $X' - x = N_A / (N_P - 1) + 0.5$ [Eq. B.5]	3.5 sites	3.17 sites
95% upper confidence limit for $X' - x = (\log 0.05 / \log f) + 0.95$ [Eq. B.6]	11.36 sites	10.36 sites
Estimated true position of eastern limit	3.10°W	< 1.75°W (no limit)
95% upper (eastern) confidence limit	2.60°W	< 1.75°W (no limit)
95% lower (western) confidence limit (coincides with observed limit)	5.68°W	2.70°W

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