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CHALLENGES TO MARINE ECOSYSTEMS

Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone

David S. Wethey · Sarah A. Woodin

Abstract Intertidal organisms are often assumed to live close to their thermal limits, and have emerged as potential early indicators of the effects of climate change. We compared our survey of the 2004–2006 geographic distribution of the barnacle *Semibalanus balanoides* to its distribution in 1872, 1955, 1963, 1971, and 1985, from surveys by Fischer, Crisp, Fischer-Piette, Barnes, Powell, and Southward. The southern geographic limit has retreated 300 km in France since 1872, at a rate of 15 to 50 km per decade. We compared our 2006 survey of the geographic distribution of the polychaete *Diopatra neapolitana* to its distribution in 1893–1923, from surveys by Saint-Joseph and Fauvel, and its distribution in 1969–1976 from surveys by Glémarec. The northern geographic limit of this species has advanced 300 km in France since 1893 at similar rates to *Semibalanus*. We used NOAA weather reanalysis data and our mechanistic simulation model of intertidal animal body temperatures to hindcast the thermal environmental change near historical geographic limits in Europe for the past 55 years. Results indicate that changes in the southern limit of *S. balanoides* are due to intolerance of winter body temperatures above 10°C, leading to reproductive failure. Results for *Diopatra* are ambiguous: based on the northern extension of its range, either cold winters or cool summers limit its range, while gaps in its distribution are consistent with limitation by cooler summer conditions. The parallel shifts of *D. neapolitana* on sedimentary shores and *Semibalanus* on rocky shores suggest that similar climatic factors control the geographic limits of both species. The intertidal zone is a model system for examining the effects of climate change on biogeographic change both because of the rapidity of its response, and because the rich historical record allows direct tests of hypotheses.

Keywords Biogeography · Climate change · Barnacle · Polychaete · *Semibalanus balanoides* · *Diopatra neapolitana*

Introduction

The European littoral zone presents an excellent opportunity to study the effects of climate change on the geographic distribution of organisms, because of the rich historical record of species distributions in Iberia, France, and the British Isles during the late nineteenth and twentieth centuries (e.g., Lafont,

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Challenges to Marine Ecosystems

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1871; Fischer, 1872; Saint-Joseph, 1898; Fauvel, 1923; Fischer-Piette, 1932; Evans, 1954; Fischer-Piette, 1955; Crisp & Southward, 1958; Southward & Crisp, 1954; Crisp & Fischer-Piette, 1959; Lewis, 1964; Barnes & Barnes, 1966; Glémarec, 1979; Southward et al., 1995, 2005; Simkanin et al., 2005; Mieszkowska et al., 2006). In addition, the oceanographic context of Europe provides a complex mosaic of climatic zones from Portugal to the English Channel. Here, we examine the climate change in relation to the present and past distributions of the intertidal barnacle *Semibalanus balanoides* (L.) and the infaunal polychaete *Diopatra neapolitana* Delle Chiaje 1841. *Semibalanus* is a northern species with its southern limits in France and Spain, and *Diopatra* is a Mediterranean species with its northern limit in France.

Numerous hypotheses have been proposed to explain the geographic limits of species. Hutchins (1947) organized several of these hypotheses into the general categories of factors that limit adult distribution and factors that limit recruitment. He proposed, for example, that equatorward limits could be set by high summer temperatures causing adult mortality, or by winter temperatures being so warm as to limit reproduction. For *Semibalanus*, the summer thermal extreme hypothesis has been elaborated by such authors as Southward (1958) and Foster (1969) who identified the heat coma (37°C) and thermal death (42°C) limits for the species. The warm winter hypothesis has support in that temperatures above 10°C have been shown in the laboratory to inhibit reproduction (Barnes, 1958; Crisp & Patel, 1969; Barnes & Stone, 1972). More recently Davenport et al. (2005) proposed that day length might set the southern geographic limit of *Semibalanus*.

Here we test the summer heat death, day length, and winter cold limitation of reproduction hypotheses by examining the changes in the southern geographic limit of the species since 1872 in relation to climate change and to the geographic and temporal changes in day length.

For *Diopatra*, the northern limit is likely to be set either by cold winter temperatures or by summer temperatures too cold for reproductive success (Hutchins, 1947; Glémarec, 1979). In contrast to *Semibalanus*, little is known of its physiological limitations. However, extensive data exist for its congener *Diopatra cuprea*, which is common on the shores of the western Atlantic and has a very similar life habit. Both are large tube-building worms that construct a 30–50 cm tube in sediments with a tube-cap decorated with debris that extends above the sediment surface. Both species sit near the mouth of the tube and extend outward to feed. Nothing is known about *D. cuprea* reproductive failure relative to temperature. However, its northern limit is immediately north of Cape Cod (Mangum et al., 1968), reflecting the species' behavioral limitations in cold temperature conditions: *D. cuprea* does not feed below 5°C (Mangum & Cox, 1971) and does not build new tubes or repair tubes below 1.8°C (Myers, 1972). Low-temperature inhibition of tube building will be limiting in sedimentary habitats with cold winters where storm-driven erosion and deposition are common, necessitating constant tube maintenance. Given the similarity between the two species of *Diopatra*, we expected *D. neapolitana* to have similar behavioral limitations during cold periods. An alternative hypothesis is that geographic distribution is limited by cool summer conditions acting on adults or juveniles at the northern geographic limit (e.g., Hutchins, 1947). Here we examine the distribution of *D. neapolitana* to ask whether both the location of the northern limit as well as gaps within its distribution are consistent with the winter cold limitation hypothesis or the cool summer hypothesis, or both.

Biophysical context

Intertidal organisms are exposed to terrestrial conditions at low tide and to oceanic conditions at high tide, therefore, they experience enormous thermal extremes over the tidal cycle. At low tide their body temperatures can rise 10°C or more above sea water temperature (e.g., Southward, 1958; Vermeij, 1971; Etter, 1988; Helmuth, 1999; Wethey, 2002). At high tide they equilibrate rapidly to seawater temperature. Therefore, one should not assume that either air temperature or sea surface temperature is a good proxy for body temperature. We use a validated biophysical model of the transient dynamics of rocky-shore intertidal animal body temperature (Gilman et al., 2006) to hindcast the conditions experienced by rocky-shore intertidal animals over the past 50 years. Meteorological variables (air temperature, wind speed, humidity, cloud cover, solar radiation, and sea surface temperature) were obtained from the

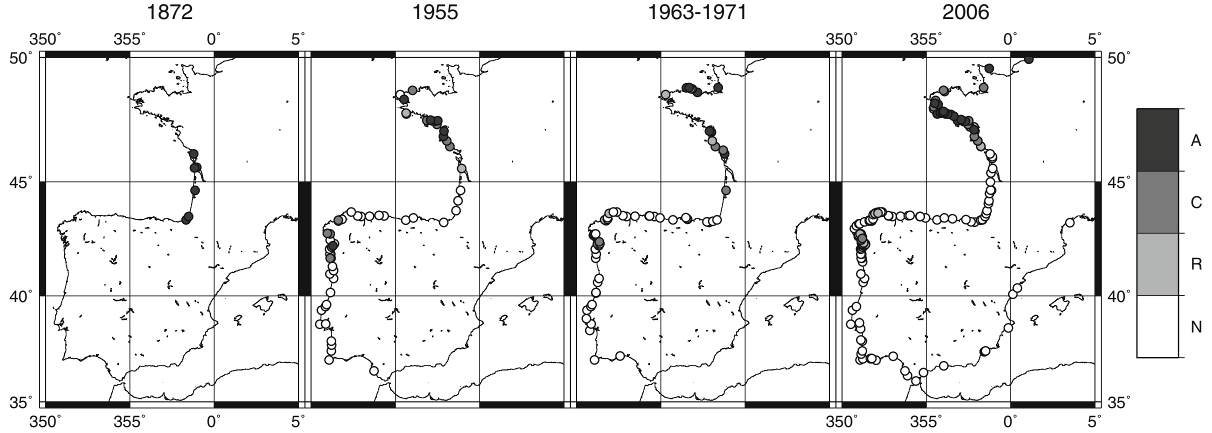

Fig. 1 Distribution of *Semibalanus balanoides* in 1872 (Fischer, 1872), 1955 (Crisp & Fischer-Piette, 1959), 1963 (Barnes & Barnes, 1966; Barnes & Powell, 1966), 1971 (Barnes et al., 1972) and 2006 (this study). Density Scale: A = Abundant, C = Common, R = Rare, N = Absent (ACFOR density scale: Crisp & Southward 1958)

NOAA global reanalysis project which estimated these variables on a worldwide 2° grid every 6 h back to 1948 (Kalnay et al., 1996). We used the reanalysis variables as inputs to our biophysical model, and calculated the average daily maximum and minimum temperature experienced by rocky-shore intertidal animals each month at sites from southern Portugal to northern France, encompassing the geographic limits of our species of interest.

Oceanographic and biogeographic context

Numerous authors beginning with Savageau (1897) have remarked that the shores and biota of northwest Spain have more in common with the shores and biota of northwest France than they do with the shores in between. This occurs because of strong upwelling in Galicia (NW Spain) and Brittany (NW France) which generates a cool oceanic and terrestrial climate. The shores in between the zones of upwelling on the northern Spanish coast and southern French Biscay coast are more like Morocco than other parts of Europe (Fischer-Piette, 1955). Floristic and faunistic surveys in the mid nineteenth to mid twentieth centuries confirmed the temperate characteristics of Galicia which contrast strongly with the rest of Iberia (e.g., Savageau, 1897; Fischer-Piette, 1955). For example, the northern algae *Fucus serratus* and *Ascophyllum nodosum* disappear in southern France and northern Spain, but reappear in Galicia and disappear again in Portugal (Fischer-Piette, 1955; Crisp & Fischer-Piette, 1959; Margalet et al., 1992, 1993).

Biogeographic surveys

The geographic distribution of *S. balanoides* (Fig. 1) was reported by Fischer (1872), Fischer-Piette (1955), Fischer-Piette & Prenant (1956, 1957), Crisp & Fischer-Piette (1959), Barnes & Barnes (1966), Barnes & Powell (1966), and Barnes et al., (1972). The geographic distribution of *D. neapolitana* (Fig. 4) was reported by Lafont (1871), Saint-Joseph (1898), Fauvel (1923), Faure (1969), Lagardère (1972a, b), Glémarec (1979) and Montaudouin et al. (2000). We resurveyed the Iberian and French coasts from Tarifa to Brittany in 2005 and 2006 at a spatial scale of 50–100 km (Figs. 1, 4). We used the geographic limits from these surveys to test the geographic hypotheses outlined in the Introduction.

Climate reconstructions

In order to hindcast the body temperature fluctuations experienced by rocky-shore intertidal animals since 1950, we used our validated biophysical model of intertidal body temperature (Helmuth, 1999; Wethey, 2002; Gilman et al., 2006). The model predictions are within 3°C of data logger averages, and 95% of predictions are within the range of datalogger observations over the US west coast from southern California to the Canadian border, for the period 2000–2004 (Gilman et al., 2006). These results indicate that the model is as good at predicting animal body temperature on rocky shores as the data loggers are at measuring it. At low tide, the model calculates the surface temperature of the organism and bare substratum based on a balance between short-wave solar radiation, convection, conduction to the substratum, evaporation, and long-wave radiation. Body temperature in the core of the animal and in the substratum is calculated by a finite-difference approximation to the thermal-conduction process. At high tide, the organismal body temperature is set to sea surface temperature. The model calculates all conditions every 30 s, so the daily cycles of heating and cooling are represented (Wethey, 2002). Historical tide levels were calculated using X-Tide (Flater, 2006). Meteorological variables (solar radiation, wind speed, air temperature, relative humidity, cloud cover, and sea surface temperature) were obtained from the global reanalysis carried out by the US National Centers for Environmental Prediction (Kalnay, 1996). The reanalysis data are available on a 2° grid every 6 h from 1948 to the present. Sea surface temperatures were obtained from the Hadley Centre GISST which has monthly worldwide values on a 1° grid from 1870 (Rayner et al., 2003). Modern sea surface temperatures were obtained from the NASA Jet Propulsion Laboratory Physical Oceanography Data Archive Center (podaac.jpl.nasa.gov). Monthly averages of 4 km grid-scale observations were obtained from the MODIS-Aqua sensor (2002–2006).

We calculate Average Daily Maximum and Average Daily Minimum body temperature for each month in our model runs (Gilman et al., 2006). These statistics give an indication of the monthly high and low temperatures experienced by rocky-shore intertidal animals. The daily maximum value is dependent largely on warming by short-wave solar radiation. The daily minimum temperature depends partly on sea surface temperature, and partly on night time conditions when animals lose heat by long wave radiation and evaporative cooling. For the equatorward limit of *Semibalanus*, the daily minimum value in the coldest month is a measure of the winter conditions associated with reproduction, and the daily maximum value in the hottest month is a measure of the summer conditions associated with adult survival.

Tests of geographic hypotheses

We examined hindcasts of body temperature maxima and minima at locations near the geographic limits of the species over the period 1950–2005. Short-term (annual scale) and long-term (decadal scale) changes in geographic limits were compared to changes in body temperature maxima and minima in order to test the hypothesis that high or low temperature could explain the species' geographic shifts. If climate change was not associated with change in the species' geographic distribution, then climate mechanisms would be falsified. If latitudinal distribution did not change over the past century then the day-length hypothesis would be corroborated.

Results

Geographic distribution and hindcasts of climate

Semibalanus balanoides

Semibalanus has a disjunct distribution, with one southern limit in France, and another in Galicia (Fig. 1). On the French coast in 1872, the southern limit was at least as far south as St. Jean de Luz, on the Spanish Border at 43.39° N (Fischer, 1872), in 1955 it was at the Pointe de Grave, 45.57° N (Crisp & Fischer-Piette, 1959), from 1963 to 1971 it expanded slightly southward from Arcachon, 44.66° N to Petit Nice, 44.57° N (Barnes & Powell, 1966; Barnes et al., 1972), and in 2006 it was at Les Sables d'Olonne, 46.49° N (Fig. 1).

On the Iberian coast in 1955 its southern limit was Teis near Vigo, Spain, 42.26° N, and its north-eastern limit was A Coruña, 43.37° N (Fischer-Piette & Prenant, 1956). In 1956 its southern limit was Viana do Castelo, Portugal, 41.70° N but the individuals there all died by 1957 (Fischer-Piette & Prenant, 1957). In 1963 its southern limit was Baiona, Spain, 42.12° N and its north-eastern limit was Serrantes, 43.38° N (Barnes & Barnes, 1966). In the mid to late 1960s its density in the Muros–Noia estuary was large enough that Barnes & Barnes (1976) used the Portosín (42.76° N) population for experiments on reproductive timing. In 1985, it was seen in Cambados, Spain, 42.52° N (A. J. Southward, personal communication). By 2006, its distribution in Galicia

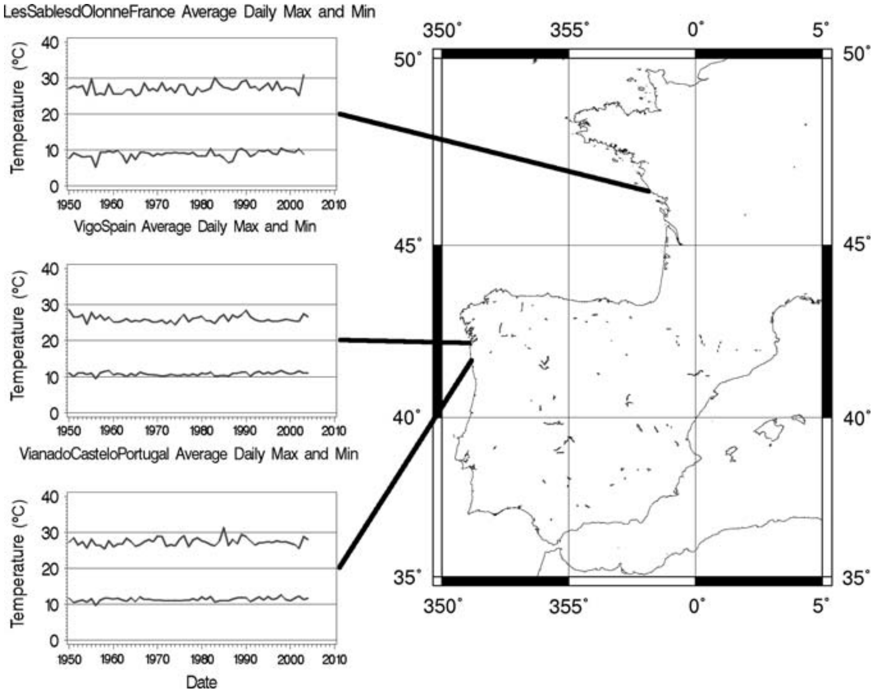

Fig. 2 Hindcasts of body temperatures of mid intertidal *Semibalanus* 1950–2004. *Top line*: average daily maximum temperature in the hottest month, *bottom line*: average daily minimum temperature in the coldest month. *Top graph*: Les Sables d'Olonne, France; *middle graph*: Vigo, Spain; *bottom graph*: Viana do Castelo, Portugal. The daily minimum body temperature in Viana do Castelo was 10°C only in 1956

consisted of an area where very rare, 10- to 15 year-old single adults were found, between Vigo, 42.20° N, and Ortiguera, 43.68° N. The only area where there was evidence of reproduction was in the Ría de Arousa between O Grove, 42.50° N, and Vilagarcía de Arousa, 42.58° N. In this region there were young adults within copulation distance of one another, and there was a broad age-structure including young of the year and older individuals. This represents a compression of the reproductive range of the species by 250 km within the past 10–15 years.

These records indicate that *Semibalanus* on the French coast shifted more than 300 km north between 1872 and 2006, half of which occurred between 1972 and 2006. The shift during the past 30 years was at a rate of 50 km per decade. On the Iberian coast, *Semibalanus* has contracted from reproductive populations throughout Galicia in the 1950s and 1960s to a single reproductive population in the Ría de Arousa in 2006. The survivors of the 1980s cohorts in Galicia have become so rare that no pairs of individuals within copulation distance remain, except in the Ría de Arousa. This is a contraction of 50 km from the south to 250 km from the north since the 1960s–1990s.

Model hindcasts based on Hadley SST and NOAA Reanalysis variables (1° and 2° grid scale) indicate that the one-year incursion of *Semibalanus* into Portugal in 1956 (Fischer-Piette & Prenant, 1956, 1957) coincided with a one-year cooling event when temperatures should have been low enough for reproduction in Viana do Castelo, i.e., below the 10°C winter minimum (Fig. 2).

Hindcasts indicate that Galicia in NW Spain has been a marginal habitat for *Semibalanus* for at least the past 50 years. The average daily minimum body temperature in the intertidal has remained slightly above 10°C for most of the period, indicating that reproduction would be unlikely based on large-scale oceanographic conditions (Fig. 2). In addition, there has been an increase in average daily minimum body temperature since the mid 1990s at all three locales modeled (Fig. 2). The grid scale of these values is problematic for an area with intense upwelling along a deeply indented coastline. Finer scale (4 km grid scale) analysis of sea surface temperature conditions can be carried out using NASA MODIS data which indicate that local upwelling occurs very close to the coast, at a much lower spatial scale than the sea surface temperature values available in the reanalysis data and the Hadley Centre GISST data. Individual Rías can be several degrees colder than the offshore water during upwelling events (Fig. 3).

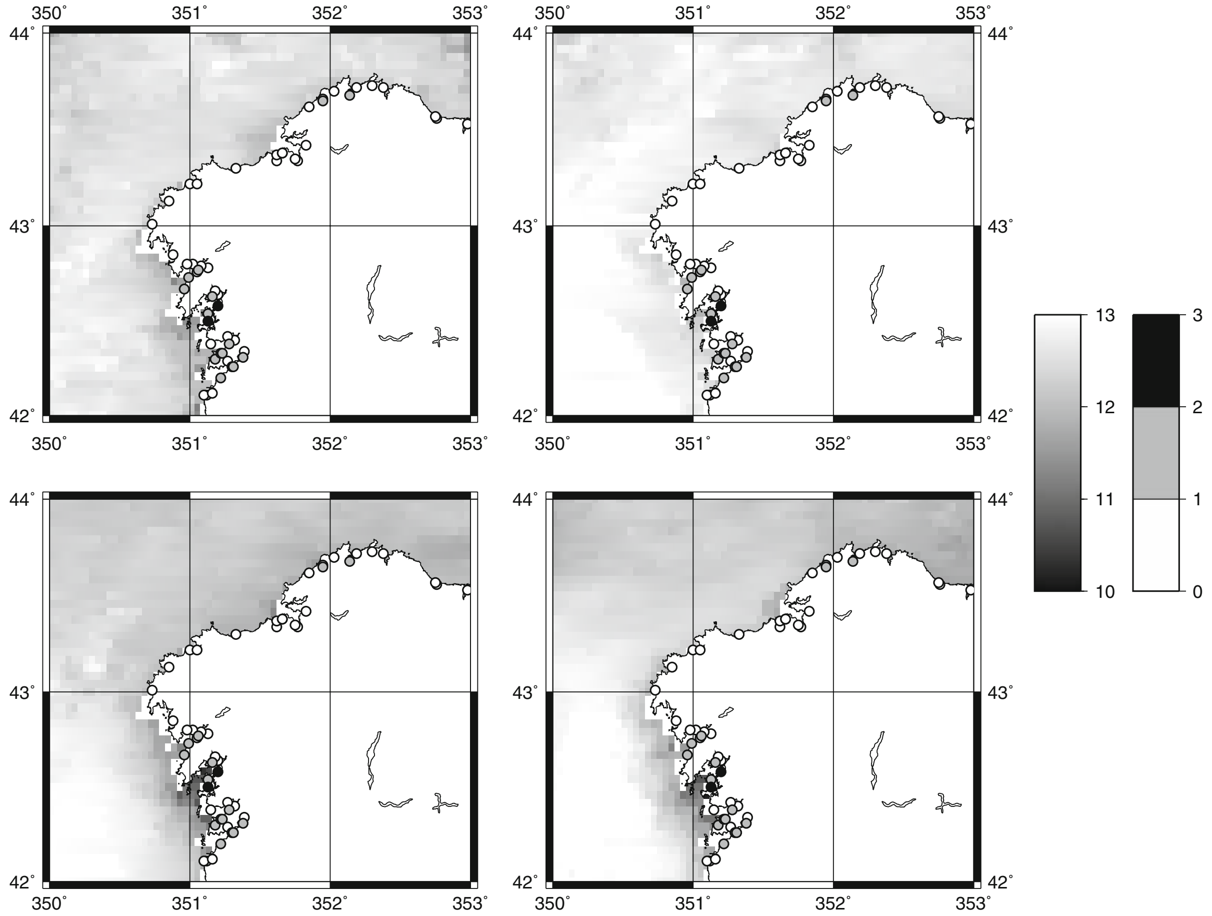

Fig. 3 Ocean temperatures in Galicia 2003–2006 from MODIS Aqua, and 2006 distribution of *Semibalanus*. Temperature scale on right. White areas in ocean next to coast indicate missing data. *Top left*: February 2003, *top right*: February 2004, *bottom left*: February 2005, *bottom right*: February 2006. *Semibalanus* abundance scale: 2–3: population with adults and juveniles; 1–2: population of old non-reproductive adults only; 0–1: absent

The 2006 age structure and restriction of *Semibalanus* reproduction to the Ría de Arousa in Galicia, NW Spain can be understood in relation to the fine scale temperature distribution in the region. The Ría de Arousa is the only estuary in Galicia where it has been cold enough for *Semibalanus* to reproduce during the years 2002–2006 (Fig. 3, dark gray color). This observation is consistent with physical oceanographic studies of the Rías Baixas estuaries in Galicia, which found that the Ría de Arousa is 1–2°C colder than the neighboring Ría de Vigo and Ría de Pontevedra (Alvarez et al., 2005).

The shift of the southern limit of *Semibalanus* on the French coast is consistent with changes in local marine conditions. The ocean climate of the Bay of Biscay has warmed during the past century. *Semibalanus* was common in Arcachon in 1972 (southern France, 44.66° N, Barnes et al., 1972), but strong warming occurred in the region between 1972 and 1993. Mean winter sea surface temperature (SST) increased from 10.6°C in 1971 to 11.8°C in 1993, and mean summer SST increased from 18.6°C to 19.9°C during the same period (Koutsikopoulos et al., 1998). By 2006, the *Semibalanus* southern limit had moved 150 km north (Fig. 1), where conditions have remained cooler (Fig. 2).

Diopatra neapolitana

Diopatra neapolitana is a Mediterranean species that occurs throughout Iberia (Fauvel, 1923). It was recorded from Arcachon, 44.66° N, in southern

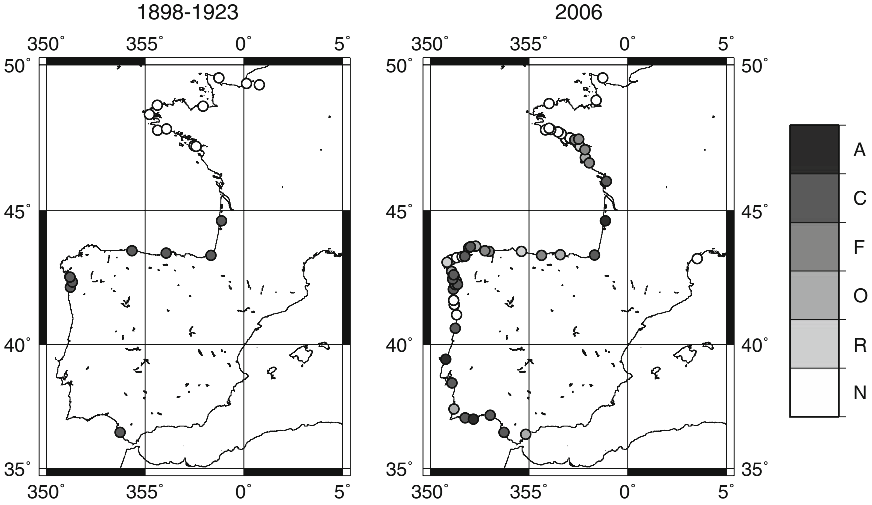

Fig. 4 Distribution of *Diopatra neapolitana* in 1898–1923 (Saint-Joseph, 1898; Fauvel, 1923) and 2006 (this study). Density scale: A = Abundant (>24 m^{-2}), C = Common (10–24 m^{-2}), F = Frequent (1–10 m^{-2}), O = Occasional (0.1–1 m^{-2}), R = Rare (<0.1 m^{-2}), N = Absent. Only presence or absence data were available from earlier work.

France, in 1869–70 (Lafont, 1871). Until 1923, the northern limit was at Arcachon; it was absent from Brittany (Saint-Joseph, 1898; Fauvel, 1923, Fig. 4). By 1966, the limit had shifted 100 km north to Châtelaillon-Plage, 46.06° N (Faure, 1969). It was also recorded from the southern tip of the Île d'Oléron, 45.85° N, (Lagardère, 1972a, b) in the late 1960s and at the mouth of the Gironde estuary, 45.57° N, (Glémarec, 1979) in 1969. By 1976 it had moved 60–130 km north to the region of St. Gilles Croix de Vie, 46.70° N (Glémarec, 1979).

Our surveys in 2006 show that the northern limit of *Diopatra* has shifted 300 km north since 1923, to Pointe de Penvins (47.50° N) in Brittany (Fig. 4). We observed the species at locations where Saint-Joseph (1898) was unable to find it although he searched for it, and we have confirmed Glémarec's (1979) observations of the species in the region between the Gironde and the Loire rivers. In addition, we identified a gap in the *Diopatra* distribution on the Portuguese coast, between Porto (41.14° N) and Viana do Castelo (41.70° N). In this gap, we searched Porto (41.14° N), Vila do Conde (41.34° N), Ofir (41.52° N), Esposende (41.54° N), Darque (41.69° N), and Viana do Castelo (41.70° N) without success. We searched semi-exposed and sheltered shores where we would expect to see *Diopatra*, based on its distribution elsewhere in Europe. This gap is in the same region of coastal upwelling where there have historically been gaps in the distribution of tropical species like *Patella rustica* (Fischer-Piette, 1955; Boaventura et al., 2002; Lima et al., 2006). The distribution within the remainder of Galicia in Spain continues as a mosaic, perhaps reflecting the hydrographic conditions. There is another mosaic distribution near the geographic limit on the French coast. In the mosaic regions, localities with abundant *Diopatra* are interspersed with localities, where it is absent (Fig. 4). For example in southern Brittany, *Diopatra* is rare but present at La Baule, 47.27° N, absent at Piriac, 47.38° N, but frequent at the Dolmen des Crapauds, 47.52° N. In southern Galicia *Diopatra* is common at Baiona, 42.12° N (Anadon & Anadon, 1973; Moreira et al., 2006; Xunta de Galicia, 2006), absent at the Playa de Foz in Vigo, 42.20° N, and is common again across the Ría from Vigo in Meira, 42.29° N and is common further up the Ría in Redondela (Xunta de Galicia, 2006). In northern Galicia, it is present in Noia, 42.79° N, absent in Baldaio, 43.30° N and Santa Cristina, 43.34° N, but common at Sada, 43.35° N. We searched extensively in appropriate habitats and did not find *Diopatra* in the locations where we recorded it as absent.

Discussion

Tests of biogeographic hypotheses for *Semibalanus balanoides* by modeling and observation

Summer heat death hypothesis

The summer heat death hypothesis (Hutchins, 1947) postulates that adult survival is restricted at the

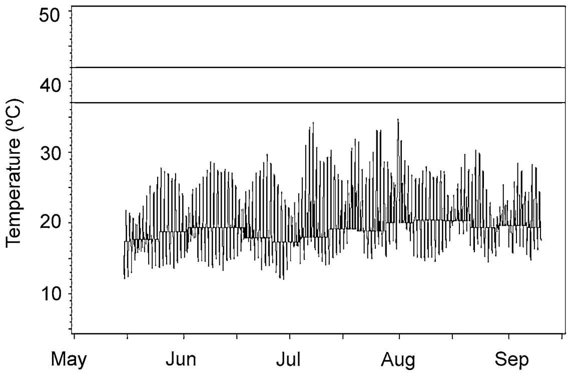

Fig. 5 Modeled summer body temperatures of *Semibalanus* on north-facing mid-shore surfaces near Lisbon, south of the southern limit of the species on the Portuguese coast. Horizontal lines are 37°C (coma) and 42°C (lethal) temperatures

southern geographic limit by high temperatures. Our hindcasts from 1950 to 2005 indicate that it is not hot enough in southern Portugal to kill adult *Semibalanus*. In shaded locations such as mid shore level north-facing slopes, temperatures are likely to be below the coma threshold of 37°C (Fig. 5). This temperature does not cause adult death (Foster, 1969) or reduction in juvenile survival (Wethey, 2002). For this reason, shaded surfaces would serve as thermal refuges for the species. We therefore reject the summer heat death hypothesis.

Day-length hypothesis

The day-length hypothesis (Davenport et al., 2005) postulates that reproduction is dependent upon shortening day length, and that there is geographic variation in response. Extrapolation of the latitude-day of year regressions indicated that the southern limit of *Semibalanus* should be either in southern France or in Galicia (Davenport, 2005). This hypothesis does not explain the geographic changes in the distribution of the species over the past 100 years, unless one hypothesizes that day length has changed over that period. It also does not explain the 1957 incursion of *Semibalanus* into northern Portugal. We, therefore, reject the day-length hypothesis.

Winter cold limitation of reproduction hypothesis

The winter cold limitation of reproduction hypothesis (Barnes, 1963; Barnes & Stone, 1972; Crisp & Patel, 1969) postulates that reproduction fails if temperatures remain above 10°C during winter months. In laboratory culture experiments, animals held at temperatures above 10°C failed to reproduce. In addition, on the Normandy coast of France, the recruitment of *Semibalanus* over the period 1983–2004 was negatively correlated with temperature in the coldest winter month, with minimum recruitment occurring in 1990 when average air temperature was 8.7°C, and maximum recruitment occurring in 1986 when average air temperature was 2.2°C (Drévès, 2001; Drévès et al., 2005). Our climate hindcasts are consistent with this hypothesis. The 1956 incursion of *Semibalanus* into Portugal was coincident with a cooling event with minimum winter body temperatures around 10°C (Fig. 2). Populations at the 2006 southern limit in France do not appear to have been at risk of reproductive failure over the past 50 years (Fig. 2). In contrast, the populations in NW Spain appear to have been very close to the reproductive failure limit over the past 50 years (Fig. 2). In 2006, the geographic distribution of populations with multiple age classes in NW Spain, and geographic distribution of successful reproduction are coincident with locations where water temperatures are in the 10–11°C range (Fig. 3). The range shift on the French coast between 1972 and 2006 was coincident with winter warming in the Bay of Biscay (Garcia-Soto et al., 2002) and a shift in the position of the 10–11°C isotherms (Koutsikopoulos et al., 1998). We, therefore, believe that the winter cold limitation of reproduction hypothesis has been corroborated by multiple lines of evidence.

Tests of biogeographic hypotheses for *Diopatra neapolitana*

Winter cold limitation hypothesis

Our prediction of limitation due to winter cold temperatures for *D. neapolitana* was by analogy to its congener *D. cuprea*. Based on data for *D. cuprea* we expected *D. neapolitana* to be limited by winter cold temperatures that interfere with normal behaviors, such as tube repair and feeding (Mangum & Cox, 1971; Myers, 1972). Thus the movement of its distribution northward, corresponding to the displacement northward of the winter 10–11°C isotherms (Koutsikopoulos et al., 1998), is consistent with this

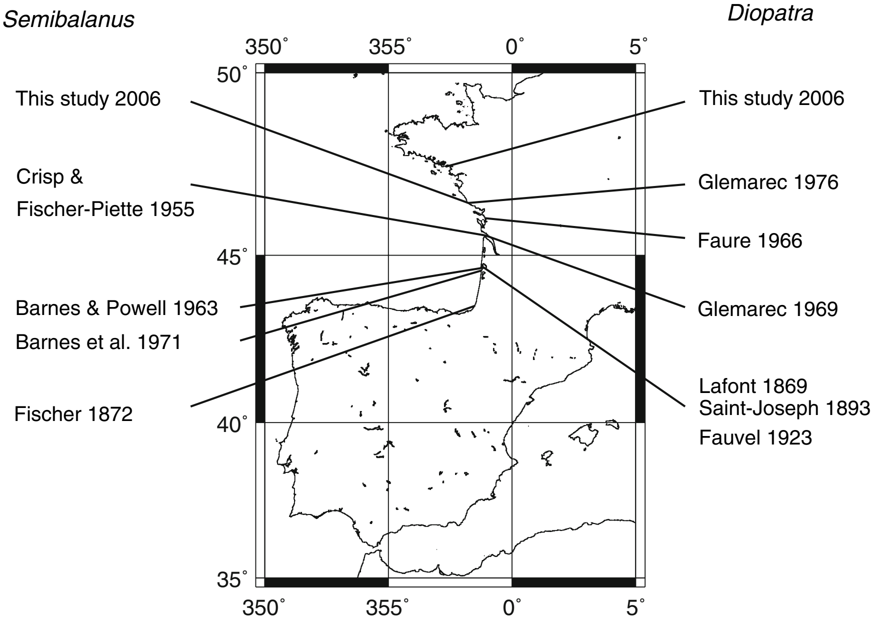

Fig. 6 Shifts in the southern limit of *Semibalanus* and the northern limit of *Diopatra* in France between 1869 and 2006. The two species overlapped by 100 km in the early twentieth century, and overlapped by the same amount both in the late 1960s and again in the early twenty-first century, but the zone of overlap has shifted 300 km north. Dates of surveys are listed, which are usually earlier than the publication dates of the papers: Fischer 1872 (Fischer, 1872), Crisp & Fischer-Piette 1955 (Crisp & Fischer-Piette, 1959), Barnes & Powell 1963 (Barnes & Powell, 1966), Barnes et al., 1971 (Barnes et al., 1972), Lafont 1869 (Lafont, 1871), Saint-Joseph 1893 (Saint-Joseph, 1898), Fauvel 1923 (Fauvel, 1923), Glémarec 1969 (Glémarec, 1979), Glémarec 1976 (Glémarec, 1979)

prediction and is consistent with the patterns of movement of both *Semibalanus* and *D. neapolitana* which have been associated in distribution pattern for over 100 years (Fig. 6).

Summer cold-limitation hypothesis

An alternative hypothesis is that *Diopatra* is restricted by cool summer conditions at its northern limit. In order to explore the possibility of a cool summer limitation, we examined MODIS sea surface temperature records for August 2005 from southern Portugal to Brittany in NW France. August is the time of warmest sea surface temperatures in this region. We used 2005 because it was the year prior to our sampling, and therefore probably had the greatest influence on the population densities that we measured. There is a summer thermal threshold in the geographic distribution of *Diopatra* near 17°C. *Diopatra* was absent in 2006 from all locations where August 2005 sea surface temperatures were below 17°C except for three sites in Galicia in NW Spain (Fig. 7). The distributional gap in Portugal occurs in locations where temperatures were between 15.9°C and 17.2°C (Fig. 7, solid triangles). This area on the central Portuguese coast has been cooler than the regions north and south at least since the 1950s (Lima et al., 2006). The northern limit of *Diopatra* in NW France also occurs where temperatures were between 16°C and 17.4°C (Fig. 7, open circles). Other locations where *Diopatra* was absent within its broadscale geographic range had temperatures between 16.8°C and 17.9°C (Fig. 7, open triangles). Clearly, we need additional data on *Diopatra* to understand these patterns, particularly asking if cool summers influence reproduction or recruitment (Figs. 4, 7). Nevertheless, cool summers appear to be stronger limiting factors than cold winters, in that they provide an explanation for both the distributional gaps and the northern limit.

Concluding remarks

The rates of climate-related geographic change that we have documented for species in the intertidal zone are

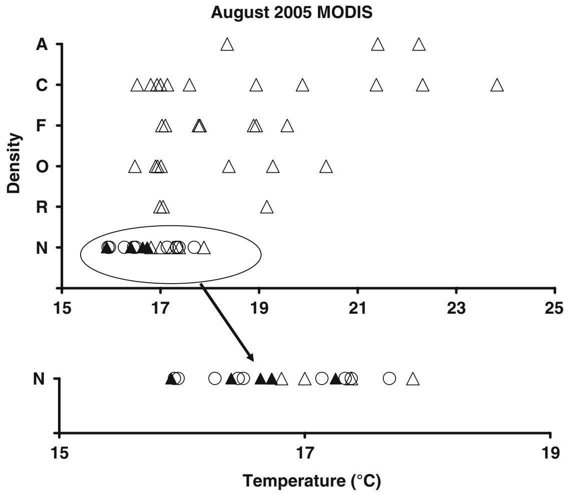

Fig. 7 Relation between semiquantitative *Diopatra* population density in 2006 and monthly mean MODIS 4 km sea surface temperature in August 2005. Density scale on the ordinate is maximum density: A = Abundant (>24 m^{-2}), C = Common (10–24 m^{-2}), F = Frequent (1–10 m^{-2}), O = Occasional (0.1–1 m^{-2}), R = Rare (<0.1 m^{-2}), N = Absent. *Solid triangles*: gap in geographic distribution between Porto, Portugal (41.14° N) and Viana do Castelo, Portugal (41.70° N). *Open circles*: locations beyond the northern limit in Brittany. *Open triangles*: mosaic region of presence and absence in Galicia and Brittany. *Lower panel* is an enlarged version of the data for density = N (absent): note temperature scale change. MODIS sea surface temperature data were not available for the location of high density populations in the Aveiro (40.63° N) estuary

much larger than those reported for most habitats. A meta-analysis by Parmesan & Yohe (2003) estimated an average rate of 6.1 km per decade for 1700 species, with a maximum shift of 25 km per decade in butterflies (Parmesan et al., 1999), and 250 km per decade for marine planktonic copepods (Beaugrand et al., 2002). Marine intertidal species in the United Kingdom have shifted 50 km over the past half century (Helmuth et al., 2006). Our observed range shifts in *Semibalanus* are 250 km in the last 10–15 years in Galicia, and 15–50 km per decade in France, measured over the past 30–100 years and those of *Diopatra* are comparable (Fig. 6). Jansen et al. (2007) have reported a range shift of 300 km since 1980 in the bivalve *Macoma balthica* in the same geographic region. These rates are consistent with the analyses of Hansen et al. (2006), who documented sea surface temperature isotherm shifts of 30–60 km per decade in Europe over the period 1975–2005.

We have documented parallel range shifts for a rocky intertidal species (*S. balanoides*) and a soft-sediment intertidal species (*D. neapolitana*). Both species' ranges overlapped by approximately 100 km in the southern Bay of Biscay in the early twentieth century (Fig. 6). By the late 1960s, they had both moved 100 km north (Fig. 6). They still overlap by the same amount in 2006, but have now shifted 300 km to the northern Bay of Biscay (Fig. 6). This parallel range shift implies that similar mechanisms are limiting the southern limit of *Semibalanus* and the northern limit of *Diopatra*. The barnacle is an intertidal species that is exposed to large thermal fluctuations every day at low tide (e.g., Wethey, 2002), and the polychaete is a mid to low intertidal species that experiences much smaller thermal fluctuations on a daily basis (e.g., Woodin, 1974; Harrison & Phizacklea, 1987). The most likely common condition influencing the two species is sea surface temperature, and possibly its effect on reproductive success (e.g., Barnes, 1963; Barnes & Stone, 1972; Crisp & Patel, 1969) and activity rates (Mangum & Cox, 1971; Myers, 1972).

As climate continues to warm, we expect that the southern limits of temperate species like *S. balanoides* will shift farther north, at least to the long term biogeographic boundary at the Cherbourg Peninsula in the English Channel (e.g., Fischer-Piette, 1932; Cabioch et al., 1977). Populations of *Semibalanus* near Plymouth have decreased in previous warm spells (Southward, 1963, 1991; Southward et al., 1995). In warming conditions we expect that the northern limits of sub-tropical species like *D. neapolitana* will shift northward in parallel with retreats of temperate species (Fig. 6). If summer sea surface temperatures around the Brittany peninsula rise 1 or 2 degrees, *Diopatra* may be able to colonize the English Channel, which is already warm enough (18–20°C in August 2005) to support dense populations. Other important rocky-shore species, such as canopy-forming algae and keystone grazers like limpets in the genus *Patella*, will most likely shift at the same time (Kendall et al., 2004; Southward et al., 1995, 2005). Other infaunal species have begun to shift northwards, apparently as a result of regional warming and consequent metabolic limitations. *Macoma balthica*, for example, is a northern species of bivalve that is no longer found in Galicia on the Iberian Peninsula (Jansen et al., 2007). Such range shifts will fundamentally change the characteristics of the European intertidal zone, so that the future intertidal of France will faunistically resemble northern Spain and Morocco. In addition, we predict concurrent changes in intertidal communities to the north and to the south. Much of the biogeographic change in the past century appears to have been concentrated in the last decade (Fig. 1), coincident with the most rapid rate of climate warming of the past century (e.g., Hansen et al., 2006). We, therefore, expect that the rate of change of species distributions will be rapid and accelerating. The intertidal zone is a model system for examining the effects of climate change on biogeographic and community change both because of the rapidity of its response, and because the rich historical record allows direct tests of a wide range of mechanistic biogeographic hypotheses.

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