

Long-term changes in the geographic distribution and population structures of *Osilinus lineatus* (Gastropoda: Trochidae) in Britain and Ireland

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Since the rate of global climate change began to accelerate in the 1980s, the coastal seas of Britain have warmed by up to 1°C. Locations close to the northern range edges of a southern trochid gastropod *Osilinus lineatus* in Britain previously surveyed in the 1950s and 1980s were resurveyed during 2002–2004 to determine whether changes in the success of near-limit populations had occurred during the period of climate warming. Between the 1980s and the 2000s, the range limits had extended by up to 55 km. Populations sampled over a latitudinal extent of 4 degrees from northern limits towards the centre of the range showed synchronous increases in abundance throughout the years sampled, suggesting a large-scale factor such as climate was driving the observed changes. These increases in abundance and changes in range limits are likely to have occurred via increased recruitment success in recent years.

INTRODUCTION

The global average surface temperature has been increasing since records began in 1861, with an acceleration in the rate of warming since the mid-1980s (Levitus et al., 2000; Houghton et al., 2001; Hulme et al., 2002) in response to increased anthropogenic emissions of greenhouse gases (Easterling et al., 2000; Houghton et al., 2001; Hughes et al., 2002). Many of the effects of global warming have been felt in the oceans (Barnett et al., 2000). The north-east Atlantic has shown some of the largest increases in sea surface temperatures globally, warming between 0.5 and 1°C over the last 20 years (e.g. Hawkins et al., 2003; Southward et al., 2005; Woehrling et al., 2005). This rise in sea surface temperature (SST) is twice the rate of any previous warming event recorded (Mann et al., 1998, 1999). Shifts in the geographic distribution and abundance of a diverse range of marine species have occurred during the current period of global warming, including macroalgae (Lubchenco et al., 1993; Navarette et al., 1993), zooplankton (Beaugrand et al., 2002; Beaugrand & Ibanez, 2004), littoral invertebrates (Bianchi & Morri, 1994; Root et al., 2003; Zacherl et al., 2003; Herbert et al., 2003), corals (Hoegh-Guldberg, 1999; Precht & Aronson, 2004) and fish (Stebbing et al., 2002; Genner et al., 2004; Perry et al., 2005). Further polewards range shifts in marine ecosystems are predicted as the climate continues to warm (Lubchenco et al., 1993; Southward et al., 1995; Lewis et al., 1996). In order to detect and quantify the extent of changes in species distributions and separate short-term and small-scale natural spatial and temporal variability from the changes driven by global climate change, the biogeographies of species need

to be characterized quantitatively. In particular, detailed information on the location of boundaries and the structure and abundance of populations at range borders is required (Maurer & Nott, 1998; Gaston, 2003; Fortin et al., 2005).

Britain and Ireland straddle a biogeographic boundary between cold, boreal waters to the north and warm, lusitanian waters to the south (Forbes, 1853) and many marine species reach their northern or southern limits of distribution close to this border (Lewis, 1964; Briggs, 1974). It is therefore an ideal location for studying the effects of climate warming on marine species. As the current warming trend continues, 'southern' warm water species are expected to extend their distributions and increase in abundance, whilst 'northern' cold water species are likely to show range contractions and decreases in abundance around the British coastline (Southward et al., 1995) in response to the polewards movement of seasonal isotherms as the global climate warms. Extensive surveys of the distribution of rocky intertidal species were made around the coastlines of Britain, Ireland and the northern European mainland from the 1930s to the 1950s (e.g. Fischer-Piette, 1936; Southward & Crisp, 1954; Fischer-Piette, 1955; Crisp & Fischer-Piette, 1958; Crisp & Southward, 1958) and during the 1970s and 1980s (Hawthorne, 1965; Bowman & Lewis, 1986; Kendall & Lewis, 1986; Kendall, 1987). These data in conjunction with resurvey data collected between 2002 and 2004 showed that the northern and north-eastern ranges of several warm water species of rocky intertidal invertebrates and algae had extended by up to 85 km in Britain since the onset of the current period of climate warming (Herbert et al., 2003; Mieszkowska et al., 2005, 2006).

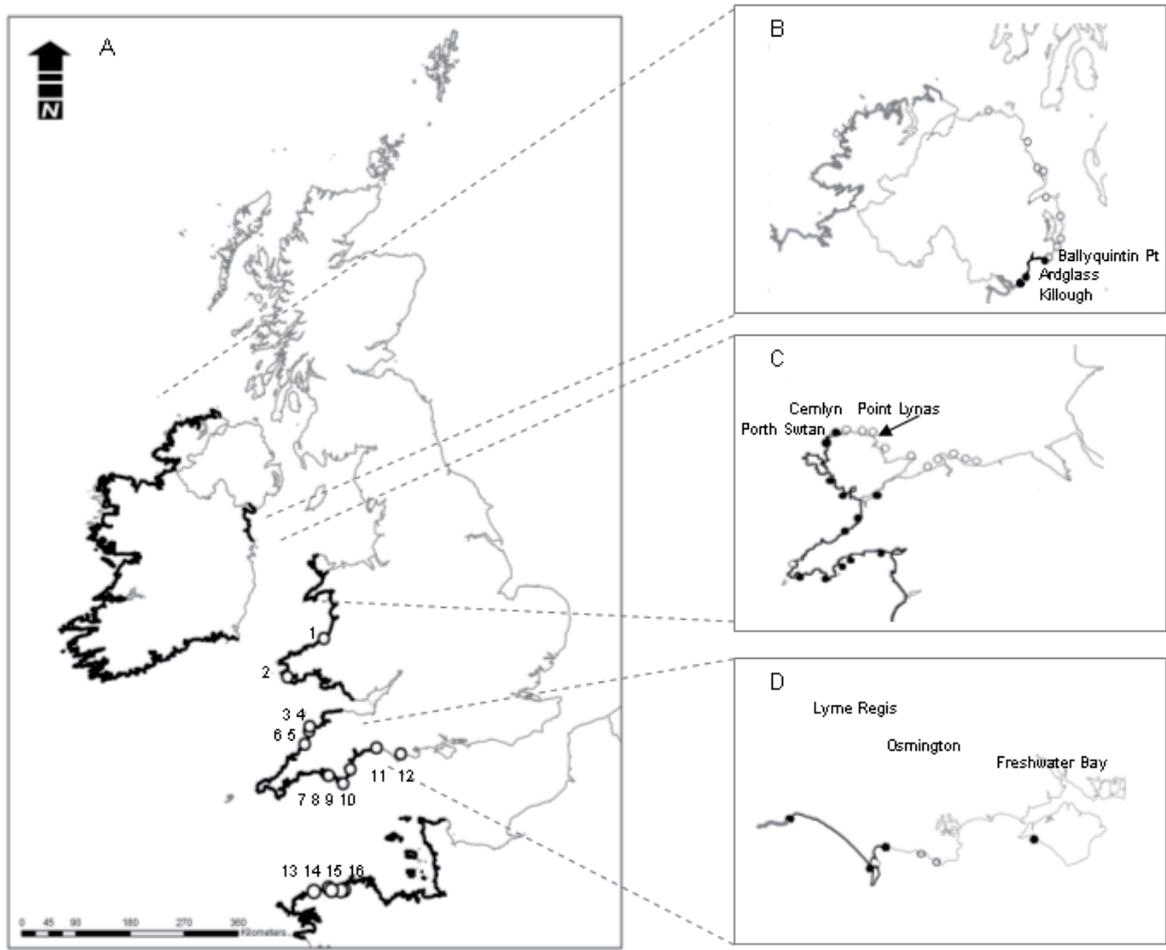


Figure 1. (A) Previous recorded north and eastern limits of distribution of *Osilinus lineatus* (black line) (from Southward & Crisp, 1954; Crisp & Southward, 1958; Lewis, 1964). Quantitative sampling sites from Kendall (1987) and 2002 resurveys in Britain and France (open circles): 1, Aberaeron; 2, West Angle Bay; 3, Hartland Quay; 4, Welcombe; 5, Widemouth; 6, Crackington Haven; 7, Wembury; 8, Noss Mayo; 9, Prawle; 10, Churston; 11, Lyme Regis; 12, Osmington Mills; 13, Locquirec; 14, Le Guersit; 15, Ile Calot; 16, Roscoff; 17, Brignogan; (B), (C) and (D) range extensions in Northern Ireland, North Wales, English Channel (black line), previous range (grey line), closed circles, *O. lineatus* present; open circles, sites where *O. lineatus* not found in 2002.

Study Species

Osilinus lineatus (da Costa) (previously *Monodonta lineata*) is a warm water species of prosobranch trochid gastropod occurring in the rocky intertidal zone (Desai, 1966) of moderately exposed shores throughout the north-east Atlantic. This species reaches its northern limits of distribution in Wales and Ireland, and its eastern limits in southern England (Southward & Crisp, 1954; Crisp & Southward, 1958). Distribution is continuous along the Portuguese, Spanish and French coastlines, and the southern limits of distribution are reached in Morocco (Lewis, 1986). *Osilinus lineatus* is one of the most abundant grazing species occurring on the rocky shores of Europe, and feeds predominantly off the biofilm on rock surfaces (Desai, 1966; Hawkins et al., 1989). The adult stage is sedentary and is found on boulders or rocky platforms in the midshore region, although some vertical movement within a shore can occur in response to daily and seasonal cycles of tides and environmental regimes (Crothers, 2001). *Osilinus lineatus* is an annual broadcast spawner (Garwood & Kendall, 1985; Bode et al., 1986; Kendall, 1987), with

a lecithotrophic larval stage lasting only a few days (Desai, 1966). New recruits settle within the same habitat on the shore as adults, but microhabitat segregation may exist as recruits tend to favour more cryptic habitats (Crothers, 2001) under boulders and in cracks and crevices. Juveniles become sexually mature at approximately two years of age as they enter the adult population (Desai, 1966; Garwood & Kendall, 1985; Crothers, 2001). Adult *O. lineatus* can live in excess of ten years (Kendall, 1987) although lifespans are thought to be shorter at lower latitudes (Bode et al., 1986).

In 1952, the northern limits of distribution of *O. lineatus* in Ireland, defined here as the last multi-age, breeding population, were recorded at Malin Head in the north and Killough in the north-east, with no animals occurring between these locations (Crisp & Southward, 1954). A population of *O. lineatus* was again recorded at Killough in 1971 by R. Anderson (J. Nunn, personal communication) but no published records exist for sites north of this location. The previous northern limit of distribution of *O. lineatus* in Britain was Point Lynas, on Anglesey, North Wales (Crisp & Knight-Jones, 1954; Lewis, 1964). An unconfirmed

record of an individual in the Great Orme in the 1940s is the only instance of individuals occurring past this location. Populations were eradicated or cut back in the severely cold winter of 1962/1963 (Crisp, 1964) to the south of the Llyn Peninsula in North Wales, and re-colonization of sites was minimal throughout the 1980s and 1990s, with only isolated individuals being found at Rhosneigr, Anglesey in the mid-1980s and in 1992 (S.J. Hawkins, personal observation). The most eastern multi-age population was recorded at Lyme Regis in the western basin of the English Channel during the 1950s, 1960s and 1980s (Southward & Crisp, 1958; Hawthorne, 1965; Kendall, 1987), with isolated individuals recorded as far east as St Aldhelm's Head (Hawthorne, 1965). A reduction in population sizes was seen in the English Channel after the 1962/1963 winter, but mortalities were not as severe as in Welsh populations (Crisp, 1964).

This paper combines archived records from the work of Crisp & Southward (1958) and the Wellcome Marine Laboratory at Robin Hood's Bay carried out during the 1970s and 1980s with resurvey data collected between 2002 and 2004 to investigate changes in the distribution of *Osilinus lineatus* since the current period of global warming began in the mid-1980s. We present resurveys of shores close to and beyond previously recorded distributional limits to determine if any extensions in range have occurred. We use abundance data collected in 1986 and 2002, 2003 and 2004 to test the hypothesis that population densities have significantly increased since the current period of climate warming began. We examine whether such changes have occurred synchronously between populations close to range limits and populations located further into the range, as would be expected if a large scale driver such as climate were responsible. Population age and size data is used to test the hypothesis that extensions in the range of *O. lineatus* in Britain and increases in population densities are being driven by increased survival of new recruits within populations at and close to distributional limits in Britain and northern France in response to warmer marine climate in the last two decades.

MATERIALS AND METHODS

Temperature data

Mean monthly sea surface temperature (SST) data from 1870–2004 were obtained from the Hadley Centre HADSST2 dataset with a spatial resolution of 1° latitude by 1° longitude for the western English Channel. From this the annual mean SST and mean winter SST were extracted.

Field surveys

The 16 sites from Kendall's 1986 quantitative survey of rocky shores close to the north and eastern range limits on English, Welsh and French coasts (Kendall, 1987) were resurveyed during 2002 (Figure 1) by the same operator as in 1986 (Kendall) and/or a cross-calibrated operator (Mieszkowska). The same methodology was used in the original surveys and resurveys. At each shore, intensive searches were made for *Osilinus lineatus* between mean tide level and mean high water neaps, focusing on the optimal habitat for *O. lineatus* of medium sized rocks over gravel, or

rock fragments in which '0' cohort individuals (animals less than 1 year old) occur. The operator randomly surveyed the shore by searching the immediate area on hands and knees, turning over small boulders and rocks and collecting all individuals found before moving to an adjacent section of the shore. At each site five replicate three minute collections of snails were made. The basal diameter of all animals collected was measured to the nearest millimetre, and individuals were aged by counting the annual growth checks on the shell to determine their year of settlement (Williamson & Kendall, 1981). These measurements were made after the collection process and all animals were subsequently returned to the shore. Repeat surveys were also made annually in the spring of 2003 and 2004 at a subset of ten sites in south-west Wales and England, using the same methods as above to provide data on inter-annual fluctuations in abundance. Additional searches were carried out in suitable habitat on rocky shores immediately beyond the previous recorded geographic limits in Northern Ireland, Wales and England (Figure 1B–D) between 2002 and 2004 (Crisp & Knight-Jones, 1954; Crisp & Southward, 1958; Crisp, 1964; Hawthorne, 1965; Kendall, 1987) to record if *O. lineatus* was present. If more than a few individuals were encountered, five replicated timed collections of three minutes duration were made according to the methods described above to allow comparisons with the existing survey sites.

Data analysis

Abundance was compared at all 16 of Kendall's sites between 1986 and 2002 using a matched-pairs *t*-test on the means. The variation in abundance between the years 1986, 2002, 2003 and 2004 was compared at a subset of ten sites where repeat data had been collected using a two-way analysis of variance (ANOVA), with site and year as the main effects. A planned comparison test was then made between 1986 and 2002–2004. This partitioned the variance associated with the 'years' effect and determined whether the inter-annual variation in abundance across the sites was less than the between-decade variation. The degree of synchrony of changes in abundance across nine sites for which data exists in 1986, 2002, 2003 and 2004 was calculated using Kendall's test for concordance, followed by a Friedman's test to determine significance. The changes in maximum size (D_{\max}), maximum age (A_{\max}), size and age at the 90th percentile (D_{90} , A_{90}) of cumulative size and age frequencies between 1986 and 2002 were tested using matched pairs *t*-tests (on log₁₀ transformed data for D_{90}) from 15 and 16 sites respectively where data exists from 1986. The 90th percentiles were obtained by calculating the diameter at the point on the size frequency curve where 90% of the sample population were included. The mean size of new recruits (year 1 cohort), animals reaching sexual maturity (year 2 cohort) and adult animals (year 4 cohort) were compared for 12 sites in 1986 and 2002 using paired *t*-tests to determine if the growth suppression that was indicated by the results of the tests on age and size could be identified within a particular life-stage. Regression analysis was carried out on the 1986 and 2002 data to examine the relationship between size (shell diameter) and abundance across all 16 sites close to range edges in both years. The

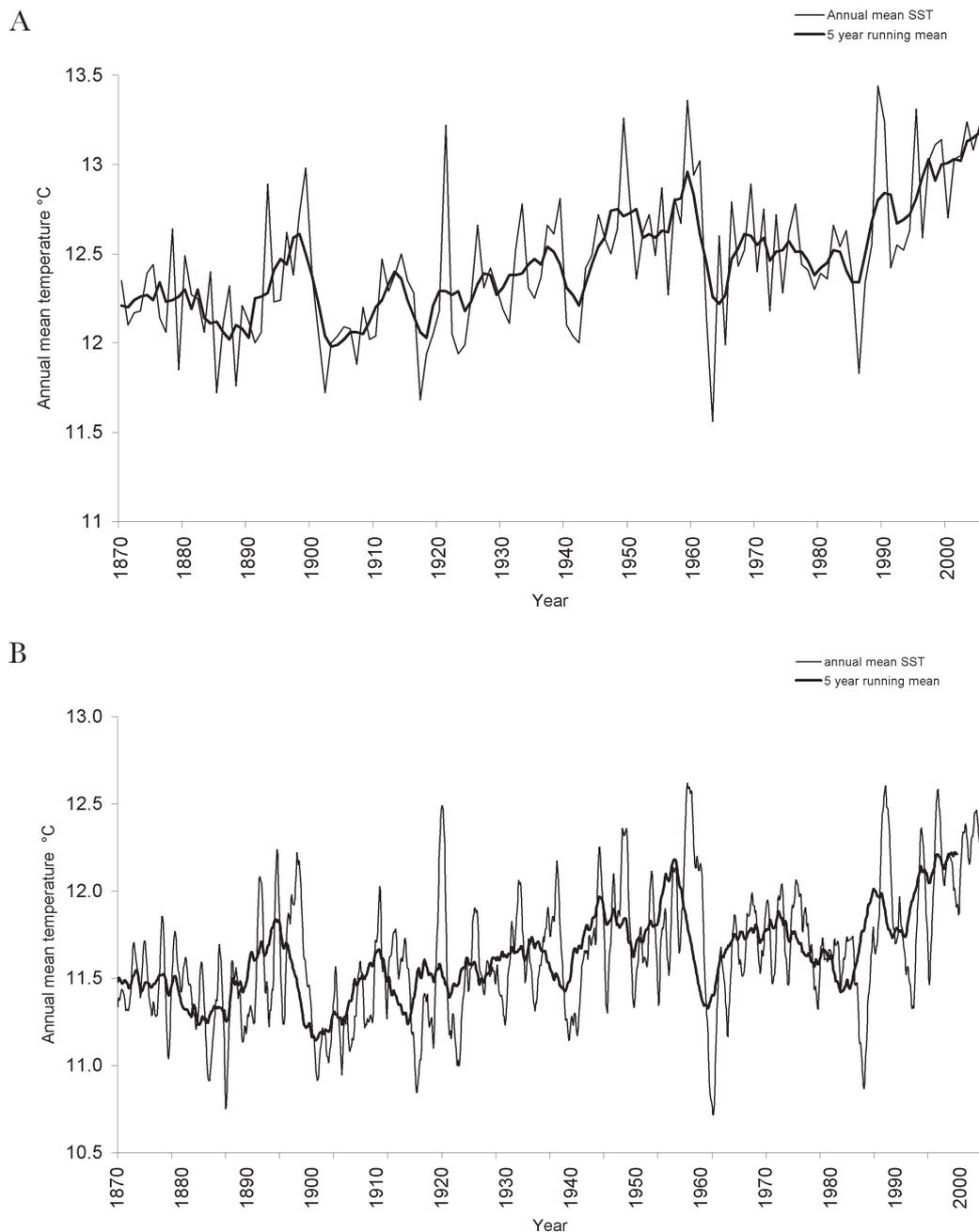


Figure 2. Annual mean sea surface temperature (SST) for (A) in the western English Channel (50–51°N 4–5°W) and (B) in the Irish Sea (52–53°N 4–5°W). Met Office - GISST/MOHSST6 SST (1870–2005) data provided to the MarClim project by kind permission of the British Atmospheric Data Centre.

variation in the slopes of the resulting regression lines was compared using an analysis of covariance (ANCOVA) to determine whether the relationship between abundance and size had altered between the 1980s and 2000s.

RESULTS

Temperature records

Temporal and spatial variation in the extent of warming has been recorded around the British coastline. Mean SST has significantly warmed by $\sim 1^\circ\text{C}$ since modern records began in 1870 ($R^2=0.56$, $F=52.49$, $P<0.0001$, $df=133$) in the western English Channel (Figure 2A). This is greater than in the Irish Sea, where mean annual SST has increased by

$\sim 0.5^\circ\text{C}$. The 1950s was a generally warm decade, with cooler weather following the extremely cold winter of 1962/1963 until the mid 1980s (Figure 2B). Winter minima decreased throughout the 1970s and early 1980s, with accelerated warming becoming apparent from 1987 onwards. Seasonal SST ranges have also decreased over the last two decades as winter temperatures have significantly increased ($R^2=0.083$, $P=0.089$, $F=3.07$, $df=34$) (Figure 3A,B) at a faster rate than the increase in mean summer temperatures.

Changes in geographical distribution

Re-colonization of sites throughout North Wales that were eradicated during the cold winter of 1962/1963 had occurred

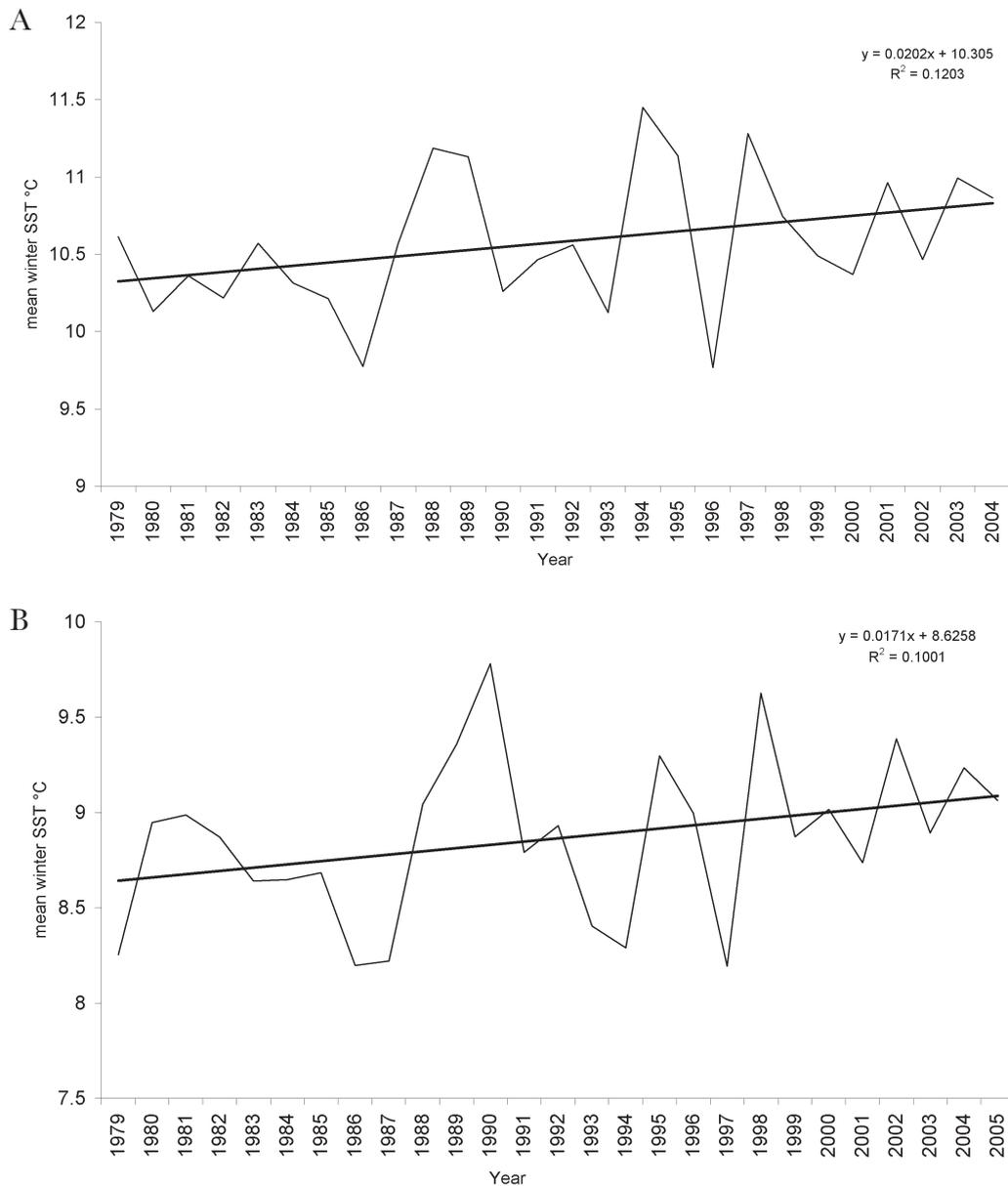


Figure 3. Mean winter (January–March) SST for (A) the western English Channel (50–51°N 4–5°W) and (B) the Irish Sea (52–53°N 4–5°W). Met Office - GISST/MOHMATN4/MOHSST6 - SST (1980–2004) data provided to MarClim by kind permission of the British Atmospheric Data Centre. Heavy line indicates regression of mean winter SST against year 1980–2004.

between the 1980s and 2002. Several individuals were recorded at Cemlyn Bay on the north coast of Anglesey for the first time since 1963 (Figure 1C). A breeding population of mixed year classes was found at Porth Swtan, Anglesey in 2002, and was still present in 2003 and 2004. The general pattern in the 2000s was of large, multi-age populations throughout North Wales, with re-colonization occurring to within 15 km of the pre-1962/1963 limits. A small population containing a range of year classes was found in the English Channel in 2002 at Osmington Mills, a site at which earlier visits in both the 1960s and 1980s had only revealed occasional large animals (Figure 1D) (Hawthorne, 1965; Kendall, 1987). This mixed age population east of the Portland Bill headland was approximately 55 km further east than the previous range edge population at Lyme Regis (Crisp & Southward, 1958; Hawthorne, 1965; Kendall, 1987). Repeat surveys in 2003 and 2004 confirmed that this

population was still present. Records of isolated individuals have also been made from Freshwater Bay on the Isle of Wight in 2004 and 2005 (S.J. Hawkins, personal observation; R.J. Herbert, personal communication). In 2003, breeding populations of *Osilinus lineatus* in Ireland had extended north by 10 km beyond the limits recorded in 1952 and 1971 to Ardglass on the north-west coast, with individuals being found 20 km further north at Ballyquintan Point (Figure 1B). This was the smallest shift observed, and coincides with the smallest increase in coastal temperatures recorded in the areas between the original surveys and resurveys.

Population structures

The abundance of *Osilinus lineatus* had significantly increased by up to six times since 1986 (matched pairs *t*-test ($t=6.87$, $df=15$, $P<0.001$)) at all of Kendall's 16 sites (UK and

Table 1. Two-way ANOVA of abundance of *Osilinus lineatus* at nine sites (West Angle Bay, Hartland Quay, Wellcome, Widemouth, Crackington Haven, Wembury, Prawle, Churstone, Lyme Regis) in 1986, 2002, 2003 and 2004, including a priori contrasts (Sokal & Rohlf, 1995) between decades and within the 2000s.

Source	df	SS	MS	F	Pr>F
Sites	8	397.68	49.71	5.77	0.0004
Years	3	442.00	147.33	17.10	<0.0001
Contrast within Years					
1980s versus 2000s	1	402.15	402.15	46.67	<0.0001
Among 2000s	2	39.86	19.93	2.31	0.1207
Error (sites by years)	24	206.82	8.62		
Total	35	1046.50			

France) revisited in 2002 (Figure 4). A simple comparison of two years separated by nearly two decades may show changes due to short-term and not long-term variation. To address the relative roles of short and long term variation, a further analysis was done on a subset of nine sites visited once in 1986, and again in 2002, 2003 and 2004. The resulting two-way ANOVA (Table 1) showed that the variation in abundance between years and between sites were both significant when using the sites by years interaction as the error term. Lack of replicates within years precluded significance testing of the interaction term. The variation among years was partitioned into two *a priori* comparisons, one between 1986 and the 2000s and the other among 2002, 2003 and 2004. The variance between 1986 and the 2000s was significantly greater ($F=20.18$, $df=1,2$, $P<0.046$) than the variance within years in the 2000s.

A significant decrease in both the maximum size, and size of animals at the 90th percentile of a size frequency histogram between 1986 and 2002 had occurred across the sites for which data exist (D_{max} : $t=2.38$, $P=0.032$, $N=15$, $df=14$, D_{90} : $t=4.94$, $P<0.001$, $N=16$, $df=15$). The regression analyses showed a significant negative relationship between mean abundance and mean size at the 90th percentile in 1986, accounting for 36% of the variance ($F=7.83$, $R^2=0.36$,

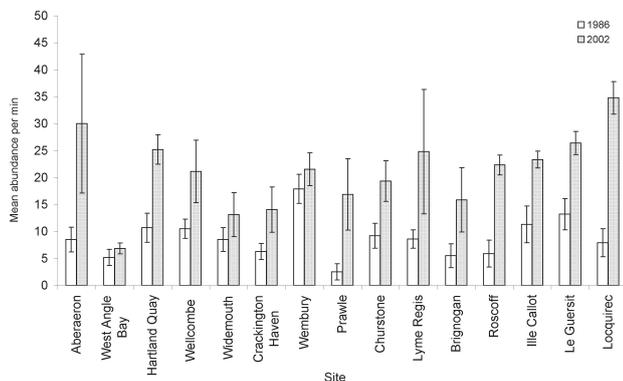


Figure 4. Mean abundance (number per minute) at 16 sites in 1986 and 2002 ($\pm 1SD$ of mean).

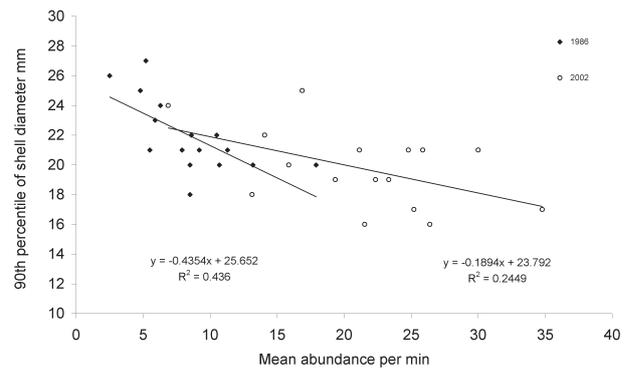


Figure 5. Linear regression of mean shell diameter at the 90th percentile against log mean abundance for all sites in 1986 (solid) and 2002 (open).

$P<0.014$, $df=14$, $N=16$, $y=-0.44x+25.53$) (Figure 5). A 1-tailed test showed that the relationship was weaker but still significant in 2002 ($F=3.85$, $R^2=0.22$, $P<0.035$, $df=14$, $N=16$, $y=-0.18x+23.08$), indicating that abundance had a much stronger negative effect on size at lower densities such as encountered in 1986 than at the higher densities found at all sites in 2002. An ANCOVA showed that the difference between the two regression lines was not significant and so a combined relationship was calculated.

A linear regression model fitted to the combined data showed a significant relationship between log abundance and D_{90} ($F=22.46$, $R^2=0.43$, $P<0.001$, $df=30$).

Across 14 sites for which comparable data were available, the age of snails at the 90th percentile of an age frequency histogram (A_{90}) had also declined significantly ($t=2.88$, $P<0.003$, $df=13$) between 1986 and 2002. There was, however, no significant change in mean size of animals in either the 1, 2 or 4 year cohorts between 1986 and 2002 across the 11–12 sites analysed (1 cohort: $t=-1.87$, $P=0.89$ NS, $df=11$, 2 cohort: $t=0.77$, $P=0.45$ NS, $df=12$, 4 cohort: $t=2.37$, $P=0.134$, $df=11$). This indicated that there had not been a reduction in the size of new recruits, nor animals reaching sexual maturity, nor of adults across the suite of sites close to the northern limit of *Osilinus lineatus*. Age frequency structures were dominated by animals between 1–2 years old in 1986. Much smaller percentages of 3+ animals were found and there was as general trend of low numbers of 0 year cohort juveniles, indicating low levels or failure of annual recruitment across the sites. In contrast, data from 2002 showed that the 0–4 year cohorts dominated all the populations, with evidence of strong recruitment of the '0' cohort at all 14 sites in recent years. An increase in the number of age classes in 2002 was recorded at seven of the 14 sites, where the maximum age cohorts had increased by between 1 and 5 years. The largest of these changes have occurred at Lyme Regis and Brignogan in the English Channel. At Lyme Regis, only young animals up to the age of 3 years were found during the 1986 survey, whereas the population was composed of both juvenile and adult animals up to 8 years old in 2002. The Brignogan population in Brittany was composed of 1,2,3 and 5-year old animals in 1986, but by 2002 this population contained individuals in every age cohort up to 10 years.

DISCUSSION

The northern and eastern distributional limits of *Osilinus lineatus* in Britain were cut back by ~120 km and 70 km respectively during the extreme cold winter of 1962/1963 due to mass mortalities within all age classes of range edge populations (Crisp, 1964). Following a cool period during the 1960s and 1970s, subsequent surveys in the 1980s showed that re-colonization of sites within 100 km of these range edges was very limited, with very few populations becoming re-established even after two decades (Kendall, 1987; S.J. Hawkins, unpublished data). From the mid-1980s to date, strong warming of surface waters and a reduction in seasonal and diurnal temperature ranges have occurred in the North Atlantic (~50–65°N) and the resulting thermal regime in Britain is now similar to that experienced further south towards the centre of the range of *O. lineatus* in Europe (Bode et al., 1987). During this time *O. lineatus* has rapidly re-extended its northern limits of distribution to the north-east coast of Anglesey. A range extension of 55 km beyond all previous records has also occurred in the English Channel, and the northern range edge in Northern Ireland has also extended by 20 km. Abundances have shown increases of up to 675% since 1985 at sites originally surveyed by Kendall (1987) and these increases are concordant across all 16 locations for which data exists. Populations within 100 km kilometres of northern limits now show close resemblance to those recorded in the centre of the range in Europe (Bode et al., 1987), with high abundances, annual successful recruitment events and bi- or trimodal size frequency structures.

Factors setting range edges

All populations of *O. lineatus* in the northern part of the range that were surveyed during Kendall's 1986 survey had low densities, missing year classes and were dominated by older individuals (Kendall, 1987). Annual recruitment failure had occurred frequently in all sites surveyed, and the relationship between abundance and size appeared to be strongly influenced by the few large, old animals that had survived. A negative relationship between density and maximum size, suggested to be the result of intraspecific competition, was observed in these range edge populations (Kendall 1987). We predicted that as the climate warmed, density-dependent effects would become stronger in response to increasing abundances as environmental conditions became more suitable for survival. This response has previously been observed in many taxa (Lawton, 1989; Gaston & Blackburn, 1996). The regression analyses indicated, however, that the relationship between abundance and size had become weaker between 1986 and 2002, with density appearing to exert less of an effect on the size of individuals within these populations as their numbers increased. Thus the negative relationship is likely to be caused by greater numbers of small, new recruits in the population rather than intraspecific competition within populations that are not severely resource-limited at present.

In 2002, 2003 and 2004 population structures showed no evidence of recruitment failure for the previous nine years, greater proportions of juveniles in all populations and an increase in the numbers of age classes present in the English

Channel populations. The decreases in the maximum age and size, age and size of animals at the 90th percentile of the population, and the larger proportions of juveniles in these populations during the 2000s were all the result of increased recruitment success occurring in recent years, rather than a reduction in the age and size of animals within the populations. Analyses of the size of individual age classes confirmed that the mean size of juveniles, immature and mature adults had not altered between 1986 and 2002. Increased numbers of individuals within populations close to distributional limits had allowed these populations to persist in recent years leading to increased total reproductive output. Greater numbers of larvae settling on shores where the local environment had become suitable for survival in recent years were also likely to have facilitated the establishment of new populations beyond previous limits. The presence of multi-age classes in these newly-established populations may be indicative of self recruitment, and/or the result of multiple inputs of larvae from long-established neighbouring populations within the range.

Osilinus lineatus is thought to spend up to four days as a pelagic, lecithotrophic larvae (Desai, 1966), and previous work has demonstrated its inability to cross small sections of sea (e.g. Northern Ireland to south-west Scotland, (Southward & Crisp, 1954), Devon to Lundy Island (Hawkins & Hiscock, 1983). Strong currents around Point Lynas on Anglesey, the tip of the Llyn Peninsula, and off Portland Bill in the English Channel were proposed as hydrographic barriers to the further spread of *O. lineatus* both eastwards and northwards (Crisp & Knight-Jones 1954; Crisp & Southward, 1958; Maddock & Pingree, 1977; Kendall, 1987). Settlement and subsequent survival of animals was thought to be prevented beyond these locations due to the small numbers of larvae produced from range edge populations being unable to breach offshore current flows. All of these populations have rapidly increased in abundance in recent years. As a result, the density of larvae in the water column may have increased to the extent that individuals have breached these hydrographic barriers and settled on shores beyond in sufficient numbers to establish new populations at locations that are now climatically suitable for habitation. Due to successful recruitment across sites in North Wales and at Lyme Regis between 2002 and 2004, these new populations will have received regular input of new recruits, helping to sustain the new populations until adult densities were sufficient to allow self-recruitment. The potential for further expansion is demonstrated by the individual found on the Isle of Wight in 2004 and 2005 (S.J. Hawkins, personal communication; R.J. Herbert, personal communication), where previous searches of shores on the island throughout the 1990s failed to find any animals (R.J. Herbert, unpublished data). Thus physical processes setting range boundaries may influence local variation in abundance at sites within the range, and changes in abundance can in turn provide information on the spatial extent of such processes (Legendre & Fortin, 1989; Maurer, 1999).

The large difference between decadal and inter-annual variance in changes in abundance, in conjunction with the concordant increases in abundance between sites and

increases in frequency and degree of recruitment success across sites in Britain and northern France suggests that the range extensions of *O. lineatus* between 1986 and 2004 were caused by a large-scale driver such as climate acting over a decadal-scale time period. Few processes operate over such a large spatio-temporal scale other than climate or hydrography. Based on the results presented here, further range expansions and increases in the success of populations close to current northern and eastern limits are predicted within the next few decades. The extent of future extensions at the north and east range edges is likely to be constrained by hydrographic barriers and lack of rocky habitat beyond existing limits, although the introduction of artificial sea defences may aid future spread by reducing the size of gaps between suitable rocky shores.

Future requirements

The changes in geographic distribution of *Osilinus lineatus* at northern and eastern limits of distribution add to the emerging pattern of warm water species extending their northern limits polewards. This type of broadscale approach to detecting biological responses to climate has its limitations, however. While correlational biogeographic studies can be used to obtain probabilistic maps of species occurrence, they cannot provide information on cause and effect (Parmesan & Yohe, 2003; Fortin et al., 2005; Helmuth et al., 2005; Parmesan et al., 2005). In addition to information on the distribution of *O. lineatus*, data on the population structures close to the range limits collected in the 1980s and 2000s has enabled the dynamics of the north and north-eastern range limits to be identified and related to climatic changes over the second half of the 20th Century. This has in turn allowed the changes in distribution observed between 1986 and the 2000s to be put into a wider context and increased the confidence in the conclusions drawn from this study. Only via the continuation of long-term data series, with emphasis on the collection of annual replicated, quantitative data can current and future spatio-temporal fluctuations in range limits be accurately mapped. In addition, by investigating the physiological responses of organisms to changes in thermal regimes, we can generate testable hypotheses of how biological mechanisms are affected by climatic fluctuations and better predict future changes in the responses of species to global climate change.

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