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Persistent border: an analysis of the geographic boundary of an intertidal species

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ABSTRACT: The biological performance of species close to their biogeographic boundaries is of critical interest in a period of rapid climate change and can inform predictions of future patterns of distribution. The classic view is that performance attributes (reproduction, growth, survival) will gradually decline from the centre towards the edge of a species range. A persistent discontinuity in the distribution of the intertidal barnacle *Chthamalus montagui* on the central south coast of England has enabled us to test hypotheses about its performance and recruitment as the range edge is approached. Although adult density was reduced by over 5 orders of magnitude along a 200 km distance, there was little evidence of impaired performance at the range edge. There have been fluctuations in abundance over the last 50 yr at shores approaching the border, which are associated with changes in temperature and suggest thermal sensitivities. A study of recruitment in *C. montagui* and in other intertidal barnacles revealed a region of very low recruitment for all species close to the border of *C. montagui*. We propose that reductions in larval supply caused by complex regional hydrography and suboptimal habitat quality, not adult performance, is most likely responsible for a steep gradient in recruitment as the border is approached, although possible reductions in larval performance cannot be totally discounted. The location of 'low recruitment cells' caused by oceanographic processes that obstruct the dispersal of propagules needs to be identified when modelling the rate of change of biological assemblages and the location and spacing of reserves.

KEY WORDS: Marine ecosystems · Oceanography · Biological performance · Recruitment · Climate change · Intertidal rocky shore

INTRODUCTION

With rising global temperatures (Hulme et al. 2002, IPCC 2007), interest and concern about the migration of species and assemblages both polewards and along elevational and bathymetric gradients has increased (Parmesan 1996, Parmesan et al. 1999, Sagarin et al. 1999, Helmuth et al. 2002, Genner et al. 2004, Perry et al. 2005). Yet research continues to be hindered by a lack of empirical evidence on the relative importance of factors that influence the rate of range expansion or retreat (Sagarin & Gaines 2002a, Gaston 2003, Parmesan et al. 2005, Gilman 2006). The occurrence of a species border has frequently been ascribed to performance attributes, such as reproduction, growth and survival (Caughley et al. 1988). Gradual decline in species density towards the range margins is thus assumed to reflect a reduction in performance as the boundary is approached (Brown 1984, Brown et al. 1995). However, a change in spatial occupancy may be dependent on multiple factors including available habitat, life history and functional traits (Sanford & Swezey 2008), competitive and predatory interactions with other species (Connell 1961, 1985, Poloczanska et al. 2008) and connectivity with source populations (Crisp 1958, Crisp & Southward 1953, Caughley et al.

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1988, Brown et al. 1995, Leonard et al. 1999, Gaylord & Gaines 2000, Wethey 2002, Lima et al. 2006) or the interaction of some or all of the above (Kinlan & Gaines 2003). In a relatively homogenous habitat with no barriers to propagule or juvenile dispersal, the rate of expansion might be cautiously projected, given knowledge of reproductive behaviour and fecundity of a species. The more likely scenario, however, is a heterogeneous environment where inshore connectivity is compromised by habitat fragmentation and restricted dispersal due to topographic or hydrographic barriers. Gaylord & Gaines (2000) suggested that biogeographic borders caused by oceanographic barriers were likely to be important and widespread. Transport processes may not only determine the dispersal of propagules but also influence the supply of food, thereby affecting a species' reproductive performance and range border (Lester et al. 2007). Unravelling the mechanisms by which species are prevented from expanding their range requires investigation of physiological performance, dispersal, recruitment, habitat availability and connectivity.

In this paper, we investigate a particularly sharp coastal discontinuity in the English Channel that has attracted attention for over 70 yr (Fischer-Piette 1936, Moore & Kitching 1939, Southward & Crisp 1956, Crisp & Southward 1958, Crisp et al. 1981, Herbert 2001, Herbert et al. 2003, Southward et al. 1995, 2005). Within this region, there is a cluster of range borders of Lusitanian intertidal species that, with the exception of some retreat during the exceptionally cold winter of 1962–63 (Crisp 1964) has remained remarkably stable since the 1930s (Crisp & Southward 1958, Crisp et al. 1981).

We have investigated the persistent border of the Lusitanian barnacle *Chthamalus montagui* (Southward) towards its adult range margin on the south coast of England. Adults occur on hard substrata across the intertidal zone along the Atlantic coast from North Africa to northeast Scotland and the Orkney Islands, and throughout the Mediterranean (Crisp et al. 1981). The pelagic larval phase is estimated to be between 18 and 75 d (Burrows 1988, Burrows et al. 1999). Prior to the separation of *C. montagui* and *C. stellatus* (Southward 1976), earlier work considered both species to be a single taxon *Chthamalus stellatus* (Poli). Intertidal barnacles have been well studied in southwest England and the relative abundance of *Chthamalus* spp. and their boreo-arctic counterpart *Semibalanus balanoides* is unequivocally linked to climatic fluctuations (Southward 1967, 1991, Southward et al. 1995, 2005), which mediate competitive interactions (Southward & Crisp 1954, Connell 1961, Poloczanska et al. 2008)). This suggests that species performance at the range edge could be linked to thermal tolerance. However, despite a decade of rising sea temperatures, the border of *C. montagui* along the south coast of England has extended by at most 8 km since 1970. Compared to other southern species, changes in the abundance of *C. montagui* at locations approaching this border have been relatively minimal (Herbert et al. 2003, Mieszkowska et al. 2006, 2007). Recruitment failure has long been suggested as a common cause of geographic range boundaries (Hutchins 1947), yet in a spatially and temporally heterogeneous environment, there may be several abiotic and biotic factors that synergistically inhibit performance, limit dispersal and hence also the expansion of populations at the range edge. However, the rate of range expansion among different taxa has so far been variable. This has led to various hypotheses on the relative importance of species performance approaching borders, as measured by survival, growth and reproduction versus that of larval dispersal and recruitment.

Focussing on the barnacle *Chthamalus montagui*, we tested the following hypotheses:

(1) The border of *C. montagui* on the south coast of England can be explained by clear gradients of reduced reproductive performance, lower growth rate and higher mortality toward the east of the region.

(2) The discontinuity in distribution can be explained by variation in recruitment of *C. montagui* and other barnacles across the region reflecting effects of oceanographic factors, habitat availability and quality.

MATERIALS AND METHODS

Study area and hydrographic context. The south coast of England (Fig. 1) straddles warm-temperate (Lusitanian) and cold-temperate (Boreo-arctic) biogeographic provinces (Forbes 1858, Southward et al. 1995); there is a summer and winter temperature gradient as continental influence increases eastwards towards the North Sea (Fig. 2a). Although the residual flow is west to east (Lee & Ramster 1981, Boxhall & Robinson 1987, Salomon & Breton 1993), the hydrography of the region is highly complex. Swanage, in the central part of the study area, has the lowest tidal range in the UK (2 m), which limits intertidal habitat (Fig. 2b). Tidal range increases both to the east and to the west and there is a 6 h difference in the time of low water spring tide over the short distance of 100 km between the western and eastern ends of this boundary region. Low spring tides in the western area occur at midday and midnight. Fast currents reaching over 3 m s^{-1}, turbulent water (Fig. 2c) and tidal eddies occur off major headlands, particularly Portland Bill (Sager & Samler 1975, Pingree & Maddock 1977, Boxhall & Robinson 1987, Guyard 2000). Summer stratified waters occur in Lyme Bay (Fig. 2c) where there is a front, to the east of which there is considerable mixing (Pingree

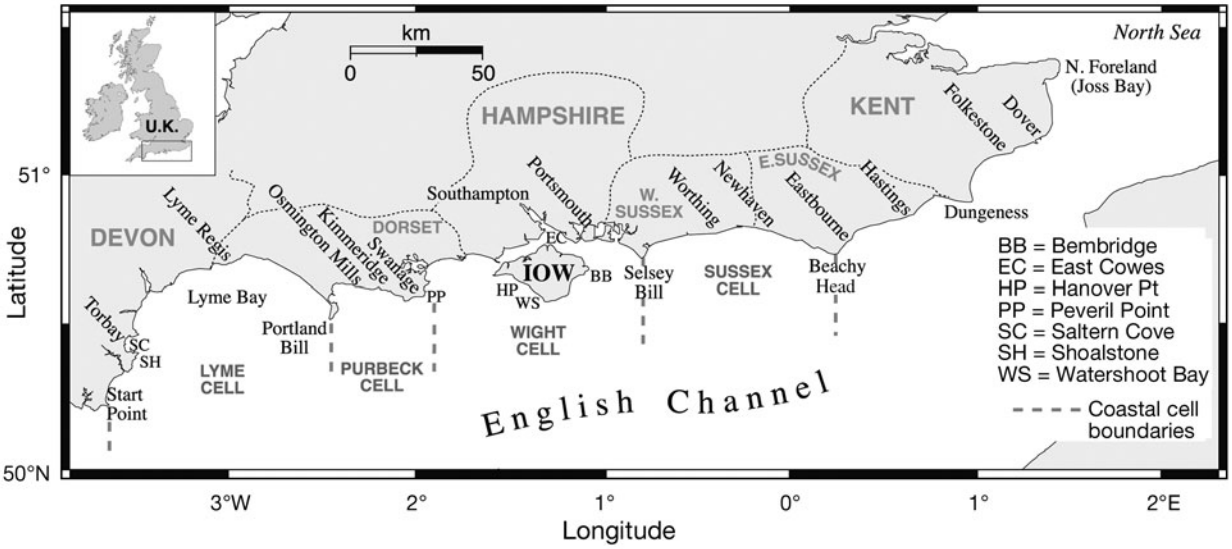

Fig. 1. Central south coast of England showing survey locations and boundaries of coastal cells referred to in the text. IOW: Isle of Wight

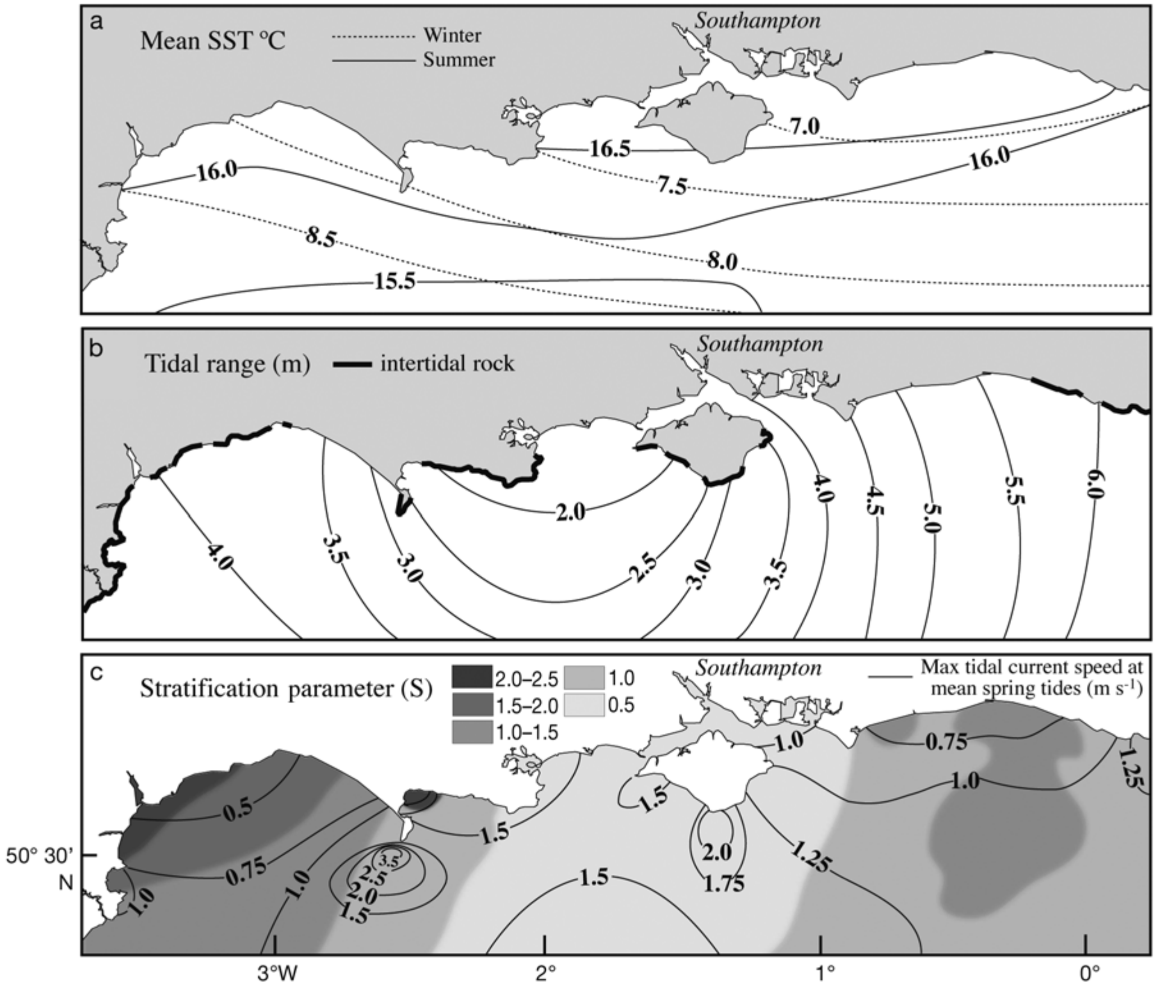

Fig. 2. The south coast of England. (a) Mean winter and summer sea surface temperature (Lee & Ramster 1981); (b) tidal range (Lee & Ramster 1981) and location of main areas of intertidal rock; and (c) mean tidal current speed (Sager & Samler 1975) and location of summer stratified waters (S > 2), transitional regions (S = 1 to 2) and regions mixed throughout the year (S < 1) (Pingree & Griffiths 1978, Simpson & Hunter 1974, R. D. Pingree pers. comm.). See Fig. 1 for place names

& Maddock 1977, Pingree & Griffiths 1978). As a consequence of thermal stratification, the spring diatom bloom develops earlier in the western part of the region, particularly around the frontal region in Lyme Bay where weak, transitory upwelling may also occur during westerly winds (Hoch & Garreau 1998). Monthly sea surface temperatures for the central English Channel (50 to 51° N, 1 to 2° W) from 1955 to 2007 were extracted from the HadISST1 data set (Rayner et al. 2003).

Adult census. Data from a time-series (1955 to 1993) of previously unpublished barnacle counts by A. J. Southward were supplemented with new survey information. Counts were made of barnacle species (*Chthamalus montagui*, *C. stellatus*, *Elminius modestus*, *Semibalanus balanoides*) at 3 tidal levels in October of each year from 1994 to 1999 and then intermittently until 2007. Locations visited (Fig. 1) and the methodology broadly followed that of Crisp & Southward (1958) and Crisp et al. (1981). Counts were made within 10 quadrats placed in each of 3 patches at heights approximating high water neap tide level (HWN), mean tide level (MTL) and low water neap tide level (LWN). The size of the quadrat varied (6 to 400 cm^2) depending on species abundance; this was previously determined for each location using a minimal area technique (Herbert 2001). The number of quadrats placed in the earlier surveys was variable, although usually a minimum of 10 were surveyed per tidal level. Counts were converted to an abundance scale (Table 1)

To investigate the response of *Chthamalus* to changes in temperature, its mean shore density at Shoalstone, Lyme Regis and Osmington Mills, where the time-series are most continuous, was correlated with mean annual and summer (July to September) sea surface temperatures between 1955 and 2007.

Reproduction. To establish the existence of any gradient in reproductive development approaching the geographic border, gonads and embryos were staged (O'Riordan et al.1992, Burrows et al. 1992) at the commencement of the breeding season in mid-May from 1994 to 1998. Rock chips colonised by adult *Chthamalus montagui* were obtained from the MTL at 7 shores along the south coast of England between Shoalstone in the west and Kimmeridge in the east of the species range. Barnacles on rock chips obtained from Shoalstone in October 1994 and fixed to the shore at the species' eastern border at Bembridge on the Isle of Wight were also sampled annually. Based on minimum sample size investigations, 40 specimens were scored from each shore. A Friedman test (Sokal & Rohlf 1995) was used to determine differences between the proportion of each population brooding in mid-May of 1997 and 1998 along the coast from west to east.

Table 1. Semi-quantitative scale to measure the abundance of barnacles. After Crisp & Southward (1958)

Abundance level	Description
Abundant:	>1 cm^{-2}; rocks well covered
Common:	0.1 to 1.0 cm^{-2}; up to 1/3 of rock space covered
Frequent:	0.01 to 0.1 cm^{-2}; ind. never >10 cm apart
Occasional:	0.0001 to 0.01 cm^{-2}; few within 10 cm of each other
Rare:	<1 m^{-2}; only a few found in 30 min searching
None:	None found

Differences in the percentage brooding of translocated *Chthamalus montagui* were compared with that of natural populations from Saltern Cove in Torbay at the western end of the study area. Barnacles settled within cleared areas of the shore and on perspex (plexiglass) settlement plates fixed to the shore at MTL. In both 1996 and 1997, plates were translocated to the eastern border at Bembridge in October after the settlement period. Control plates were also moved within Saltern Cove to simulate disturbance due to translocation. In May 1997 and 1998, 2 replicate samples of 40 specimens were obtained per treatment, including natural populations on the shore at Saltern Cove. A 2-way replicated ANOVA was used to test for differences in percentage brooding of *C. montagui* between treatments, with 'year' being treated as a random factor.

Through monthly sampling, the number of broods produced by the translocated animals per year was determined. This was calculated using the formula of Burrows et al. (1992):

$$N_B = L_B/L_E$$

where N_B is the no. of broods released; L_B is the effective length of time that an individual spends in carrying embryos and L_E is the time for complete development of embryos from oviposition to release. L_B was calculated as:

$$L_B = \Sigma P_B \times \Delta t$$

where P_B is the average proportion of the population with embryos over the brooding season and Δt is the time interval between successive samples.

Recruitment. To establish the pattern of recruitment of all common intertidal barnacle species across the region, a broad-scale survey was made on shores to the east and west of the *Chthamalus* border in 1999. The south coast of England from Torbay to Beachy Head (Fig. 1) was divided into 4 regions differentiated largely by major headlands and similar to those used by sediment dynamicists (Motyka & Brampton 1993) to define 'coastal cells'. As in coastal sediment dynamics, where cell boundaries or headlands might cause barriers to sediment transport, it is hypothesised that cell boundaries or headlands might cause barriers to the dispersal of larval propagules. The cells were named 'Lyme', 'Purbeck' 'Wight' and 'Sussex' (Fig. 1). Within each cell, 3 shores were chosen and 3 random patches of 100 cm^2 clearances (n = 10) were made at each of 3 tidal heights approximating HWN, MTL and LWN tide levels. Clearances were made ahead of the commencement of settlement of *Semibalanus balanoides,* which begins in March and early April. Recruits were counted in May when new clearances in different areas of each shore were created prior to the settlement period of *Chthamalus* and *Elminius modestus*, which settle later in the summer.

With the null hypothesis that there are no significant differences in recruitment between 'cells', a multifactorial ANOVA was carried out for each barnacle species with the factors 'cell' being fixed, 'shore' being random within 'cell', 'level' being fixed and factor 'patch' being random within all other factors.

Growth and mortality. The growth and mortality rates of the 1995 cohort of *Chthamalus montagui* were monitored until August 1997 from photographs of fixed patches within shores at Shoalstone, Saltern Cove and Lyme Regis in the western Lyme cell, Portland Bill and Kimmeridge within the Purbeck cell and 3 shores within the Wight cell. Six fixed patches were established at HWN, MTL and LWN at each location. From October 1995, photographs were taken each May, August and October until August 1997, when the barnacles were about 2 yr old. Between 15 to 25 recruits were randomly selected for monitoring within each photograph and the presence/absence of each recruit was established in subsequent images. On the Isle of Wight, where recruitment density was very low, individual recruits of *C. montagui* identified within permanent quadrats from 3 shores (Colwell, Watershoot Bay and Hanover Point) were photographed. ANOVA was used to test the null hypothesis that the winter mortality rate of the 1995 cohort did not differ between the western cell Lyme and the combined Purbeck and Wight cells to the east. The factor 'cell' was fixed and factors 'shore' and 'patch' were treated as random within each cell.

To determine the existence of any gradient in growth rate as the range boundary was approached, ~15 recruits of the 1995 cohort were measured across the basal diameter, rostro-carinal (R-C) axis and opercular tergal–scutal (T–S) axis on projected images at each photographic station. A 2-way replicated ANOVA was used to test the null hypotheses that growth rate [expressed as Ln (opercular diameter Aug 1997) – Ln (opercular diameter Oct 1995)] did not differ among shores and shore levels. The factor 'shore' was treated as a random factor. A second nested ANOVA was used to test the null hypothesis that the opercular diameter measured after 2 yr did not differ among shores.

To establish any impairment of growth at the extreme range boundary, barnacles of the 1995 cohort were translocated to Bembridge on the Isle of Wight and growth was compared with that within natural and control (locally translocated) populations at Saltern Cove in the west. Perspex settlement plates (100 cm^2) were fixed to the shore at the MTL at Saltern Cove in May 1995. Four were removed in October and translocated to the MTL at the range boundary at Bembridge. Plates left at Saltern Cove were re-secured to a different patch of rock as a control for translocation. Growth on the translocated plates, control plates and in natural populations at Saltern Cove was measured as above from photographs taken in May, August and October of each year until August 1997.

A nested ANOVA of the opercular diameter of the 1995 cohort measured in May 1996 and August 1997 was carried out to test the null hypothesis of no significant difference among locations. Four random replicate patches of 10 ind. were measured per treatment.

RESULTS

Adult census

Adult abundance of *Chthamalus montagui* at the western edge of the study area (4 to 5 cm^{-2}) is similar to that observed in the centre of the range in southern Portugal (Crisp & Southward 1958, Boaventura et al. 2002, R. J. H. Herbert pers. obs). Yet 50 km east of Lyme Regis, as the promontory of Portland Bill is rounded, the density diminishes rapidly towards the border on the Isle of Wight, where only a few individuals may be found in 30 min of searching (Fig. 3). Population density estimates were combined with the earlier time-series (Southward & Crisp 1954, Crisp & Southward 1958, Southward 1967, Southward et al. 1995, 2005, A. J. Southward unpubl. data). The abundance of the boreo-arctic species *Semibalanus balanoides* is significantly inversely correlated with that of *C. montagui* at Shoalstone ($r = -0.72$, $n = 25$, $p = < 0.001$) and Lyme Regis ($r = -0.38$, $n = 30$, $p = 0.04$), but not so at the most eastern shore at Osmington Mills ($r = -0.38$ $n = 22$, $p = 0.08$) (Fig. 4). The mean shore *Chthamalus* density was correlated with both annual and summer SST. Except for Lyme Regis, correlations with mean summer SST were more significant than that with mean annual SST. However, the most statistically significant correlations were those between *Chthamalus* density and summer SST in the previous year (Table 2).

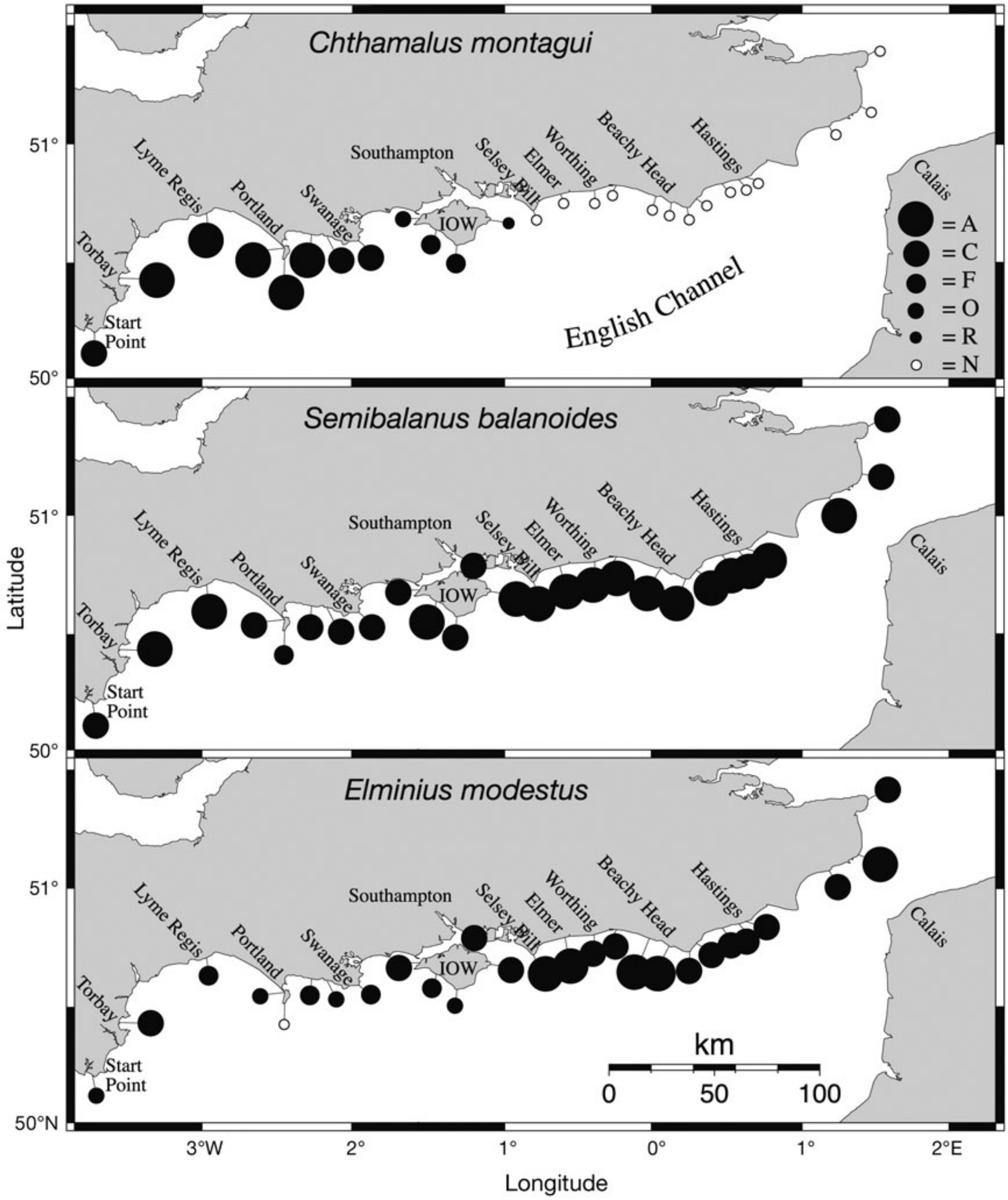

Fig. 3. *Chthamalus montagui*, *Semibalanus balanoides* and *Elminius modestus*. Distribution of barnacles along the central south coast of England (Figure based on, and updated from, Herbert et al. 2007). Symbols show maximum mean shore abundance observed during 1999 to 2008. A: abundant; C: common; F: frequent; O: occasional; R: rare; N: none. See Table 1 for abundance scale parameters. IOW: Isle of Wight

Reproduction

Although there was considerable annual and spatial variation in the stages of reproductive development at the onset of the breeding season, there was no evidence of retarded development at the more eastern shores, nor at the range boundary where individuals had been translocated (Fig. 5).

Two Friedman non-parametric tests (Sokal & Rohlf 1995) were used to assess differences between years in the proportion of brooding individuals. For each of 7 shores (Saltern Cove control shore data was incomplete), the years were placed in rank order of percentage of brooding embryos. The result showed a highly significant difference between years ($\chi^2 = 18.8$, df = 3, $p < 0.001$), with the coolest spring (1996) and the

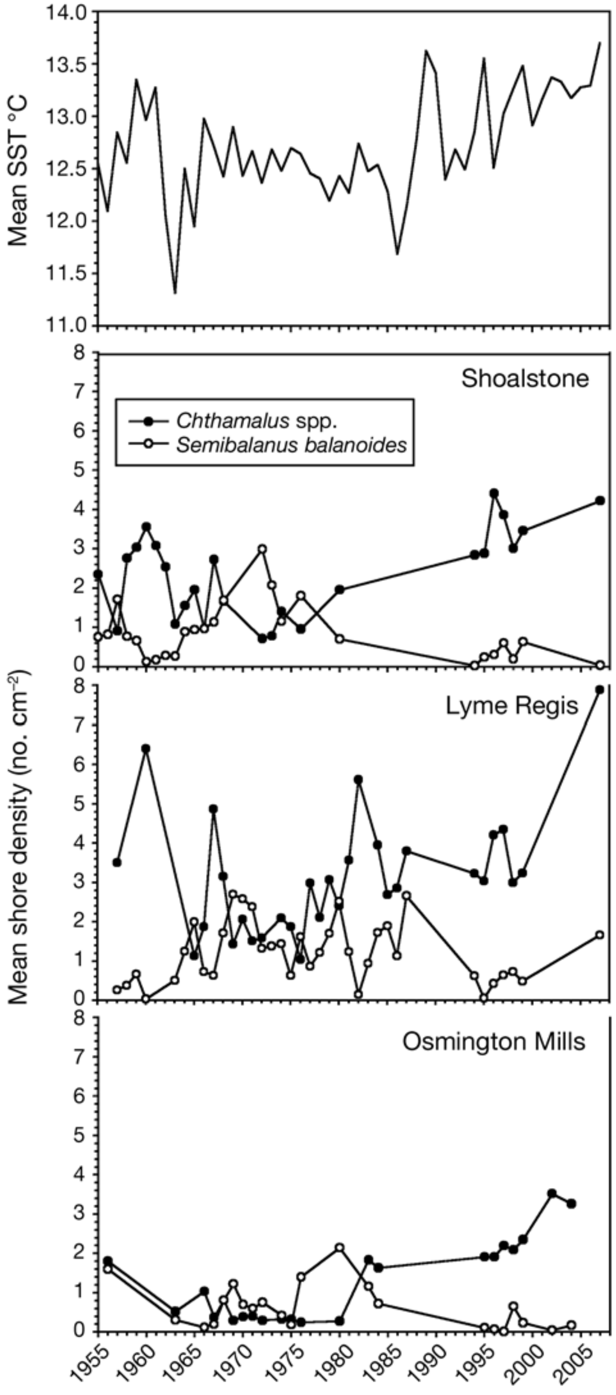

Fig. 4. *Chthamalus* spp. and *Semibalanus balanoides*. Time-series of mean shore barnacle density at shores along the central south coast of England. Shoalstone is the most western in location. Unpublished data for 1955 to 1993 by A.J.S. is included. Sea surface temperature (SST) of central English Channel (50 to 51° N, 2 to 3° W) are from 1955 to 2007. Data were extracted from HadISST1 data set (Rayner et al. 2003)

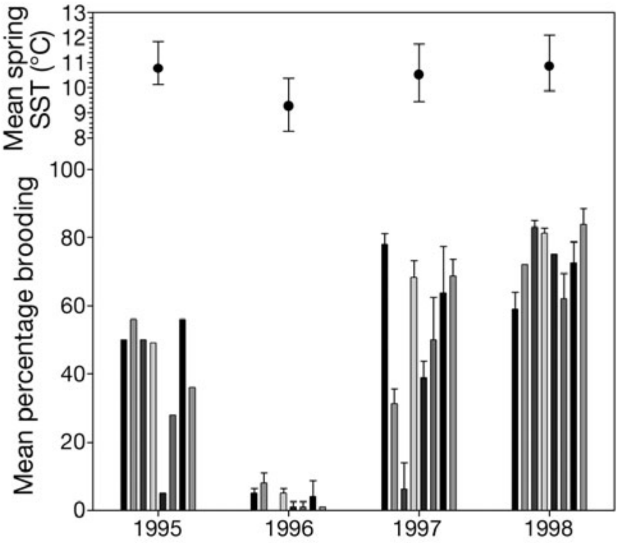

Fig. 5. *Chthamalus montagui*. Proportion (+SE) of brooding barnacle embryos at mean tidal level in mid to late May at shores along the south coast of England during 1995 to 1998. Mean, maximum and minimum spring sea surface temperatures (March to May for 50 to 51° N, 1 to 2° W) are also shown. Data were extracted from HadlSST1 data set (Rayner et al. 2003). Shores west to east from left bar: Shoalstone, Saltern Cove, Saltern Cove Controls, Lyme Regis, Portland Bill, Osmington Mills, Kimmeridge, Bembridge translocation. Those at Bembridge were translocated from Saltern Cove. At Saltern Cove, samples were taken from both natural populations and from controls. Controls were lost in 1996. Estimates for 1995 were from single samples (n = 40). From 1996 to 1998, estimates are means of 2 samples, each n = 40

warmest spring (1998) having the fewest and highest proportion of brooding embryos respectively, in mid to late May. A second Friedman test (Table 3) applied to determine differences between shores with respect to proportion of brooding individuals (by ranking shores within each year separately) showed insignificant results (p = 0.34).

A 2-way replicated ANOVA was used to determine differences in brooding frequency of *Chthamalus montagui* translocated to the range boundary at Bembridge and at Saltern Cove 200 km west, in both 1997 and 1998. Results (Table 4) indicate no differences in percentage brooding among the treatments, but the significant treatment × year interaction shows that the treatment differences varied between years. Specifically, the procedural control barnacles brooded less than those in the other treatments in 1997, but not in the second year when all 3 treatments had higher brooding. The respective percentage brooding among treatments (1) natural, (2) procedural control and (3) translocated were 31, 6 and 69 % in 1997, but all data were higher at 70, 83 and 84 % in the second year. This large interaction effect means that there are no statistically significant differences in average brooding among treatments (cf. Table 4). Overall, percentage brooding was at least as high at the range border at Bembridge as at the more westerly shore at Saltern Cove.

Table 2. Pearson correlation (r) tests between mean shore *Chthamalus* density and mean summer (July to September) sea surface temperatures (SST) in the same and previous years

	Mean SST			SST 1 yr earlier			SST 2 yr earlier		
	r	n	p	r	n	p	r	n	p
Shoalstone	0.514	25	0.0085	0.694	25	0.0001	0.377	25	0.062
Lyme Regis	0.347	30	0.0599	0.447	30	0.0133	0.263	30	0.160
Osmington	0.599	22	0.0032	0.745	22	<0.0001	0.571	22	0.005

Table 3. Shores ranked by order of percentage brooding *Chthamalus montagui* examined in mid to late May for each year between 1995 and 1998. In 1995, only a single sample (n = 40 barnacles) was examined; in subsequent years, 2 samples. Rank 1 is highest percentage brooding (in bold). Friedman test (Sokal & Rohlf 1995) $\chi^2 = 6.83$, n = 4, df = 6, p = 0.337. See Fig 5 for values

	1995	1996	1997	1998	Median rank
Shoalstone	3	2.5	**1**	7	2.75
Saltern Cove	**1.5**	**1**	7	5	3.25
Lyme Regis	4	2.5	3	2	2.75
Portland Bill	7	6	6	3	6
Osmington Mills	6	6	5	6	6
Kimmeridge	**1.5**	4	4	4	4
Bembridge	5	6	2	**1**	3.5

Table 4. Two-way replicated ANOVA of percentage brooding *Chthamalus montagui* by treatment and year (1997 and 1998); treatments were (1) natural populations at Saltern Cove, (2) barnacles grown on settlement plates at Saltern Cove (procedural control); and (3) barnacles grown on plates at Saltern Cove and translocated to Bembridge; there were 2 replicate samples, each of 40 ind. treatment^{-1} yr^{-1}. Data were arcsine transformed; Year was treated as a random factor

Source	df	MS	*F*	p
Treatment	2	0.1702	1.01	0.497
Year	1	0.7947	4.73	0.162
Treatment × Year	2	0.1681	12.93	0.007
Samples (Residual)	6	0.0130		
Total	11	1.5495		

Table 5. Kolmogorov-Smirnov 2-sample test probabilities (p) between shores showing greatest maximum differences (D) in cumulative probability distribution of stage of embryonic development of *Chthamalus montagui*, as shown in Fig. 6. Samples taken from mean tidal level in mid to late May. In 1996, insufficient numbers in the populations were brooding embryos. Samples from Bembridge had been translocated (T)

Year	Shore 1 (n)	Shore 2 (n)	D	p
1995	Osmington Mills (11)	Saltern Cove (20)	0.77	<0.001
1997	Portland Bill (30)	Kimmeridge (50)	0.40	0.005
1998	Portland Bill (67)	Bembridge TL (59)	0.35	0.001

The stages of embryonic development in all natural populations and translocated samples were assessed in mid-May of each year and plotted as cumulative frequency graphs (Fig. 6). Kolmogorov-Smirnov 2-sample tests (Sokal & Rohlf 1995) were applied to the pairs of shores showing the greatest differences in cumulative percentage frequency of stages of embryonic development (Table 5). Although highly significant differences were obtained, there was no evidence of retarded development at the most eastern shores. Indeed, localities close to the species border generally showed either moderate or relatively advanced development.

A range of stages of embryonic development were observed at any one time, even at the species border, providing evidence of asynchronous multiple broods. For barnacles translocated to Bembridge, the first broods were observed on May 20, 1995 (33 % of the sample) and the last on September 15 (10 % of the sample). Moreover, there was evidence of ovarian regeneration and development of eggs as embryos within the mantle cavity matured. The effective length of time that an individual spends in carrying embryos L_B was calculated as 66.2 d (May: 9.9 d; June: 18 d; July: 18 d; August: 17.3 d; September: 3 d). Using an embryonic development period L_E = 23 d (Burrows et al. 1992), the number of broods produced by the translocated animals at Bembridge is estimated at 2.9. These estimates assume that each brood has an equal development period.

Recruitment intensity

The broad-scale survey of barnacle recruitment in 1999 revealed that the region of most rapid attenuation for *Chthamalus montagui* was the same as that for the other intertidal barnacle species *Semibalanus balanoides* and *Elminius modestus* prevalent in the region (Fig. 7); the shores within the cells Purbeck and Wight had relatively little overall recruitment compared to neighbouring cells. The 4-way multifactorial ANOVA showed significant differences between cells for each species, and also between shores within each cell (Table 6, Fig. 7).

Growth

The opercular diameters of recruits growing at MTL on plates from Saltern Cove and those translocated to Bem-

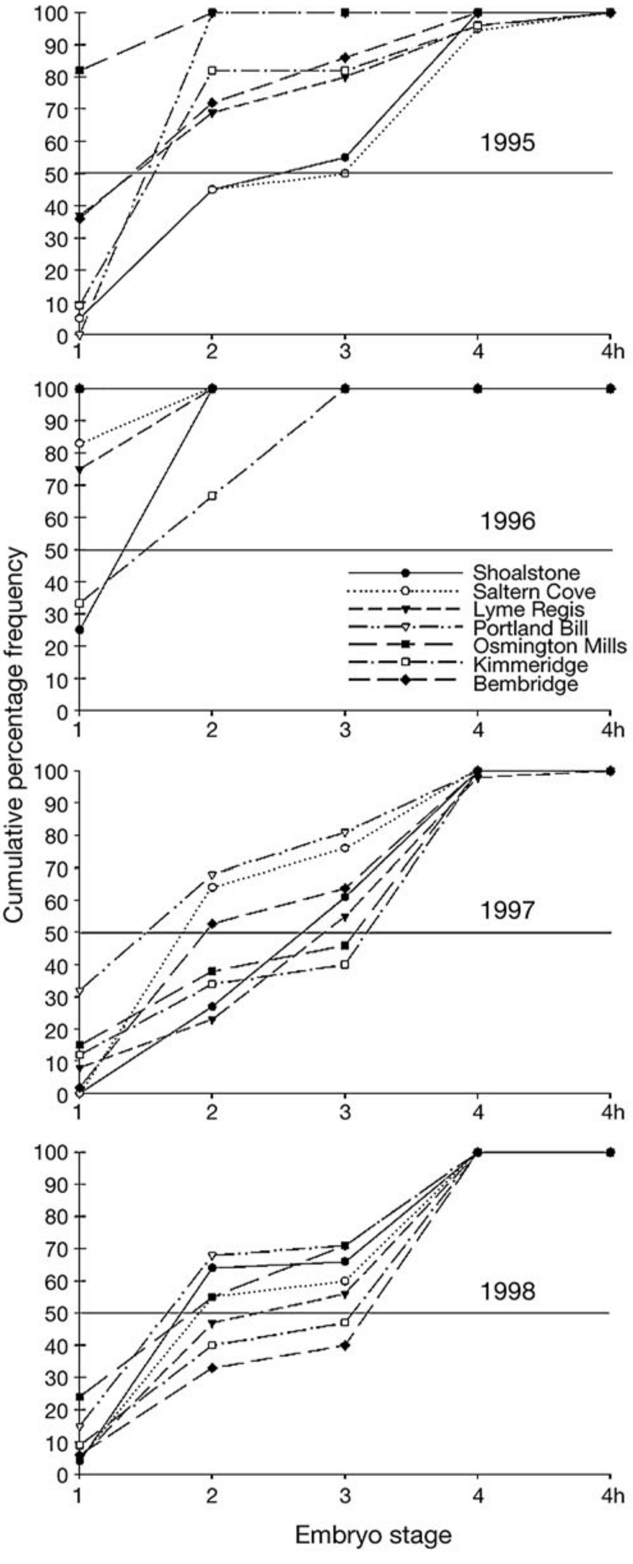

Fig. 6. *Chthamalus montagui*. Cumulative percentage frequency of barnacle embryonic development stages at mean tidal level in shores along the south coast of England sampled in mid-May 1995 to 1998. Horizontal lines show 50% cumulative frequency of embryonic developmental stage

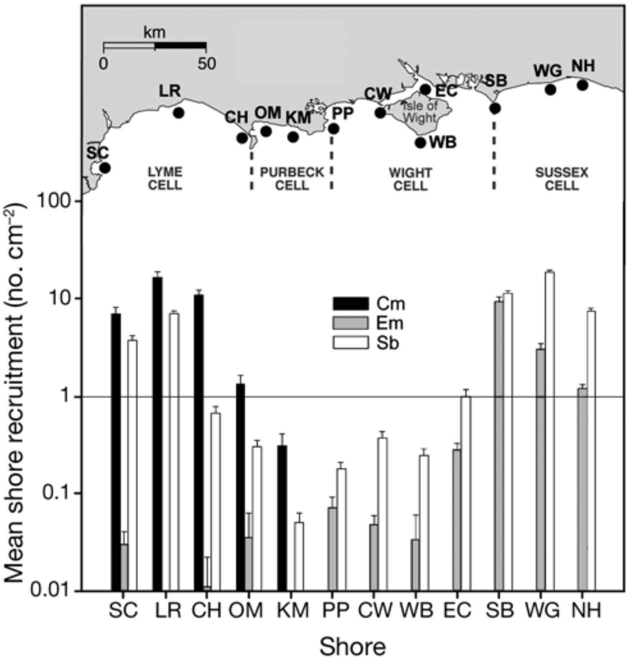

Fig. 7. *Chthamalus montagui* (Cm), *Elminius modestus* (Em), and *Semibalanus balanoides* (Sb). Mean shore barnacle recruitment (+SE) along the south coast of England in 1999. Note log scale. Horizontal line indicates mean shore density of 1 recruit cm^{-2}. SC: Saltern Cove; LR: Lyme Regis; CH: Chesil; OM: Osmington Mills; KM: Kimmeridge; PP: Peveril Point; CW: Colwell Bay; WB: Watershoot Bay; EC: East Cowes; SB: Selsey Bill; WG: Worthing; NH: Newhaven

bridge were compared with those on the other shores (Fig. 8). Differences in the opercular diameter observed shortly after recruitment in October 1995 were maintained over the 2 yr study period (Table 7). By August 1997, there were statistically significant differences ($p = 0.002$) among the 4 shores, with average diameter being highest at Portland Bill (mean ± SE = 2.16 ± 0.06) and lowest at Kimmeridge (1.58 ± 0.02). There were no statistically significant differences in opercular diameters between random sampling patches within shores ($p = 0.462$). Size was not dependent on density.

The mean growth rate of the 1995 cohort over 2 yr (Table 8) did not reveal any statistically significant differences among the 3 shores investigated (Saltern Cove, Portland Bill and Kimmeridge). However, the significant shore × level interaction ($p < 0.001$) indicates that the pattern of spatial variation in growth rate differs between shores (i.e. growth rate was highest on the middle shore level at Kimmeridge, but highest on the upper level at Saltern Cove).

A nested ANOVA was carried out to determine whether the mean opercular diameter of the 1995 cohort growing at Saltern Cove was different from those translocated to Bembridge at the species' eastern

Table 6. Four-way multifactorial ANOVA for recruitment of barnacle species in the 4 coastal cells. Data were double square-root transformed. Factor Cell was fixed, factor Shore was random within cell, factor Level was fixed and factor Patch was random within all other factors

Source	df	*Chthamalus montagui*			*Semibalanus balanoides*			*Elminius modestus*		
		MS	*F*	p	MS	*F*	p	MS	*F*	p
Cell	3	174.122	40.12	<0.001	100.703	20.12	<0.001	74.983	9.93	0.004
Shore (Cell)	8	4.340	4.80	0.004	5.005	6.54	0.001	7.548	9.63	<0.001
Level	2	0.409	0.45	0.644	11.971	15.64	<0.001	0.770	0.98	0.396
Cell × Level	6	0.355	0.39	0.872	1.932	2.53	0.065	0.193	0.25	0.954
Level × Shore (Cell)	16	0.904	3.54	<0.001	0.765	1.37	0.180	0.784	3.44	<0.001
Patch (Cell Level Shore)	72	0.256	4.87	<0.001	0.557	24.06	<0.001	0.228	8.18	<0.001
Quadrats	972	0.053			0.023			0.028		

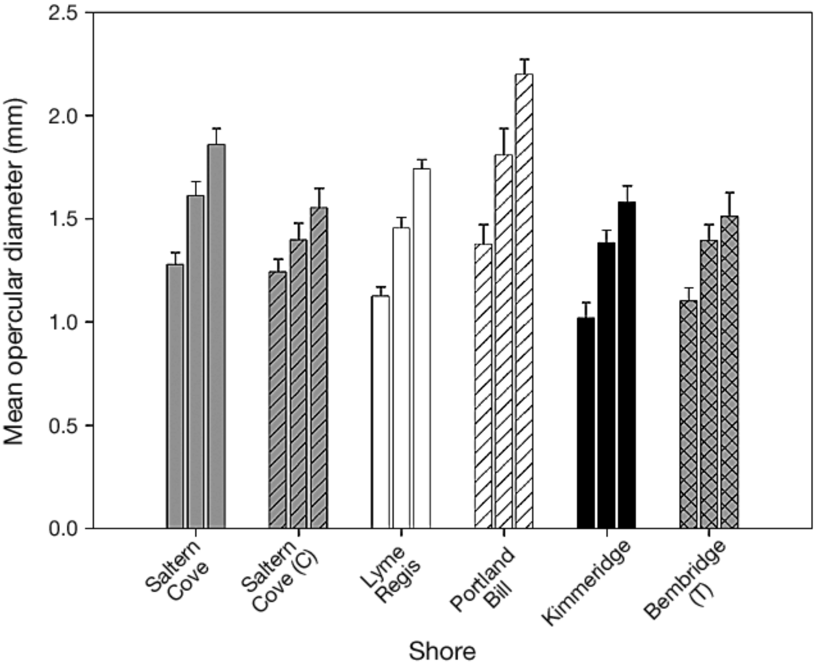

Fig. 8. *Chthamalus montagui*. Mean opercular size (+SE, from 4 patches, n = 10) of the 1995 barnacle cohort at mean tidal level along the south coast of England from the west to range border at Bembridge. Left bar: May 1996; Mid bar: October 1996; Right bar: August 1997. Barnacles at Bembridge were translocated (T) from Saltern Cove, Saltern Cove 'C' are procedural control plates

boundary. There were statistically significant differences in opercular diameter among treatments in May 1996 after the first winter (Table 9); Tukey pairwise tests showed that this was entirely due to the smaller diameter of barnacles translocated to Bembridge (both tests $p < 0.006$). By August 1997, there were no longer any statistically significant treatment differences in barnacle opercular diameter (Table 9). However, the differences among patches within treatments became highly significant ($p < 0.001$), indicating increasing spatial heterogeneity in barnacle size (i.e. opercular diameter) among patches.

Mortality

Overall mortality of the 1994 cohort during the relatively mild winter of 1994–1995 was 31% at the most western shore compared to only 4% at the eastern border on the Isle of Wight. The winter of 1995–1996 had the second coldest record over the study period,

Table 7. Two-way nested ANOVA of opercular diameter for the 1995 cohort of *Chthamalus montagui* measured at mean tidal level after 2 yr in August 1997 at 4 shores (Saltern Cove, Lyme Regis, Portland Bill, Kimmeridge); n = 10 per patch, 2 patches per shore. Mean of 2 patches: Saltern Cove 1.95 mm; Lyme Regis 1.77 mm; Portland Bill 2.16 mm; Kimmeridge 1.58 mm

Source	df	MS	*F*	p
Shore	3	1.2446	42.62	0.002
Patch (Shore)	4	0.0029	0.91	0.462
Residual	72	0.0320		
Total	79			

Table 8. Two-way replicated ANOVA of growth rate for the 1995 cohort of *Chthamalus montagui* in relation to shores (Saltern Cove, Portland Bill and Kimmeridge) and shore level (lower, middle, upper); based on 10 ind. for most Shore–Level combinations; Shore was treated as a random factor

Source	df	MS	*F*	p
Shore	2	0.0826	0.54	0.620
Level	2	0.2844	1.85	0.266
Shore × Level	4	0.1656	5.10	0.001
Residual	72	0.0325		
Total	80	0.0440		

Table 9. Nested ANOVA of opercular diameter for the 1995 cohort of *Chthamalus montagui* measured at mean tidal level in May 1996 and August 1997; treatments were (1) natural populations at Saltern Cove, (2) barnacles growing on settlement plates at Saltern Cove (procedural control), and (3) barnacles that settled on plates at Saltern Cove and were translocated to Bembridge in October 1995; there were 4 random replicate patches of 10 ind. treatment^{-1} yr^{-1}

Source	df	May 1996			August 1997		
		MS	*F*	p	MS	*F*	p
Treatment	2	0.5125	15.08	<0.001	1.0563	3.62	0.070
Patches	9	0.0340	1.72	0.093	0.2914	5.21	<0.001
Individuals	108	0.0198			0.0559		

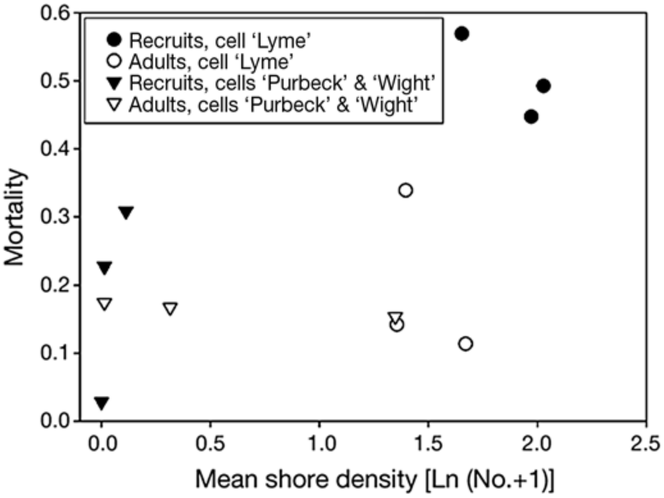

Fig. 9. *Chthamalus montagui*. Mean shore mortality rate of adult barnacles and the 1995 cohort plotted against mean shore density, Ln (No. cm^{-2} + 1). Recruit mortality expressed as Ln (No. Oct 1995 +1) – Ln (No. May 1996 +1). Adult mortality expressed as Ln (No. Oct 1995 +1) – Ln (No. Aug 1996 +1)

Table 10. Nested ANOVA of winter mortality for the 1995 cohort of *Chthamalus montagui* at mean tidal level within 3 shores in the western cell (Lyme) and 3 shores within the eastern cells combined (Purbeck & Wight). Mortalities were arcsine square-root transformed. Factor Cell was fixed, factors Shore and Patch were random

Source	df	MS	*F*	p
Cell	1	0.011	0.03	0.866
Shore (Cell)	4	0.351	5.60	0.002
Patch (Shore)	24	0.062		

yet the winter mortality rate of the 1995 cohort was highest at the milder western end of the study area where populations were largest and recruitment was greatest (Fig. 9). Of the 14 recruits observed in marked quadrats on Isle of Wight shores in October 1995, only 1 had died by the following May. A nested ANOVA to determine differences in winter mortality of the 1995 cohort at MTL among the 3 shores in both the western cell (Lyme) and adjacent eastern cells (Purbeck and Wight combined) indicated statistically significant differences among shores within cells, but not between cells (Table 10).

Mortality curves of the 1995 cohort on the lower tidal level from the most western shore at Shoalstone and at Kimmeridge, monitored from photographs between October 1995 and August 1997, revealed that the greatest mortality occurred during the summer months (Herbert 2001). Mortality of adult *Chthamalus* on shores along the south coast of England between October 1995 and August 1996 did not show any significant density-dependent relationships or any east–west gradient (Fig. 9).

DISCUSSION

Adult performance

In this discussion, we first consider the evidence to reject hypothesis 1 based on the experimental and observational studies undertaken. We then synthesise available oceanographic evidence coupled with knowledge of habitat availability in the central English Channel to support hypothesis 2. Despite a reduction in *Chthamalus montagui* density of 5 to 6 orders of magnitude over a distance of 200 km, no evidence of impaired adult performance could be found at the species border. Gonads appeared to develop normally in near-edge populations and in translocated samples. In some years, gonads of eastern populations close to the species border developed faster than populations further west. Burrows et al. (1992) estimated that *C. montagui* has an average of 1.5 to 3.6 broods yr^{-1} in southwest England, which is comparable with the estimate of 2.6 broods obtained from animals translocated to the range border at Bembridge. Growth rate was variable, yet no gradient was apparent. Winter mortality of recruits was greatest at the milder western shores where recruitment density was also much higher. Adult mortality showed little variation and was more dependent on shore, season and tidal level: greatest mortality occurred in the summer months when there is potential damage from desiccation and possibly higher activity of bulldozing limpets (Hawkins 1983) and dogwhelks (Burrows & Hughes 1989). Variation in annual sea temperature also influenced the magnitude of *Chthamalus* recruitment and subsequent adult abundance, as demonstrated at several locations including near-edge populations. However, higher recruitment in warmer years has so far not caused any significant range extension from that which has persisted for at least 70 yr (Fischer-Piette 1936, Crisp & Southward 1958, Crisp et al. 1981, Herbert et al. 2007).

Although species borders have been attributed to competitive or predatory interactions mediated by local climate conditions (Leonard et al. 1999, Wethey 2002), the important and significant observation that the range border of *Chthamalus montagui* coincided with very low recruitment of other intertidal barnacles strongly suggests that oceanographic factors are of overriding importance in this species. With its complex hydrography and convoluted coastline, the south coast of England could present several barriers to the supply of larvae from both east and west. In the case of *Elminius modestus*, which is capable of fouling the undersides of boats, penetration of oceanographic barriers has undoubtedly been facilitated by this vector (Crisp 1958). With *Semibalanus balanoides*, the existing distribution along the entire coast, including estuarine populations, could be explained by a higher overall supply of larvae from the east of the region, enabling the establishment of critical breeding densities. Co-existence with *C. montagui* is probably mediated by changing temperatures over the past 70 yr: *S. balanoides* benefiting during the colder periods when *C. montagui* has been less successful. With space occupation of *S. balanoides* now decreasing at some southern locations (R. J. H. Herbert pers. obs.), populations of *S. balanoides* could become fragmented as the species retreats eastwards and disappears with changing climate (Poloczanska et al. 2008).

The production of several broods is advantageous as it reduces the risk of failure during the hazardous pelagic larval phase and could be especially important at the species border in a region of complex hydrography. Crisp (1950) was the first to suggest that unlike *Semibalanus balanoides, Chthamalus stellatus* gives rise to a succession of broods in British waters. A higher fecundity will increase the probability of breaching barriers. The breeding period of *Chthamalus montagui* is known to commence earlier in lower latitudes (Burrows 1988, O'Riordan 1992). Higher temperatures in 1995 and 1998 appear to have caused an earlier development of embryos at nearly all shores, whereas the late spring of 1996 severely delayed brooding. Cooler water may affect the production cycle and therefore food supply to the developing embryos (Patel & Crisp 1960a). Patel & Crisp (1960b) note that in cirripedes, the release of nauplii is frequently delayed after embryos have become fully developed and is dependent on the secretion of a hatching substance (reviewed by Clare et al. 1985), which is highly correlated with feeding. It is possible that the retention times of the different broods vary due to food availability.

Although self-fertilization is known in *Chthamalus* (Barnes & Crisp 1956), an examination of *Chthamalus montagui* at Colwell on the Isle of Wight showed that the frequency of brooding in isolated *C. montagui* was 33% compared to 70% in contiguous animals (Herbert 2001). Isolation is typically the norm within these small populations; on average, only 10% of all *C. montagui* mapped on Isle of Wight shores were contiguous (Herbert 2001). This could considerably influence the larval output from small populations at the species border. Because adult densities become so low at the range limit, there could be an Allee effect (Allee 1931) since the minimum distance between individuals necessary for cross-fertilization is seldom reached.

Habitat availability

Shores approaching the species border have a lower tidal range and the area of rock habitat is reduced by nearly 80% before rising again to the east of the Isle of Wight. Some shores in this region are characterised by large amounts of available space for potential colonists, supporting the hypothesis that the region is generally poor for the recruitment of a variety of species, not just barnacles. A potential competitive interaction between *Chthamalus montagui* and *Semibalanus balanoides* (Connell 1961) does not cause the range of *C. montagui* to terminate abruptly because density and recruitment is low for both species. Further east, beyond the existing border, soft and friable chalk shores predominate. Recruitment of *C. montagui* may be quite high on this rock type, but post-recruitment mortality can limit the persistence of populations (Herbert & Hawkins 2006). Poor habitat quality is therefore likely to inhibit population growth and potential larval output. However, the proliferation of new hard sea defences built from granite and limestone along this coastline, may provide significant barnacle habitat in the longer term (Moschella et al. 2005, Herbert & Hawkins 2006).

Recruitment limitation

Many studies have demonstrated that recruitment correlates well with larval settlement rate (Sutherland 1987, Holm 1990, Minchenton & Schiebling 1991). Although physical and biological factors may cause mortality among settling cyprids and newly calcified recruits, Dayton (1971), Hawkins (1983), and Kendall & Bedford (1987) concluded that poor recruitment of

Chthamalus montagui was a result of low numbers of cyprids reaching the shore, rather than post-settlement mortality. Here, greater recruitment was recorded in the warmest summers. Higher temperatures can reduce the larval development period and the duration and distance of dispersal (O'Conner et al. 2007), which could increase recruitment. Warm summer days can also cause the formation of onshore seabreezes that may facilitate recruitment (Hawkins & Hartnoll 1982). Between 1994 and 2004, annual recruitment at the species border on the Isle of Wight was significantly correlated with the number of summer days (July to September) when the wind was onshore; the pulse of high recruitment in the summer of 2000 coincided with the second highest frequency of onshore breezes over that decade (Herbert et al. 2007).

In areas of significant upwelling, onshore advection of warm water has been significantly correlated with invertebrate settlement causing major spatial and temporal variability in recruitment (Broitman et al. 2005, Narváez et al. 2006). There is no evidence of seasonal or cyclical upwelling along the shallow south coast of England, although a retentive gyre occurs to the east of the Isle of Wight in the summer months (Guyard 2000).

The oceanographic complexity of the region precludes a precise identification of process. Gaylord & Gaines (2000) predicted that where regional currents converge or diverge, 2-way boundaries could be established causing division in the supply of propagules to the shore that would have an inevitable impact on adult abundance and assemblage structure (Gaines & Roughgarden 1985, Underwood & Fairweather 1989). Along the south coast of England, there is likely to be significant larval dispersal around prominent headlands where there are strong tidal races. Using a combination of genetic analyses and a hydrodynamic model, Gilg & Hilbish (2003) confirmed the presence of a strong barrier to mussel (*Mytilus* spp.) larval dispersal at Start Point at the western end of Lyme Bay.

Although little evidence of impaired performance at the border has been identified for adult *Chthamalus montagui*, the larval stages have not been investigated. The long pelagic phase and potential for significant dispersal could expose larvae to a wide variation in food and predatory environment that may affect fitness and mortality. The summer plankton assemblages in western stratified and eastern mixed regions are likely to be spatially and temporally variable (Hoch & Garreau 1998). In culture, the barnacle naupliar development period is known to be affected by food (Moyse 1963, Lang & Marcy 1982, Hentschel & Emlet 2000) and there could be interactions between feeding and temperature, as reported in copepod nauplii (Cook et al. 2007). In barnacles, the final cyprid stage is non-feeding, so settlement close to the species border is not necessarily indicative of local naupliar survival. However, Stage II nauplii of *Chthamalus* were collected at the species border in the highly eutrophic Southampton Water between 2000 and 2001 (Muxagata et al. 2004, E. Muxagata pers. comm.). Unless there is an interaction with food type, sea temperature should not limit survival of *Chthamalus* larvae in the eastern Channel, which experiences higher summer SST than the western region.

CONCLUSIONS

The available evidence allows us to reject hypothesis 1. The balance of evidence supports hypothesis 2 in this species: the persistent discontinuity of *Chthamalus montagui* on the south coast of England is considered to be due to recruitment limitation and is not caused by any gradient in adult performance. The decline in recruitment likely reflects massive reductions in larval abundance within the water column and the supply of cyprids to the shore, which are caused by complex hydrographic and habitat constraints. This study supports other work that challenges the classic view that a species' geographic limit is largely determined by continuous processes acting on populations as the range boundary is approached (Sagarin & Gaines 2002b, Gilman 2005). While this may occur for some species with short-distance dispersal over areas that cover the entire species range, it does not explain steep gradients in recruitment for species with long-distance passive dispersal (Gaylord & Gaines 2000). Regions or cells of generally low recruitment are important to identify as they may be vulnerable to re-population following disturbances. Identification of these areas and locations of consistently high recruitment will influence the siting and spacing of marine reserves (Shanks et al. 2003). Modelling the rate of change in biological assemblages in response to rising SST needs to incorporate the characteristics of such regions, which appear to be more critical for some species than for others. For example, the trochid *Gibbula umbilicalis,* which has a short larval phase lasting at most a few days (Fretter & Graham 1994), has now managed to penetrate its hitherto persistent border and extended its range eastwards along the Channel through rapid recruitment over the past 10 yr (R. J. H. Herbert & S. J. Hawkins pers. obs.). Monitoring progress in penetrating such barriers by different species will also provide further insight into the importance of life-history traits influencing the capacity for extension and retreat in response to climate change.

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