Influence of recruitment and temperature on distribution of intertidal barnacles in the English Channel

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The central English Channel is a region of complex hydrography where many warm-water (Lusitanian) species reach their limits, failing to penetrate to the North Sea. In this area we have re-surveyed the eastern limits of the Lusitanian intertidal barnacles *Chthamalus montagui* and *C. stellatus*, from 1994 to 2004, a decade of exceptionally high sea temperatures. Compared to the early 1950s and the 1970s there have been range extensions on both sides of the Channel. Annual recruitment of *Chthamalus* on the English coast was monitored during the survey. There was a consistent gradient of low recruitment to the east of Portland Bill, with significant reductions coinciding with prominent headlands. Highest recruitment occurred during the warmest years. Cluster analysis revealed a high degree of similarity of annual recruitment within coastal cells suggesting that local processes are also important. In 1999 recruitment was studied in the other common intertidal barnacles, the boreal *Semibalanus balanoides* and the non-native *Elminius modestus*, to compare with *Chthamalus*. There was low recruitment of all species in the region between Selsey Bill and Portland Bill, suggesting habitat limitations and/or hydrographic mechanisms. Annual recruitment of *Chthamalus* at existing limits on the Isle of Wight was positively correlated with the number of days of westerly and south-westerly winds during the summer, coinciding with the pelagic larval phase. A 'pulse' of high *Chthamalus* recruitment on the Isle of Wight, measured during the warm summer of 2000, reversed population decline. Only a higher frequency of such pulses will maintain populations at existing limits and increase the rate of range extension towards the North Sea. Any such extension will still be limited by lack of suitable hard substrata, though this has increased in recent years with proliferation of coastal defence schemes.

INTRODUCTION

The British Islands straddle a biogeographic boundary zone where southern (Lusitanian) and northern (Boreal) species overlap (Forbes, 1858; Crisp & Southward, 1958; Lewis, 1964). Many species of intertidal rocky shore invertebrates have been surveyed in this region for 75 years, particularly for the English Channel where many Lusitanian species reach their geographic limits (Fisher-Piette, 1936; Moore & Kitching, 1939; Crisp; 1950; Crisp et al., 1981; Southward & Crisp 1952, 1954, 1956; Crisp & Southward, 1958, Herbert et al., 2003). These studies provide an excellent baseline against which to judge the influence of global climate change. There is an east-west gradient of shallow water species in the English Channel, with Lusitanian species commoner in the western basin and cold-water species commoner in the eastern basin, reflecting the difference in temperature regimes. A time series on fluctuations in abundance of barnacles of the Lusitanian genus *Chthamalus* (*Chthamalus montagui* Southward and *C. stellatus* Poli) and the Arctic-Boreal species *Semibalanus balanoides* (L.) has provided evidence of climatic influence (Southward, 1967; Southward, 1991; Southward et al., 1995). During cooler periods, for example in the 1970s, *Semibalanus* was found to predominate, whereas during warmer years such as the 1950s and the 1990s *Chthamalus* were more abundant (Southward, 1967, 1991). Annual counts near Plymouth (Southward, 1991) show that the proportion of adult *Chthamalus* at mean tide level (MTL) and mean low water neap tide level (MLWN) is positively correlated with annual mean sea surface temperature (SST) two years earlier, whereas *S. balanoides* is negatively so correlated. Good settlement as a result of greater larval output resulting from more broods during warmer years is considered to be a major factor causing an increase in the adult *Chthamalus* population. In contrast, in the single brooder *Semibalanus* the survival of juveniles is noticeably higher during the cooler periods (Southward, 1991).

Surveys from 1950 to the late 1970s showed a major discontinuity in the abundance of *Chthamalus* and *Semibalanus* along a line between the Isle of Wight and the Cotentin Peninsula (Figure 1). East of this region *Chthamalus* was virtually absent (Crisp & Southward, 1958; Southward, 1964; Crisp et al., 1981) and *Semibalanus* much more abundant. It was suggested that the trends in distribution of barnacles and other intertidal animals surveyed were broadly related to temperature differences, with eastern limits determined not from a lethal winter minimum temperature, but from lower competitive ability compared to northern species, as the temperature falls (Crisp & Southward, 1958; Connell, 1961). Additionally, other factors appeared to be involved in the abrupt change of species distribution in the central region of the Channel, including barriers to larval dispersal and settlement created by the complex hydrography and lack of habitat for settlement in the eastern Channel. Around Swanage in Dorset there is a very small tidal range (2m) and potential barnacle habitat is reduced in the vicinity. Moreover, this area has many shores consisting of soft bedrock, including chalk, which appear inimical to barnacle settlement (Moore & Kitching, 1939). The tidal range increases both to the east and west of this area in Dorset, reaching 4m at Portsmouth and in Torbay. Distortion of the tidal curves is a common feature of the region and there are other unusual tidal phenomena, with double high and low waters from east of Portland Bill to the Isle of Wight (Pingree & Maddock, 1977; Barne et al., 1996). Tidal ranges increase farther away from the central Channel region, reaching maxima of 8-9m around Jersey and the Gulf of St. Malo on the north coast of France. While weak (<0.5 $m.s^{-1}$) inshore tidal currents occur in Lyme Bay and off parts of the Sussex coast, fast streams occur in many areas, reaching between 1.75-3.0 $m.s^{-1}$ off Portland Bill during spring tides (Barne et al., 1996; Bruce & Watson, 1998). Fast currents and turbulence also occur off other major headlands such as St. Albans Head in Dorset and at the Needles and St. Catherines Point on the Isle of Wight. Either side of these headlands, tidal eddies may occur such as at Portland Bill (Pingree & Maddock, 1977). A major gyre circulation reducing the easterly residual flow occurs at the eastern end of the Isle of Wight between Bembridge and Selsey Bill during the summer months (Boxall & Robinson, 1987 Guyard, 2000).

The present study had two main aims. First, to examine evidence for range extension of *Chthamalus* spp. during a period of increasing SST (Figure 2). Secondly, to examine the role of hydrographic barriers and habitat availability on recruitment, and hence in setting biogeographic boundaries in the region. To this end, levels of recruitment were measured and a simple model created to simulate larval output.

While coastal marine ecosystems are often considered highly open (Roughgarden et al, 1985; Gaines & Bertness, 1992; Johnson, 2005), recent genetic studies shows a greater degree of small-scale differentiation of populations than might be expected (Duran et al, 2004; Paz et al, 2004; Mair et al, 2005). This study contributes to the debate about connectivity in coastal ecosystems and shows evidence for the existence of barriers that will interfere with the advance or retreat of species during periods of climate change.

MATERIALS AND METHODS

Initial Survey

A broad-scale re-assessment of barnacle species distribution was made along the central south coast of England in the autumn of 1994 and repeated in subsequent years to 2004. In the autumn of 2001 and 2002, sites along the French coast between the Gulf of St Malo and Calais were also re-surveyed. Sites included those visited earlier (Crisp & Southward, 1958; Crisp et al., 1981; Southward, unpublished database), thus extending the long time series (>50 y) for those places. The density of barnacle species *Semibalanus balanoides*, *Elminius modestus* Darwin and *Chthamalus* spp. was recorded at three tidal levels using quadrats of various sizes between $6cm^2$ and $400cm^2$ depending on abundance. Surveys were carried out on flat or gently sloping surfaces except where these were not a characteristic feature of the shore. In such cases, species densities were obtained on all accessible surfaces and aspects, including man-made substrata such as sea walls and groynes. If a species was not observed within any of the quadrats, a 30 minute timed search was carried out to check presence. Species abundance was converted to a semi-quantitative scale (Table 1.), consistent with Crisp & Southward (1958). References to species abundance using this scale are shown in parentheses.

Recruitment of Chthamalus along the central south coast of England

In June 1994, prior to settlement of the species, six 400cm^2 clearances were created on the upper, middle and lower section of the limpet-barnacle zone (eulittoral zone, *sensu* Lewis, 1964) at five sites between Torbay in Devon and Swanage in east Dorset. Clearances of 400cm^2 incorporated the range of microhabitat and surface topography thought to be important at low recruitment sites. For sites where population densities were low, the same clearance squares were re-scraped annually. At the end of the *Chthamalus* settlement season in mid-October, the number of recruits was counted with the aid of a hand-lens. The two species of *Chthamalus* could not be separated immediately post-settlement, however careful examination of quadrats the following May, when the recruits were larger prior to re-clearance, revealed only the occasional *C.stellatus* throughout the whole study period. Where densities of *Chthamalus* were very high, at least five sub-samples were taken. Each site was also checked in August during the middle of the settlement season to determine if there was any delay in settlement at the eastern localities and whether a higher density of recruitment was evident that may not have survived until the end of settlement.To avoid damage to the small populations at the extreme eastern limits on the Isle of Wight, counts of new recruits were made within un-scraped areas of the shore at Hanover Point (Brook), Watershoot Bay and Bembridge where barnacle cover was generally less then 75%. Ten quadrats (400cm^2) were placed within two patches at each of three tidal levels. Adult density of all barnacle species was also recorded. The recruitment surveys and adult census were repeated annually between 1994 & 2004.

Recruitment of Semibalanus balanoides, Chthamalus spp. *and Elminius modestus on vertical surfaces along the south coast of England in 1999.*

To establish the pattern of recruitment of other intertidal barnacle species a broad-scale study was carried out to include neighbouring coastal cells east and west of the Isle of Wight. For consistency, it was decided to survey only vertical surfaces including walls, groynes and pier piles as they are more frequently distributed than natural platforms in the eastern cells. The coast from Prawle Point to Beachy Head was divided into four cells (Figure 1), broadly based on those cells or sub-cells identified as having independent sediment transport characteristics (which are likely to be correlated with tidal or wind driven currents) and differentiated largely by major headlands or hydrographic barriers (Motyka & Brampton, 1993). These were named: '*Lyme*' (Prawle Point to Portland Bill); '*Purbeck*' (Portland Bill to Handfast Point near Swanage; '*Wight*' (Handfast Point to Selsey Bill; and '*Sussex*' (Selsey Bill to Beachy Head). Within each cell, three representative shores were chosen. To determine within-shore variability, three random patches of ten 100cm^2 clearances were made at each of three tidal heights approximating to mean high water neap tide (MHWN), MTL and MLWN. Settlement of *S. balanoides* begins in March and early April (Crisp, 1959; Hawkins & Hartnoll, 1982; Jenkins et al., 2000; Kent et al., 2003) so clearances were made well in advance during January and February. New clearances in different areas of each shore were made in May, prior to the settlement of *Chthamalus* and *Elminius modestus*. Each quadrat was scanned with a hand lens and sub-sampling used to calculate the mean density within each 100 cm^2 clearance.

Simulation model of barnacle larval output and recruitment within coastal cells

Early hypotheses concerning the discontinuity of intertidal species along the English Channel (Crisp & Southward, 1958) suggested that larval dispersal within fast offshore currents or retention within eddies and gyres may be associated with headlands and might cause abrupt reductions in recruitment further along the coast in the direction of residual drift. The influence of coastal promontories and embayments upon recruitment was assessed by calculating recruitment as a proportion of estimated larval output from different localities along the south coast, up to the species eastern limits. Consistent and significant reductions in the estimated percentage recruitment in localities of hydrographic dynamism and complexity would support the hypothesis that larval supply to the shore at these locations was generally limited.

To determine the magnitude of *Chthamalus* and *Semibalanus* larval production within cells and sub-cells and hence recruitment as a percentage of larval output, the population density of the adult barnacle population had to be estimated. The area of intertidal rock along the south coast of England between Prawle Point and Beachy Head was calculated using GIS (*MapInfo v5*). Based on vertical species zonation shown in Lewis (1964) and a visual assessment along this moderately exposed-exposed coast two-thirds of this was considered to approximate to the limpet-barnacle zone. This zone was divided equally in to the three areas 'upper' 'middle' and 'lower' and the adult population was calculated within each zone based on mean counts. An estimate of total larval output within cells was calculated for both taxa. For *Chthamalus*, a mean figure of 1000 eggs per brood with 2.6 broods per year was taken from Burrows et al., (1992). For *Semibalanus*, which has just a single brood, a mean figure of 2000 eggs per brood was taken from estimates by Barnes & Barnes (1968) from shores in southern England. Recruitment was measured from counts as described above.

RESULTS

Re-surveys

Compared to earlier surveys (Crisp & Southward, 1958; Crisp et al., 1981) *Chthamalus* has shown a small extension eastwards on both sides of the English Channel and an increase in abundance at earlier limits (Figure 3). There are two species of *Chthamalus* in Europe, *C. stellatus* Poli and *C. montagui* Southward; (Southward, 1976). Both show similar patterns of geographical distribution with eastern limits on the Isle of Wight (Figures 4 & 5) and although counted separately they are often treated as a single taxon for comparison with the abundance of *Semibalanus balanoides* (Southward, 1991). Single individuals of *C. montagui* were found on limestone platforms near the lifeboat station at Bembridge in 1995 and 2001 (Figure 4), which is 8 km east of earlier limits at Bonchurch recorded in the late 1970s (Crisp et al., 1981). The eastern limits of *C. stellatus* were also found at Bembridge (Figure 5) approximately 26 km east of previous records at Hanover Point (Crisp et al., 1981).

West of Portland, *C. montagui* was the most abundant barnacle between MTL and MHWN. On favourable substrata between MHW and MLWN mean densities of *C. montagui* between 4-6 per cm^2 were recorded at sites in Lyme Bay where a maximum of 10.25 per cm^2 was measured at MLWN at Lyme Regis. To the east of Portland Bill the density of adult *C. montagui* decreased along the Purbeck coast from 2-3 per cm^2 at Osmington to 0.5-1 per cm^2 at Kimmeridge. Although still 'common' (Table 1) on the Long Groyne at Hengistbury Head, the density of *Chthamalus montagui* diminishes rapidly on the Isle of Wight. While a few individuals occur on the north-west coast of the island, the largest densities are on the southern shores at Hanover Point (Brook) and between St. Catherine's Point and Ventnor, where the maximum density can reach 5 per dm^2 ('frequent') with a significant number of adjacent individuals. These shores may now be capable of forming an outlying breeding population as previous surveys indicated that densities were generally one or two orders of magnitude less (Figure 3) The species was found on a variety of rock types including the chalk boulders below Culver Cliff near Bembridge. *Chthamalus stellatus* was less abundant than *C. montagui*, with mean shore densities never rising above 1 per cm^2. As noted by Crisp et al (1981), in the western Channel *C. stellatus* is most abundant in the lower regions of the limpet-barnacle zone, but it was occasionally observed to extend above *C. montagui* near its eastern limits on the Isle of Wight. A similar phenomenon has been recorded at the limits of *Chthamalus* in north-east Scotland (Crisp, unpublished data). Maximum densities of 0.75 per cm^2 were measured on the mid shore at Portland Bill although the species still only accounted for less than 5% of the total *Chthamalus* recorded. Mean densities diminished east of Portland, yet maximum counts continued to be relatively high east along the Purbeck coast with 0.6 per cm^2 recorded at Kimmeridge; densities accounting for over 12% of total *Chthamalus* on the lower shore were recorded there in 1994. On the Isle of Wight the species was generally classed as ‘occasional’ along the south-coast, yet due to aggregated settlement could be a cross-fertilizing population.

Semibalanus balanoides was ubiquitous although mean shore densities were higher east of the Isle of Wight. Densities of up to 11 per cm^2 were measured on the sandstone rocks at Cow Gap near Eastbourne in Sussex and mean densities at MLWN were over 5 per cm^2 (Figure 6). On the chalk at Seaford, mean shore densities of nearly 3.5 per cm^2 were recorded and up to 12 per cm^2 on the flints. Even at MHWN tide level the species was common with up to 2 per cm^2 recorded at Shoreham. In contrast, at shores in Lyme Bay the species was hardly ever seen at this tidal level, where *Chthamalus* can occupy nearly 100% cover. However at MLWN, maximum densities of 1 to 1.5 per cm^2 were recorded for *Semibalanus balanoides* at Shoalstone and Saltern Cove and at Lyme Regis maxima of 2.5 per cm^2 were measured at MTL.

Elminius modestus was also most common in the eastern Channel and particularly near estuarine localities (Figure 7). Highest densities were measured at Southsea where maxima of 4 per cm^2 were recorded at MHWN. At Selsey Bill and at Worthing the species was ‘common’ or ‘abundant’. At Shoalstone in Torbay, a maximum of 2.3 per cm^2 was recorded at MLWN. East of Portland Bill, abundance was comparable with earlier surveys (Crisp, 1958; Crisp & Southward, 1958), however further west at Lyme Regis, where between 1948-1950 the species was unseen, it is now ‘occasional’ and at Brixham it was ‘abundant’ when previously ‘occasional’.

France

On the French coast both species of *Chthamalus* were found right across the northern shores of the Cotentin Peninsula to Barfleur (Figures 4 and 5). This is approximately 50 km east of previous records in the 1970s where the limits were just east of Cap de la Hague (Crisp et al., 1981). *C. stellatus* was the most abundant of the two species on these exposed granite shores and 'frequent' to Cap Levy, where no *Chthamalus* was found in the 1950s (Crisp & Southward, 1958). At Baie d’Ecalgrain, immediately south of Cap de la Hague, mean-shore densities of *C. stellatus* were 0.06 per cm^2 ('frequent') in 2000 compared to 0.02 per cm^2 in 1979 (Crisp et al., 1981) but an order of magnitude greater at mean high water springs (0.2 per cm^2) than the earlier survey. *C. montagui* was 'frequent' here in 2000 compared to 'rare' in 1979 (Crisp et al., 1981). Shores on the north coast of the Cotentin Peninsula are now likely to have breeding populations of both *Chthamalus* species. The density of *Semibalanus balanoides* appears to be relatively unchanged in the surveyed locations compared to earlier surveys (Crisp & Southward, 1958) although an increase of between one and two orders of magnitude was recorded in the abundance of *E.modestus* on the west side of Cotentin, where in 1954 it was ‘rare’ or ‘occasional’ (Crisp & Southward, 1958).

Recruitment of Chthamalus

From west to east, a consistent pattern was observed along the coast (Figure 8) with shores in Lyme Bay having much greater recruitment of *Chthamalus* than those east of the major promontory at Portland Bill, Weymouth Bay and along the Purbeck coast. In Lyme Bay, all three shores studied had mean recruitment densities of at least 1 per cm^2, except for Shoalstone in 1997 (0.8 per cm^2). The highest mean recruitment recorded in Lyme Bay was 20 per cm^2 on the lower shore at Lyme Regis in 1999, when a maximum count of 27 per cm^2 was recorded from one quadrat. There was an order of magnitude reduction in recruitment at Osmington Mills immediately east of Portland with densities exceeding 1 per cm^2 in 1999 only. Densities were further reduced along the Purbeck coast to Peveril Point where the mean was never greater than 0.02 per cm^2 (8 per 400cm^2 quadrat). At some shores there were also consistent differences in recruitment with tidal level. Shoalstone, Saltern Cove and Osmington

Mills generally had higher recruitment on the middle shore, whereas at Lyme Regis, Portland Bill and Kimmeridge, densities were usually greater at lower tidal levels. The annual data between 1995-1999 were subject to three-way analysis of variance (Table 2) with the main hypothesis being that recruitment was significantly different in the western cell (Lyme) compared to the eastern cell (Purbeck).To ensure a balanced design for this analysis the highly wave-exposed shore at Portland Bill was omitted. Factor 'Coastal Cell' is orthogonal and fixed; factor 'Shore' was nested in 'Coastal Cell' and is random; factor shore 'Height' is orthogonal and fixed. There were six replicates at each shore level sampled. The results indicate that there was a significant ($p<0.05$) or highly significant ($p< 0.001$) difference in recruitment between coastal cells each year except 1997. In 1998 the difference was dependent on tidal height examined with differences being apparent at middle and lower levels. Apart from 1998 there were highly significant differences between shores and each year the recruitment at a particular tidal height varied on different shores. Even in 1997 the mean recruitment in the western cell was three orders of magnitude greater than that in the eastern cell. Differences between shores in the eastern cell were not resolved by Student-Newman-Keuls (SNK) multi-comparison procedure because of the much larger variances. A separate analysis was carried out on the eastern cell, which showed that the recruitment at Osmington Mills was greater than at both Kimmeridge and Peveril Point but there was again a significant Height x Shore interaction ($p<0.05$). Observations in August did not show signs of mortality of newly settled *Chthamalus* related to high summer rock temperatures. No cyprids or metamorphosing recruits were seen during shore visits at localities east of Portland Bill.

Highest mean recruitment of *Chthamalus* occurred during the warmest year (1999) except at Saltern Cove, where recruitment was marginally greater in 1995. All shores, except for Shoalstone, had their lowest recruitment in the cooler years of 1996 and 1998.

A Friedman test (Sokal & Rohlf, 1997) on the rank-order of recruitment of *Chthamalus* at sites along the south coast (Table 3) showed that between 1995 and 1999 there was a high degree of concordance in the magnitude of *Chthamalus* recruitment ($\chi^2 = 22.8$, n = 8, df 4, $p <0.001$). This implies that broad-scale factors, such as temperature and (or) wind direction, are likely to have an overriding influence on annual recruitment variability.

To determine the level of similarity in recruitment variation between individual sites (and cells) a cluster analysis (Figure 9) using Bray-Curtis Similarity Indices (Bray & Curtis, 1957) was undertaken of mean-shore *Chthamalus* recruitment over the period 1995-99. The three main clusters show remarkable association with the location of known coastal process cells. Cluster 2 consists of all sites within 'Lyme' cell, with the two sites in Torbay, Shoalstone and Saltern Cove, separated as a sub-grouping. The shores in Cluster 3 are all within 'Purbeck' cell. The sub-group consisting of Osmington Mills and Portland Bill is unsurprising considering their close proximity. Cluster 1 consists of the two most eastern sites used in the analysis; Peveril Point on the Dorset coast and Hanover Point on the Isle of Wight. This shows that in spite of overriding broad-scale influences, local meteorological and hydrographic processes are still important factors that can affect variation in recruitment and degree of spatial synchrony between cells.

Recruitment on vertical surfaces along the south coast of England during 1999

Recruitment of *Semibalanus* was highest along the Sussex coast (Figure 10A). Densities were greatest on the piles of Worthing Pier, where mean and maximum densities of 22 and 30 per cm^2 respectively were measured on the upper shore. There is a marked contrast between the high recruitment densities observed along the Sussex coast and that measured round the Isle of Wight and in east Dorset. In the Solent the recruitment density at East Cowes was, in comparison, relatively low with a mean of 1.6 per cm^2 at one patch on the lower shore. At Kimmeridge, where *S. balanoides* recruitment on flat surfaces was almost zero, there were higher densities on vertical ledges, with a mean of 0.2 per cm^2 at one patch on the lower shore. In the east of Lyme Bay, relatively high mean-shore recruitment densities were observed at Saltern Cove and Lyme Regis of 8 and 11 per cm^2 respectively. However at each of these sites there was considerable variability both between tidal levels and within tidal level. The main conclusion from a four-way ANOVA, followed by SNK procedure, was that there is a significant difference in recruitment between coastal cells (F = 10.98, $p < 0.01$) with the Sussex cell having greater recruitment than the other three cells further west ($p < 0.01$). The differences between shores were dependent on tidal height examined (Height x Shore interaction $p < 0.01$). There was a highly significant correlation ($p<0.001$) between recruitment and background density of adults, R^2 = 0.74.

Highest counts of *Elminius* were along the Sussex coast (Figure 10B) with 16 and 23 per cm^2 being the mean and maximum recorded for a single patch at Selsey Bill. Yet ANOVA failed to resolve any differences between cells and differences between shores were dependent on tidal height examined; generally recruitment was greater on the lower level. There was a highly significant correlation ($p<0.001$) between recruitment and background density of adults, $R^2 = 0.65$.

The general pattern of *Chthamalus* recruitment on vertical surfaces (Figure 10B) mirrored the pattern observed on shore platforms in Figure 8. Very high densities of recruits were measured in Lyme Bay with significant reductions east of Portland Bill, diminishing rapidly along the Purbeck coast. No recruitment of *Chthamalus* was recorded east of Watershoot Bay on the Isle of Wight. The highest mean patch density was 28 per cm^2 on the lower shore at Lyme Regis. There was considerable variability between patches at each tidal level. The results of a four-way ANOVA and SNK test showed a significant difference between cells, with the 'Lyme' cell having a significantly higher recruitment than the other cells further east (F = 13.12, $p < 0.01$). A strong Height x Shore interaction indicated that differences between shores is dependent on tidal height examined. There was a highly significant correlation ($p<0.001$) between recruitment and background density of adults, R^2 = 0.94.

Between 1994 and 2004 recruitment of *Chthamalus* measured at Hanover Point on the south-west coast of the Isle of Wight (Figure 11) was either nil or extremely low. Yet there was a significant 'pulse' in 2000 that arrested adult population decline. A similar pulse was also measured at Watershoot Bay on the southern tip of the island. Over the decade, the summer (July-September) of 2000 had the second highest number of days when the wind was either from the west or south-west which may have facilitated larval transport from the larger populations further west along the Dorset coastline. In this area, between 1994-2004, annual recruitment was significantly correlated with the number of summer days the wind was from west or south-west ($r = 0.67$, $p= 0.03$, $n = 10$). The highest number of such days occurred in 2004 but there was also an unusual number of particularly strong winds that may have caused greater dispersal and been responsible for the relatively low recruitment measured, albeit the second highest since records began.

DISCUSSION

Subsequent to the previous survey of *Chthamalus* along this coast (Crisp et al., 1981), from the late 1980s there has been a succession of exceptionally warm summers and mild winters, with SST much higher than in the 1970s (Figure 2). Large range extensions of other southern species have been observed in the eastern Channel (*Balanus perforatus*, Herbert et al 2003; *Gibbula umbilicalis*, Hiscock et al, 2004; R.J.H. Herbert, S.J. Hawkins and N. Miezkowska pers.obs.) yet there have been considerably smaller eastward extensions of *Chthamalus*. The ten-year time series and the broad-scale study of *Chthamalus* recruitment in 1999 all showed a steeply declining recruitment gradient of *Chthamalus* east of Portland Bill. Yet, importantly, recruitment along the Purbeck and Isle of Wight coast was found to be low for all species of intertidal barnacles including *S. balanoides*. Additional recruitment data for *S. balanoides* obtained in 1998 and 1999 (Kent et al 2003) is consistent with this. Compared to sites further west, recruitment of *Chthamalus* measured on the Isle of Wight may have been slightly elevated as quadrats were not cleared of adults and as a consequence could be more attractive to settlers. It is suggested that this considerable reduction in intertidal barnacle recruitment in the 'Purbeck' and 'Wight' cells is mainly the effect of physical and hydrographic barriers created by Portland Bill and Selsey Bill, which reduce both east and westward transport of larvae and subsequent settlement on the shore. Very low adult densities and considerably higher space availability observed on shores along the Purbeck and Isle of Wight coast support this view. Portland Bill was considered to be an important barrier to the westward dispersal and colonisation of *Elminius modestus* (Crisp, 1958). Should *Semibalanus balanoides* retreat from the extreme south-west of England following higher temperatures, as occurred in the 1950s (Southward, 1967), then any subsequent recolonisation from shores in the eastern Channel might be inhibited by large headlands.

A simple simulation model of *Chthamalus* recruitment within each coastal cell, incorporating estimates of habitat area, adult density and potential larval production (Tables 4 & 5) shows that recruitment as a percentage of estimated larval production is reduced by between one and two orders of magnitude between Lyme

Bay and the Purbeck coast. This could be indicative of greater larval retention within Lyme Bay and higher larval loss on the eastern side of Portland Bill on the Purbeck coast. Fewer recruits per adult reaching the shore could also be symptomatic of an Allee-effect (Allee, 1931; Kent et al 2003) where because adult densities are so low, the minimum distance between individuals necessary for cross-fertilisation is seldom reached. However in *Chthamalus*, this difficulty may be partly overcome by self-fertilisation (Barnes & Crisp, 1956; Barnes & Barnes, 1958). Between 1995-1998, investigations in to the development of gonads and brooding of embryos in non-isolated individuals of *C. montagui* on the south coast of England found no evidence of impaired or delayed development at the extreme eastern limits of distribution (Herbert, 2001). The simulation for *Semibalanus balanoides* (Table 6) from data obtained in 1999 also shows an order of magnitude reduction in percentage recruitment along the east Dorset coast and around the Isle of Wight compared to the more embayed coastline both to the east and west of these locations. Certain generalisations have necessarily been made; fecundity of *Chthamalus* and *S. balanoides* is known to be subject to annual variation, degree of wave exposure and shore level (Barnes & Barnes, 1968; Burrows et al 1992). Estimates of recruitment obtained from clearances may be excessive at sites where space is limited because of high density of adults. The estimate of shore surface area makes no allowance for shoes with varied topography that includes boulders and overhangs.

During the study, highest *Chthamalus* recruitment occurred in the warmest summer of 1999 and lowest in the less warm years of 1996 and 1998. Moreover there has been remarkable concordance in the level of recruitment at different locations along the whole coast. This suggests that in spite of the locally variable tidal regime, rock type and shoreline configuration, the magnitude of recruitment appears to be ultimately determined by some climatic or meteorological factor. Lewis (1991) suggested a correlation between *Chthamalus* recruitment and summer temperatures in Scotland, but the relatively poor regional synchrony also pointed to strong wind influences on this highly irregular coastline, as with *Semibalanus* in the same area (Barnes & Barnes, 1977; Hawkins & Hartnoll, 1982). Comparison of spatial synchrony in the abundance of 40-plus intertidal species on rocky shores in north Scotland showed *Semibalanus* to have the most synchrony over a 20 year time series, which could be partly as a result of the comparatively long pelagic phase and hence dispersal period (Burrows et al., 2002). At Aberystwyth, on the Welsh coast, Kendall

& Bedford (1987) did not find any association between recruitment of *C. montagui* and summer air temperature. Hawkins & Hartnoll (1982) found that settlement of *S. balanoides* around the Isle of Man was strongly correlated with onshore winds. Relatively calm seas with light onshore winds, often associated with warm summer anticyclonic conditions, are likely to provide good conditions for larval settlement of any intertidal species, and so it is difficult to separate wind effects from sea temperature. The greater frequency of easterly winds during the summer of 1995 may have been responsible for the particularly high recruitment of *Chthamalus* observed at Shoalstone and Saltern Cove within Torbay, which has an eastern aspect and may aid larval retention in other larger embayments along the coast. The small but significant 'pulse' of *Chthamalus* recruitment observed on Isle of Wight shores during 2000 is likely to have been caused by the favourable coincidence of several variables including a greater frequency of winds from the direction of larger populations, and high sea temperature. Pulses of settlement may also have occurred on the French side of the Channel during the warm climate phase of the 1950s: a single *Chthamalus montagui* (recorded as *C.stellatus* at the time) was found 1 km west of Cap Gris Nez in May 1961 (Southward, 1964).

The probability of further eastward range extension of *Chthamalus* along the south coast of England, overcoming the barrier created by Selsey Bill, is therefore dependent on a higher frequency of recruitment pulses on Purbeck and Isle of Wight shores which would increase the adult population and larval output at existing limits.

The range extension of *B. perforatus* (Herbert et al, 2003) may have been facilitated by sublittoral populations. The rapid range extension of the trochid *G.umbilicalis* is less easy to explain as the short pelagic of 4-5 days (Fretter & Graham, 1994) is much less than barnacles. However short-range dispersal and subsequent metamorphosis may be more effective at penetrating hydrographic barriers than a lengthy and vulnerable pelagic phase. Yet other factors such as poor survival on the soft, friable chalk substrate (Herbert & Hawkins in press) and competitive interactions with large populations of *Semibalanus* (Connell,1961) may also be partially responsible for limiting the establishment of *Chthamalus* in the eastern Channel.

New habitat created by sea defence works, such as those at Elmer (Moschella et al., in press) may facilitate further eastward range extensions along the English coast, although during a survey of artificial substrata in 2004 no *Chthamalus* were seen east of the Isle of Wight.

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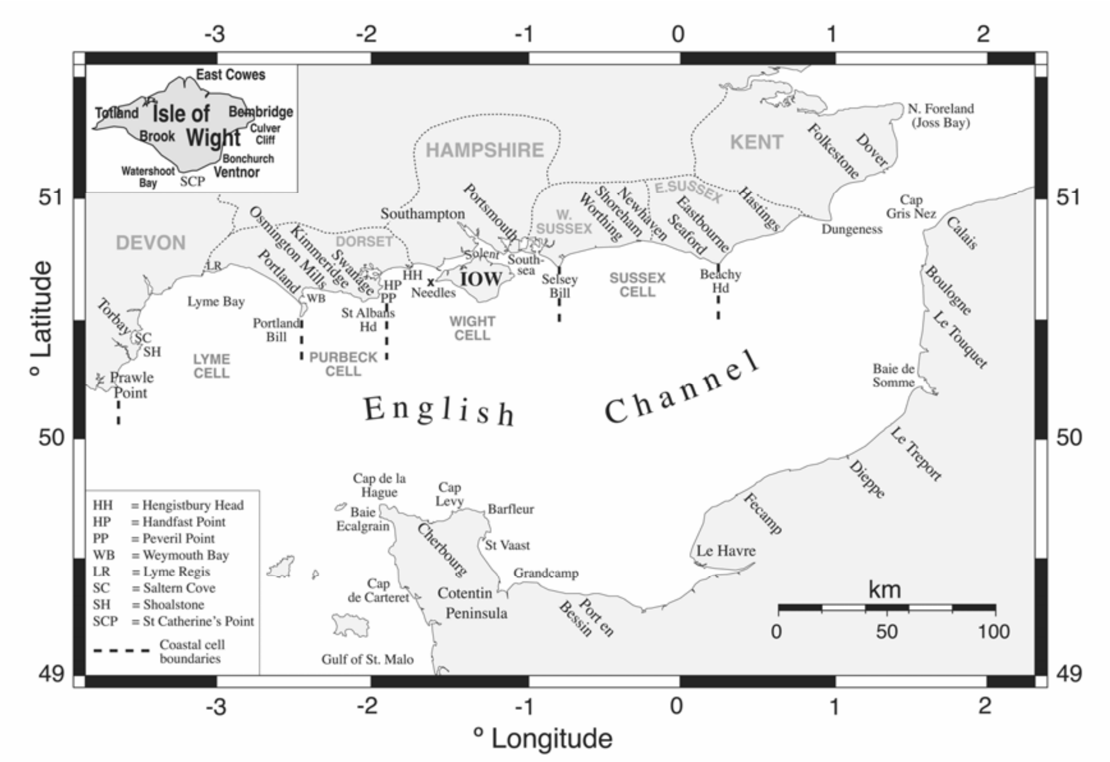

Fig 1. Central English Channel showing survey locations and boundaries of coastal process cells on the south coast of England that are referred to in the text.

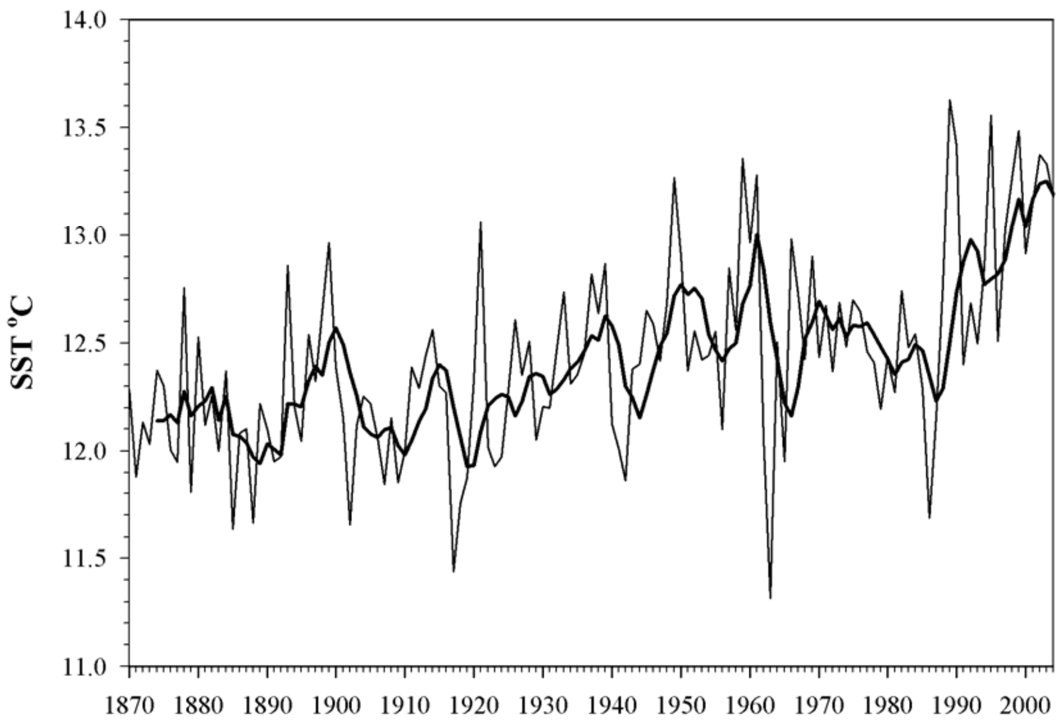

Fig 2. Sea surface temperature (SST) of central English Channel (50-51° N, 1-2° W) from 1870-2004, shown as annual mean (thin line) and smoothed 5 year mean (thick line). Data extracted from the HadlSST1 data set (Raynor *et al.*, 2003).

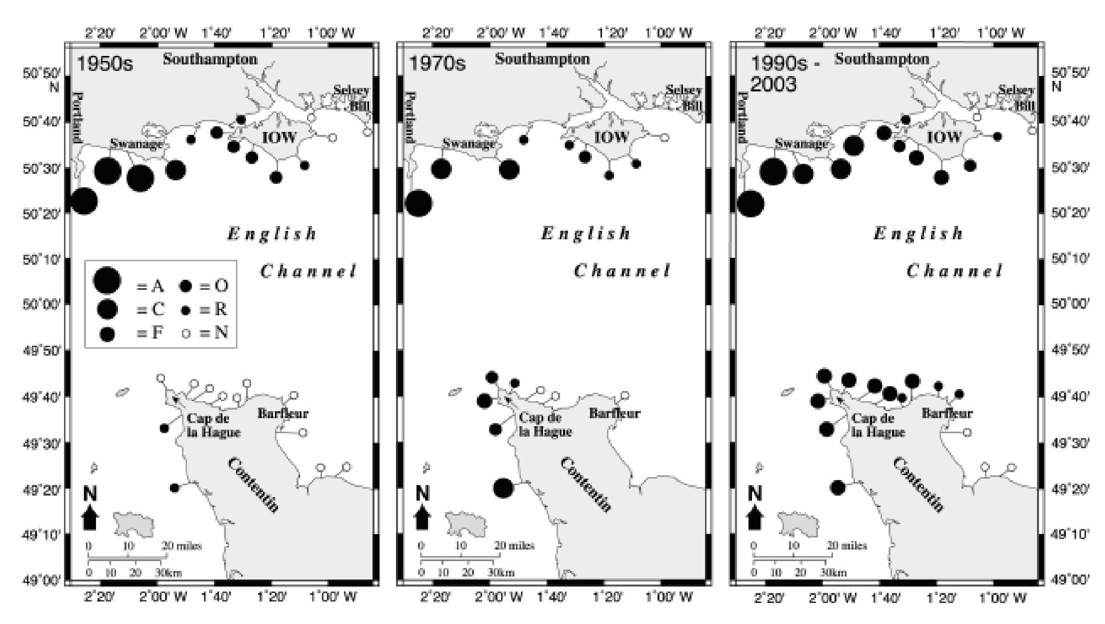

Fig 3. Mean Shore abundance of Total *Chthamalus* along the central English Channel. Data from 1950s from Crisp & Southward (1958) and 1970s from Crisp et al (1981) and AJS unpub. Prior to Southward (1976) all *Chthamalus* was recorded as *C.stellatus.*

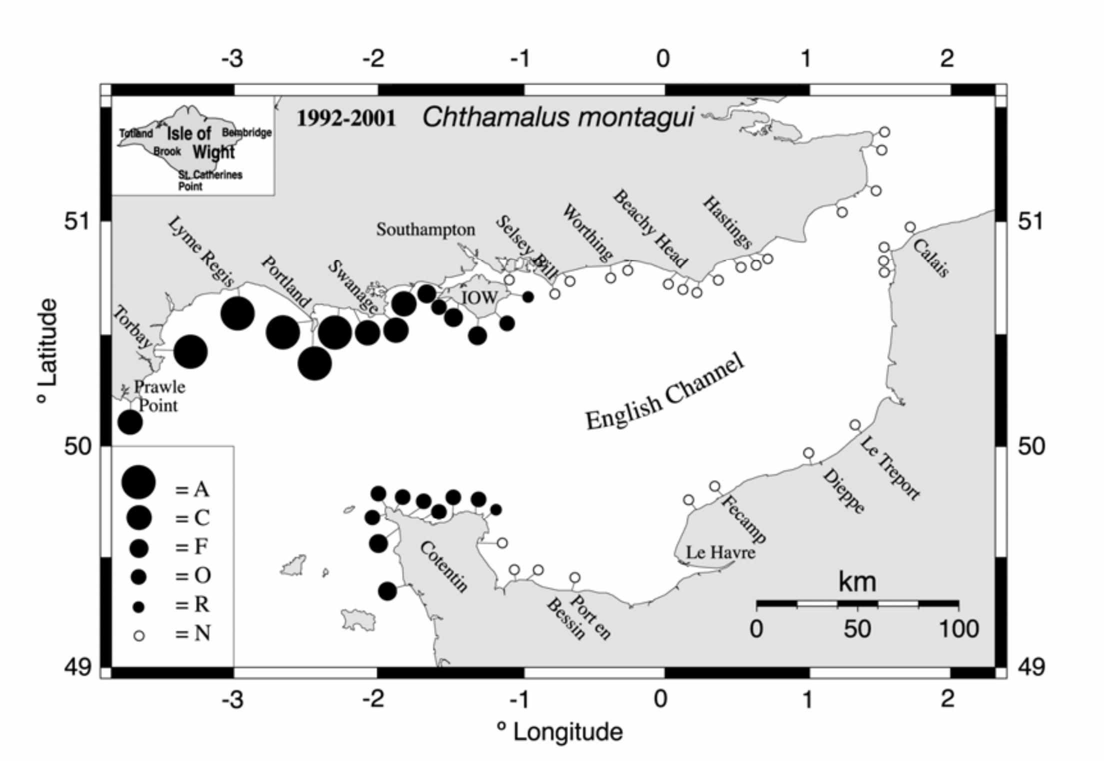

Fig 4. Distribution of *Chthamalus montagui* east to existing limits in the central English Channel. Symbols along south coast of England show the maximum mean-shore abundance observed during period 1994-1999. On the French coast, symbols show the mean-shore abundance recorded during surveys in 2000 and 2001.

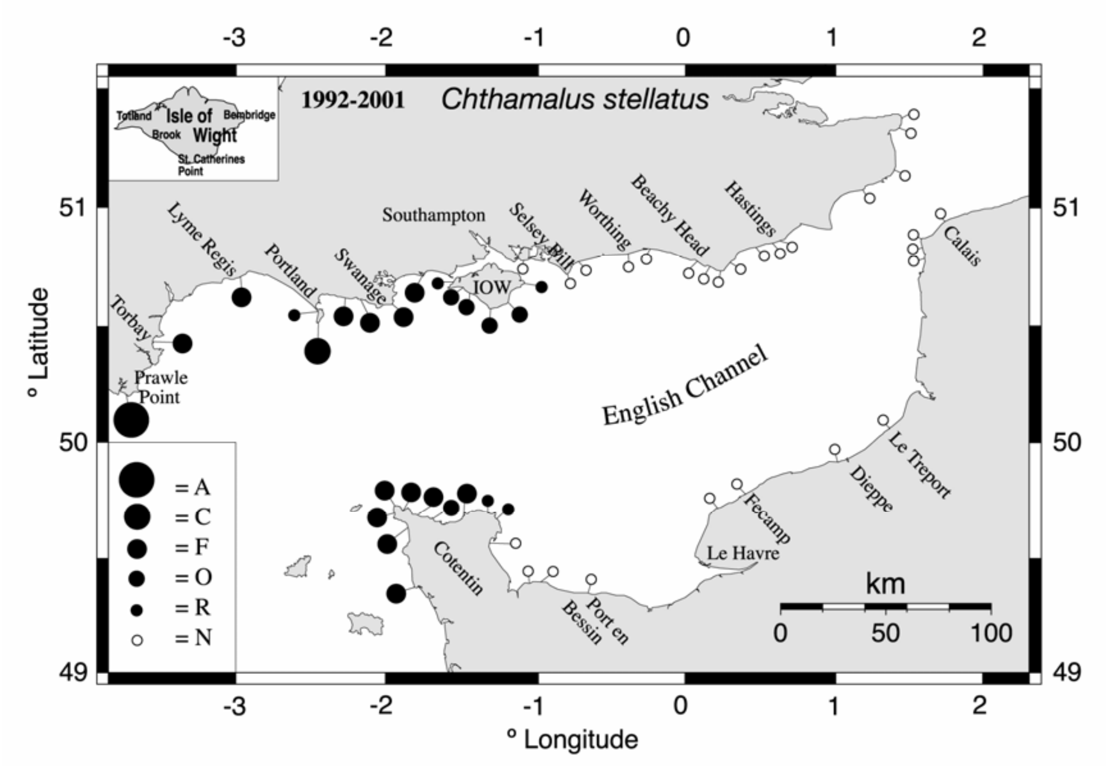

Fig 5. Distribution of *Chthamalus stellatus* east to existing limits in the central English Channel. Symbols along south coast of England show the maximum mean-shore abundance observed during period 1994-1999. On the French coast, symbols show the mean-shore abundance recorded during surveys in 2000 and 2001.

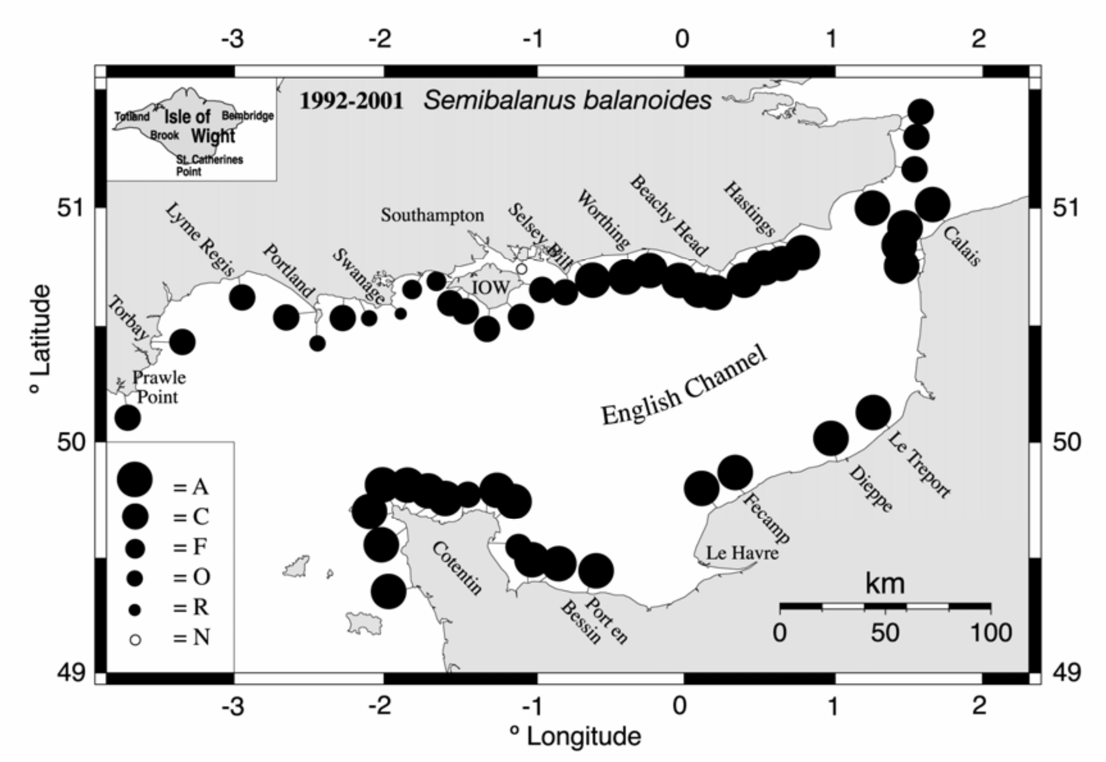

Fig 6. Distribution of *Semibalanus balanoides* in the central English Channel. Symbols along south coast of England show the maximum mean-shore abundance observed during period 1994-1999. On the French coast, symbols show the mean-shore abundance recorded during surveys in 2000 and 2001.

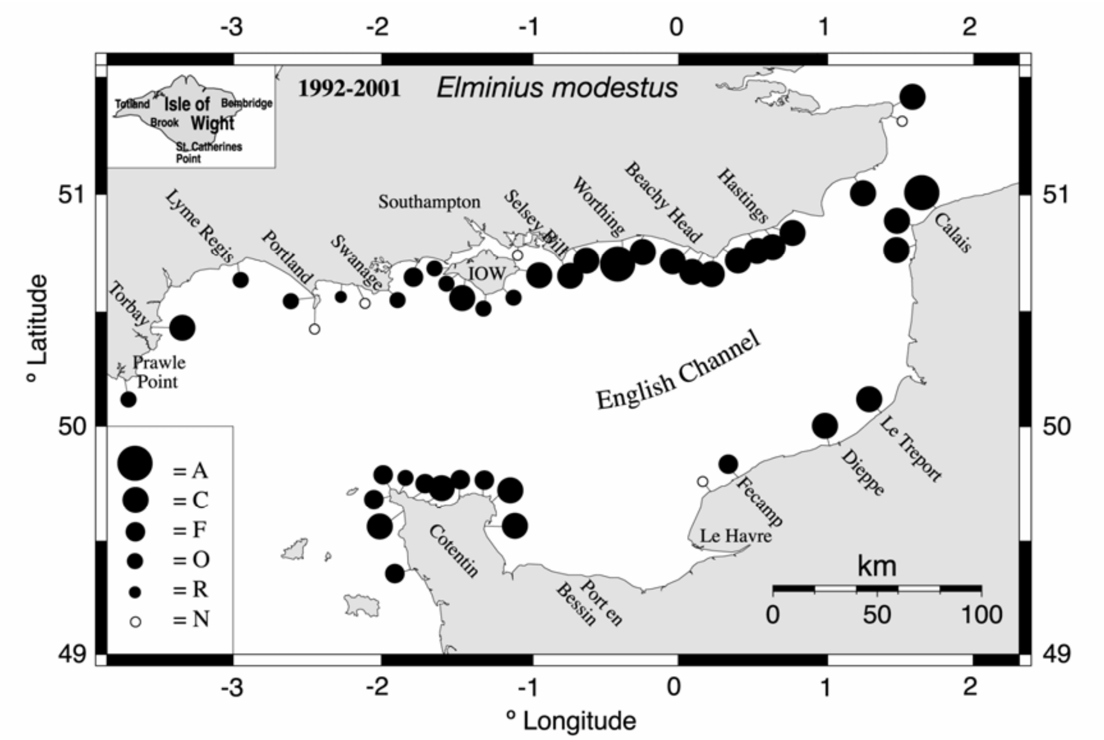

Fig 7. Distribution of *Elminius modestus* in the central English Channel. Symbols along south coast of England show the maximum mean-shore abundance observed during period 1994-1999. On the French coast, symbols show the mean-shore abundance recorded during surveys in 2000 and 2001.

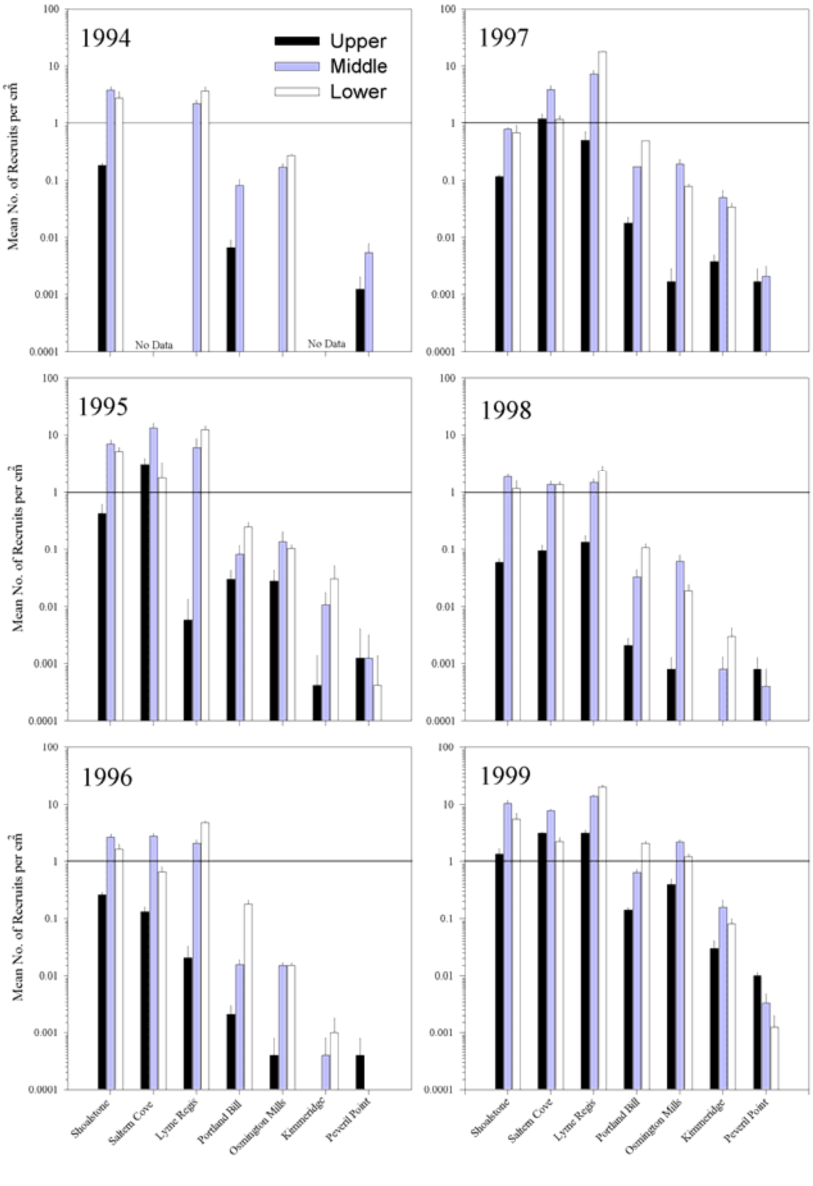

Fig 8. Mean *Chthamalus* recruitment at three tidal levels along the south coast of England from 1994 to 1999. Counts made in mid-autumn within cleared 400cm^2 quadrats (n = 6 at each level). Note Log scale. Error bars show +SE. Sites at Saltern Cove, Kimmeridge and lower shore of Portland Bill were not established until 1995.

Fig 9. Dendrogram following cluster analysis of Bray-Curtis Similarity Indices using square-root transformed mean shore recruitment of *Chthamalus montagui* at eight shores along the central south coast of England between 1995-1999.

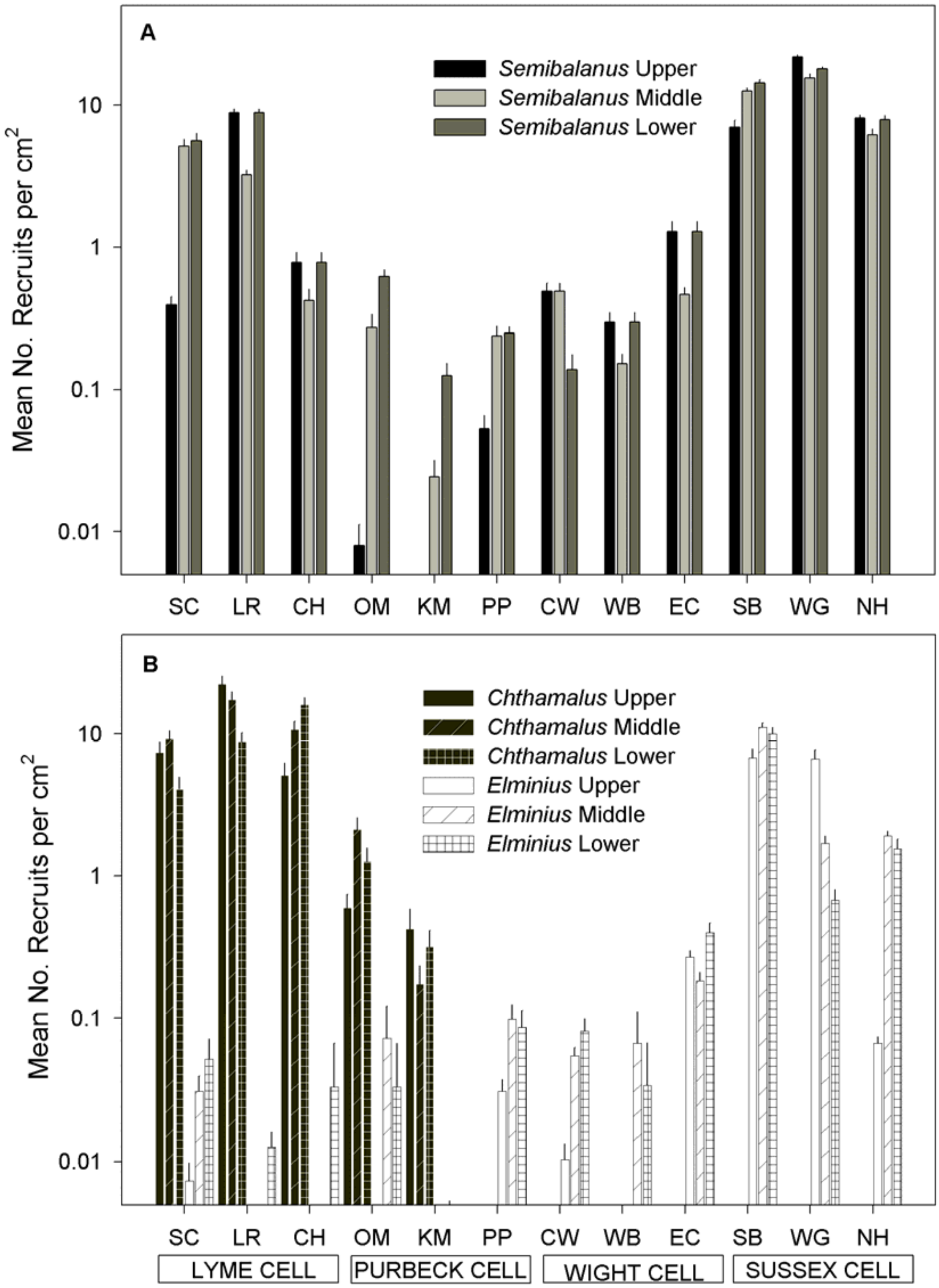

Fig 10. A: Mean recruitment of *Semibalanus balanoides* and **B**: *Chthamalus* and *E.modestus* at three tidal levels on shores along the central south coast of England in 1999. Note Log Scale. Most western site is Saltern Cove on left side of graph. Each bar represents mean recruitment of each patch of three 100cm^2 quadrats (n =10). Error bars show + SE. Key: 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).

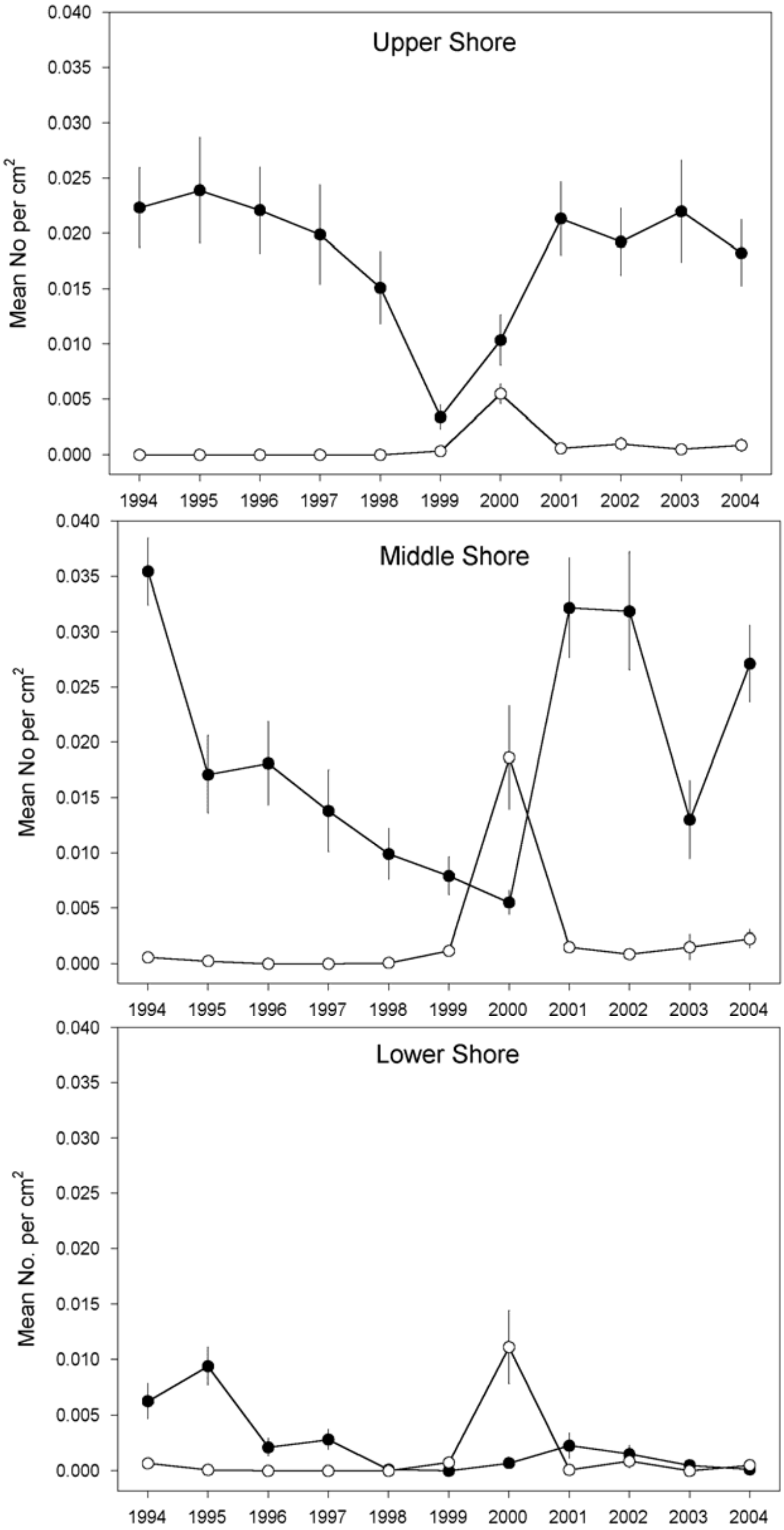

Fig 11. Mean Annual recruitment and adult census of *C.montagui* at Hanover Point, Isle of Wight 1994-2004. Error bars show +SE.

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

Abundant:	More than 1 per cm^2; rocks well covered
Common:	0.1 to 1.0 per cm^2; up to one third of rock space covered
Frequent:	0.01 to 0.1 per cm^2; individuals never more than 10 cm apart.
Occasional:	0.0001 to 0.01 per cm^2; few within 10 cm of each other.
Rare:	Less than 1 per m^2; only a few found in 30 minutes searching.
None:	None found.

Table 2. Three-way ANOVA of annual mean *Chthamalus* recruitment density (No. per cm^2) within cleared patches at shores West and East of Portland Bill (known as West and East coastal cells). Data are untransformed. *P* values: * denotes p< 0.05,** denotes p < 0.01,*** denotes p<0.001

YEAR		1995			1996	
Source of variation	**df**	**MS**	***F***	**df**	**MS**	***F***
Cell = C	1	805.38	73.85***	1	74.38	25.06***
Shore = S (C)	4	10.91	5.48***	4	2.97	9.34***
Height =H	2	141.02	2.11	2	15.82	2.69
C X H	2	138.00	2.07	2	15.68	2.67
H X S (C)	8	66.81	33.6***	8	5.88	18.5***
Residual	90	1.99		90	0.32	

YEAR		1997			1998	
Source of variation	**df**	**MS**	***F***	**df**	**MS**	***F***
Cell = C	1	369.05	2.22	1	32.06	86.22***
Shore = S (C)	4	166.00	169.35***	4	0.37	1.32
Height =H	2	83.04	1.04	2	6.92	12.86
C X H	2	80.85	1.02	2	6.68	12.41**
H X S (C)	8	79.61	81.22***	8	0.54	1.91**
Residual	90	0.98		90	0.28	

YEAR		1999	
Source of variation	**df**	**MS**	***F***
Cell = C	1	1530.6	11.12*
Shore = S (C)	4	137.6	13.35***
Height =H	2	134.89	1.33
C X H	2	97.20	0.96
H X S (C)	8	101.1	9.81***
Residual	90	10.31	

SNK tests. '=' denotes no significant differences. * denotes p< 0.05,** denotes p < 0.01.

YEAR	**1995**	**1996**	**1997**	**1998**	**1999**
Cells	W>E	W>E	W = E	W>E	W>E
Means	5.5>0.035**	1.66>0.004**	3.74=0.04	1.01>0.01**	7.98>0.45*

Table 3. Rank order recruitment of *Chthamalus* at sites along a 100km section of the south coast of England between 1995-1999. Sites listed from west to east. Rank 1 is highest recruitment. SST is the maximum monthly mean recorded between July-September for central English Channel (50-51^{o}N, 1-2^{o}W) from HadISST1 data set (Raynor et al, 2003). Results of Friedman test applied with H_o 'Years have same median recruitment'χ^2 =22.8, n= 8, df 4, p <0.001***. Reject H_o and accept H_1 that years differ.

	1995	**1996**	**1997**	**1998**	**1999**
Shoalstone (Devon)	4	3	1	2	5
Saltern Cove (Devon)	5	2	3	1	4
Lyme Regis (Dorset)	3	2	4	1	5
Portland Bill (Dorset)	3	2	4	1	5
Osmington (Dorset)	3	1	4	2	5
Kimmeridge (Dorset)	3	1	4	2	5
Peveril Point (Dorset)	3	1	4	2	5
Hanover Point (Isle of Wight)	4	1.5	1.5	3	5
Median Rank	**3**	**1.75**	**4**	**2**	**5**
Max Mean SST ^{o}C (July-Sept)	**17.92**	**16.70**	**17.42**	**17.30**	**17.97**
Rank SST	**4**	**1**	**3**	**2**	**5**

Table 4. Model of *Chthamalus* recruitment within Cells and sub-cells along the central south coast of England for 1995. Intertidal Rock Area (column b) determined using GIS (MapInfo v5). Barnacle Zone Area (column c) is considered to be two-thirds of intertidal rock area. Columns d, e and f, are mean adult densities within equal divisions of Barnacle Zone. Column g is estimate of total number of barnacles in each cell and sub-cell. Mean No. of broods per year (column g) and No. of eggs per brood (column i) is taken from Burrows et al (1992). Column j is an estimate of larval release per cell and sub-cell. Mean recruitment densities are from counts obtained in the autumn. Column 'o' shows recruitment as a % of total larval output.

			Mean Adult Density per cm^2							Recruitment on shore No. per cm^2				
a	**b**	**c**	**d**	**e**	**f**	**g**	**h**	**i**	**j**	**k**	**l**	**m**	**n**	**o**
Coastal Cell	**Intertidal Area Km^2**	**Barnacle Zone Area cm^2**	**Upper Zone**	**Middle Zone**	**Lower Zone**	**Total No. in Cell**	**No. of broods per year**	**Eggs per brood**	**Total No. of larvae per Cell**	**Upper Zone**	**Middle Zone**	**Lower Zone**	**Recruits per Cell**	**% Recruitment**
Lyme	2.53	6.33×10^{9}	2.20	5.4	2.7	6.5×10^{10}	2.6	1000	1.7×10^{14}	1.2	8.8	6.5	1.0×10^{11}	6×10^{-2}
Purbeck a	0.18	4.61×10^{8}	0.80	3.0	3.4	3.3×10^{9}	2.6	1000	8.5×10^{12}	0.03	0.1	0.2	1.4×10^{8}	$2 \times 10\text{-}^{3}$
Purbeck b	0.34	8.41×10^{8}	0.07	0.4	0.7	9.3×10^{8}	2.6	1000	2.4×10^{12}	0.0004	0.01	0.03	3.5×10^{7}	1×10^{-3}
Purbeck c	0.03	7.76×10^{7}	0.13	0.0	0.0	1.4×10^{7}	2.6	1000	3.6×10^{10}	0.001	0.001	0.0004	2.3×10^{5}	6×10^{-4}
Wight	1.10	2.75×10^{9}	0.02	0.0	0.0	1.1×10^{8}	2.6	1000	2.8×10^{11}	0.0	0.0003	0.0001	9.2×10^{5}	3×10^{-4}
Sussex	2.70	6.75×10^{9}	0.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Purbeck sub-cells

Purbeck a = Portland Bill to White Nothe; Purbeck b = White Nothe to St Albans Head; Purbeck c = St Albans Head to Handfast Point

Table 5. Annual Recruitment of *Chthamalus montagui* in coastal cells and sub-cells expressed as % of estimated larval output (column 'o' Table 5) 1995-1999.

Cell	**1995**	**1996**	**1997**	**1998**	**1999**	**1999 on vertical surfaces**
Lyme	8×10^{-2}	2×10^{-2}	5×10^{-2}	2×10^{-2}	1×10^{-1}	1×10^{-1}
Purbeck a	2×10^{-3}	8×10^{-4}	3×10^{-3}	8×10^{-4}	2×10^{-2}	4×10^{-2}
Purbeck b	2×10^{-3}	1×10^{-4}	4×10^{-3}	3×10^{-4}	1×10^{-2}	1×10^{-2}
Purbeck c	8×10^{-4}	2×10^{-4}	2×10^{-3}	9×10^{-4}	5×10^{-3}	1×10^{-2}
Wight	4×10^{-4}	0	0	2×10^{-4}	6×10^{-3}	3×10^{-3}

Table 6. Simulation model of *Semibalanus balanoides* recruitment within coastal cells and sub-cells along the central south coast of England in 1999. Intertidal Rock Area (column b) determined using GIS (MapInfo v5). Barnacle Zone Area (column c) is considered to be two-thirds of intertidal rock area. Columns d, e and f, are mean adult densities within equal divisions of Barnacle Zone. Column g is estimate of total number of barnacles in each cell and sub-cell. Mean No. of broods per year (column g) and No. of eggs per brood (column i) is mean brood size for animal from southern England of 1.5mg dry body weight Barnes & Barnes (1968). Column j is an estimate of larval release per cell and sub-cell. Mean recruitment densities are from counts obtained in the spring. Column 'o' shows recruitment as a % of total larval output.

			Mean Adult Density per cm^2							Recruitment on shore No. per cm^2				
a	**b**	**c**	**d**	**e**	**f**	**g**	**h**	**i**	**j**	**k**	**l**	**m**	**n**	**o**
Coastal Cell	**Intertidal Area Km^2**	**Barnacle Zone Area cm^2**	**Upper Zone**	**Middle Zone**	**Lower Zone**	**Total No. in Cell**	**No. of broods per year**	**Eggs per brood**	**Total No. of larvae per Cell**	**Upper Zone**	**Middle Zone**	**Lower Zone**	**Recruits per Cell**	**% Recruitment**
Lyme	2.53	6.33×10^9	0.01	0.8	3.1	2×10^{10}	1	2000	4×10^{13}	3.35	2.92	5.10	6×10^{10}	1×10^{-1}
Purbeck a	0.18	4.61×10^8	0.00	0.3	0.3	3×10^8	1	2000	5×10^{11}	0.01	0.27	0.62	4×10^8	7×10^{-2}
Purbeck b	0.34	8.41×10^8	0.00	0.1	0.6	5×10^8	1	2000	1×10^{12}	0.003	0.02	0.13	1×10^8	1×10^{-2}
Purbeck c	0.03	7.76×10^7	0.10	0.4	0.7	8×10^7	1	2000	2×10^{11}	0.053	0.24	0.25	4×10^7	2×10^{-2}
Wight	1.10	2.75×10^9	0.35	0.5	0.4	3×10^9	1	2000	6×10^{12}	1	0.37	0.57	5×10^9	7×10^{-2}
Sussex	2.70	6.75×10^9	2.93	1.7	2.7	4×10^{10}	1	2000	9×10^{13}	12	11.46	13.43	2×10^{11}	2×10^{-1}

Purbeck sub-cells

Purbeck a = Portland Bill to White Nothe; Purbeck b = White Nothe to St Albans Head; Purbeck c = St Albans Head to Handfast Point

SUGGESTED KEY WORDS

KEY WORDS: Barnacles, Recruitment, Coastal Cells, Climate Change, Range extension, Rocky Shores, Biogeography.