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Spatial and temporal variation in settlement and recruitment of the intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale

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Abstract

Variation in the level of settlement and recruitment in the intertidal barnacle *Semibalanus balanoides* was studied using a hierarchical sampling programme. The effect of three spatial scales, 10s of metres (sites), 1000s of metres (shores) and 100s of kilometres (locations), was determined. The largest spatial scale represented the distance between four widely separated locations, Sweden, the Isle of Man, SW Ireland and SW England, covering a large part of the range of *S. balanoides* in Europe. Temporal variation was determined by comparison between two years, 1997 and 1998. The settlement period of *S. balanoides* varied in length and timing, being earlier and shorter at the most northerly location, Sweden. The duration of settlement showed little difference among shores within locations, but the pattern of settlement did vary. Estimates of total settlement throughout the settlement period and of recruitment at the end of this period both showed substantial variation among locations which was dependent on the year of study. There was little consistency in the ranking of locations between the two years. Recruitment showed significant variation at the lower spatial scales of shore and site. In addition, examination of variance components showed a high degree of variation between replicates within sites in 1997. There was a significant relationship between settlement and recruitment at three of the four locations. Across all locations variation in settlement explained between 29 and 99% of variation

in recruitment. However, locations showed distinct differences in the level of post-settlement survival.   © 2000 Elsevier Science B.V. All rights reserved.

1. Introduction

The majority of benthic invertebrates exhibit a complex life cycle that includes separate planktonic and bottom dwelling phases, linked by a settlement event (Thorson, 1950). Variation in the level of settlement and recruitment has been documented for a wide range of benthic species (e.g., Hawkins and Hartnoll, 1982; Kendall et al., 1982, 1985; Caffey, 1985; Davis, 1988; Hughes, 1990; Katz et al., 1994; Pineda, 1994; Hunt and Scheibling, 1996), but few studies have been undertaken in a framework that allows a quantitative understanding of the temporal or spatial scales at which variation occurs. One way of achieving this is to adopt a hierarchical sampling programme to measure variation at different spatial and temporal scales using nested ANOVA (Underwood, 1981). Analysis of spatial and temporal patterns in nature is essential to gain an understanding of the scales at which important ecological processes are acting (Levin, 1992).

The settlement rate, defined as the rate at which planktonic larvae of benthic organisms establish permanent contact with the substrate, depends on a number of different processes which operate over different spatial and temporal scales. The size of the larval pool obviously determines the number of larvae potentially available to settle. Factors operating over large scales such as those controlling the timing and intensity of phytoplankton blooms are likely to determine the number of available larvae through their influence on larval food supply (Barnes, 1956). Additionally, large scale variation in levels of reproduction in adult populations can influence larval abundance (Wellington and Victor, 1988). Settlement from this larval pool will be influenced by various factors. At the largest scale, physical transport processes, ranging from upwelling systems (Roughgarden et al., 1988) to local wind patterns (Bennell, 1981; Hawkins and Hartnoll, 1982; Bertness et al., 1996; Shanks, 1998) and flushing rates of bays (Gaines and Bertness, 1992) determine the rate of arrival of larvae in a particular area. At a smaller scale, local hydrodynamics (Gaines et al., 1985; Minchinton and Scheibling, 1991), larval behaviour (e.g., Knight Jones, 1953; Crisp, 1955; Pineda, 1994) and substratum characteristics (e.g., Crisp and Barnes, 1954; Strathmann et al., 1981; Thompson et al., 1998) are important. An understanding of the scales at which variation in settlement occurs will allow identification of those processes most important in determining the settlement rate at any particular site.

Studies examining recruitment of benthic organisms have frequently failed to distinguish between settlement and recruitment. Keough and Downes (1982) consider a larva to have settled at the moment it irreversibly attaches to the substratum, whilst a settler is considered to be a recruit once it has survived the period up to observation. On

this basis the true settlement rate is difficult, if not impossible, to measure in the field since it assumes no post-settlement mortality. However, if sampling is frequent enough such that post-settlement mortality is negligible, then a good estimate of settlement may be made (Minchinton and Scheibling, 1993). Connell (1985) considered daily census sufficient to give a good estimate of settlement rate in barnacles. The time taken from settlement to metamorphosis in *S. balanoides* is relatively short. Connell's (1961) estimate of an average time to metamorphose of 1.5 days is supported by observations on the Isle of Man (Hawkins, Jenkins, independent unpublished observations). Because of the short period to metamorphosis we consider the number of attached unmetamorph-osed cyprids constitutes a good estimate of settlement. The accumulated number of metamorphosed individuals at the end of the settlement season was used as a measure of recruitment. This represents the maximum size of the cohort available to proceed to subsequent age groups and hence subsequent entry to the adult population.

The overall aim of this work was to investigate the spatial and temporal variation in the levels of settlement and recruitment of the intertidal barnacle *Semibalanus balanoides*. We examined this variation at three spatial scales, 10s of metres (sites), 1000s of metres (shores) and 100s of kilometres (locations), and one temporal scale (years). The general hypothesis to be tested was that there is variation at each of the specified scales. Barnacles are frequently used as model organisms to examine supply and recruitment variation in benthic organisms, owing to their abundance and the ease of identification and census of both planktonic larvae and newly settled individuals. *S. balanoides* is an extremely abundant intertidal barnacle with a wide distribution. It is a boreo-arctic species found on both sides of the north Atlantic. In Europe it extends over a large latitudinal range, from NW Spain (Barnes, 1958) to Spitzbergen (Barnes, 1957). The four locations used, SW England, SW Ireland, the Isle of Man and the west coast of Sweden, cover a large part of the latitudinal range of this species in Europe and a variety of environmental conditions. In particular, the macrotidal shores of the British Isles and Ireland contrast with the microtidal environment of the Swedish west coast.

2. Methods

The intensity and duration of settlement and the level of recruitment of the intertidal barnacle *Semibalanus balanoides* were assessed during 1997 and 1998 at four locations within northern Europe: the west coast of Sweden, the Isle of Man, the south west coast of Ireland and the south west coast of England (Fig. 1). At each location three shores were studied. These were as follows: Sweden (1) Svartskär, (2) Ramsö, (3) Krugglö; the Isle of Man (1) Port St. Mary, (2) Derbyhaven, (3) Niarbyl; SW Ireland (1) Crosshaven, (2) Castlepark, (3) Castlefreke; SW England (1) Wembury, (2) Heybrook, (3) Prawle.

2.1. Sampling design

Spatial (three scales) and temporal (one scale) variation in settlement and recruitment of *S. balanoides* were assessed by using a nested sampling design within each of the years 1997 and 1998. At each of the four locations a number of accessible exposed
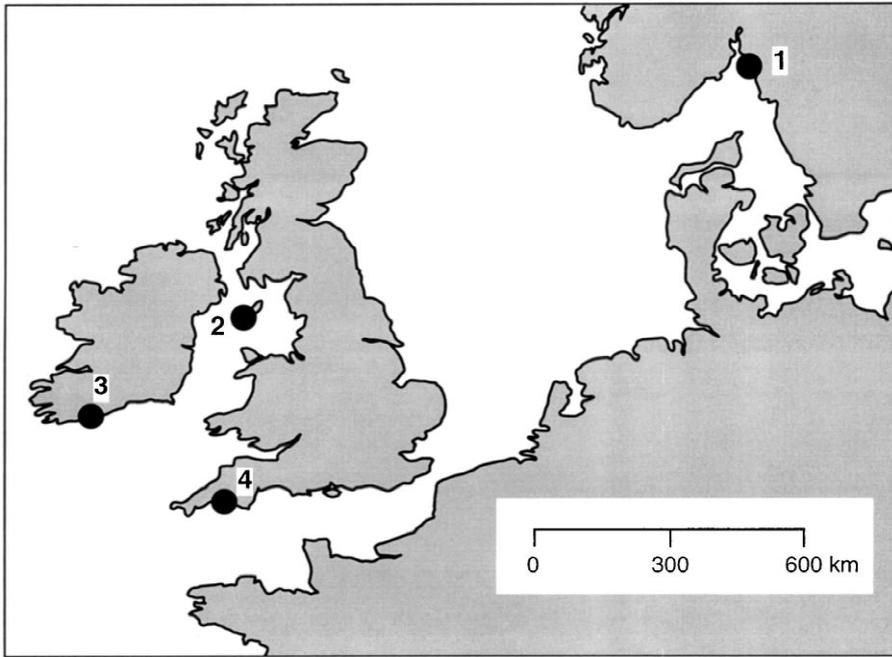
Fig. 1. Map of northern Europe showing the positions of the four sampling locations: (1) Sweden, (2) Isle of Man, (3) SW Ireland, (4) SW England.

shores were selected and three chosen at random between 3 and 50 km apart. At each shore, three sites at mid tide level were chosen between 5 and 30 m apart. All sites were in well drained, barnacle dominated areas with an abundance of *S. balanoides* and with between 20 and 50% bare space available for settlement. Steep slopes ($>45°$), shaded rocks and algal dominated areas were avoided. Sites were selected at random within the specified criteria. Sampling was undertaken weekly throughout the settlement season of *S. balanoides*, from the time when settled cyprids were first observed until settlement had ceased.

At each site on each sampling date five 5×5 cm quadrats were positioned at random within an area of 4 m^2. Quadrats placed on substrata unsuitable for barnacle settlement (e.g., algal turf) were relocated. The number of cyprids and the number of metamorphosed individuals in each quadrat was counted, and the percentage cover of bare space estimated using the intersection points of a 25-point grid. New sites were selected on each sampling date using the criteria described above. Variation in settlement and recruitment was therefore examined at three spatial scales, 100s of kilometres (location), kilometres (shore) and 10s of metres (site).

2.2. Analysis

Relative levels of total settlement during the settlement season of each year were

estimated by calculating the area under the curve of cyprid numbers (settlement) plotted against time. Since random quadrats and sites were used on each sampling date, 'total settlement' was calculated for each shore, thus preventing examination of spatial variation at scales below location. Recruitment was determined as the number of metamorphosed individuals present at the end of the settlement season. This single point estimate allows examination of the spatial variation at the three spatial scales specified.

Estimation of the percentage cover of bare space in each quadrat allowed determination of the level of settlement per unit area of bare space. However, for the accumulated number of metamorphs (recruitment) the meaningful estimate of bare space is not that at the time of sampling, but that prior to the beginning of settlement. Since this was not estimated, recruitment was calculated as number of metamorphs per quadrat. This approach may be justified because of the criteria used in selecting sampling sites; all sites were chosen on the basis of a defined cover (20–50%) of bare space.

Data were analysed using analysis of variance (ANOVA). Both the factors location and year were considered fixed, whilst shore and site were random. Cochran's test (Winer, 1971) was used to test for heterogeneity of variance and, where necessary, data were transformed. In two analyses data were heterogeneous even after transformation. In these cases ANOVA was still applied since in large designs this technique is robust to departure from homogenous variances (Underwood, 1997). However, results from these analyses must be viewed with caution owing to the increased probability of type I error. Multiple comparisons of levels within significant factors were made using Student Newman Keuls (SNK) tests.

From the mean square estimates, ANOVA allows a quantitative measure of the variation associated with each factor in the analysis. Components of variation were calculated for random factors only using the hierarchical model described by Winer (1971). The fixed factor location was not included in this analysis owing to the illogicality of comparisons between fixed and random variance components (Underwood, 1997). The percentage of variation for each level of the analysis was calculated as that component of variation divided by the sum of all components of variation multiplied by 100.

3. Results

3.1. Settlement periods

The settlement period ranged from 30 days (Sweden, 1997, 1998) up to 71 days (Isle of Man, 1997), and at all locations settlement occurred in the spring and early summer (Table 1, Fig. 2). In both years the settlement period in Sweden was the shortest and began relatively early. There was, however, no consistent latitudinal gradient in either the start of settlement or the length of the settlement period. It is interesting to note, however, that the early start and short duration of the settlement period in Sweden meant that in 1997 there was virtually no overlap in settlement period between the most

Table 1
Duration of the period of settlement of *Semibalanus balanoides* at four European locations in 1997 and 1998

Location	Year	Settlement period	Duration (days)
Sweden	1997	March 8–April 7	30
	1998	March 23–April 22	30
Isle of Man	1997	April 1–June 10	71
	1998	April 20–June 3	44
SW Ireland	1997	April 8–June 4	57
	1998	March 19–May 7	49
SW England	1997	April 5–May 27	52
	1998	March 29–May 7	39

northerly locality and the other three. There was no relationship between the duration of the settlement period and total settlement ($n = 8$, $r = 0.524$, $P > 0.05$).

3.2. Settlement and recruitment patterns

The pattern of cyprid settlement throughout the season displayed considerable variation both among locations, and often among shores at a single location (Fig. 2). For example, in SW Ireland in 1997 the settlement pattern at shore 1 differed markedly from the other two shores, with peak settlement occurring 2 weeks earlier. Despite such variation the general trend was unimodal, with highest rates of settlement occurring in the middle or early part of the season, and tailing off in the later stages. The plots of cumulative metamorphosed individuals (recruitment) (Fig. 3) tend to rise consistently through the season, as expected. In a number of instances numbers declined towards the end of the season when input of settlers was at a low level.

3.3. Variation in settlement and recruitment

Analysis of 'total settlement' throughout the settlement period revealed the same results whether considering settlement per square centimetre of bare space or per quadrat. Therefore, in order to facilitate comparison with recruitment results, level of settlement per quadrat was used. 'Total settlement' showed substantial variation among locations, with 12 times less settlement in Sweden compared to SW Ireland averaged over two years (Fig. 4). Variation among locations, however, was dependent on the year, indicated by the significant location×year interaction (Table 2). There was no consistent ranking of locations between the two settlement periods other than the low ranking of Sweden. Comparison between years within each location shows the enormous difference in settlement level which can occur. In SW England, for example, overall settlement, averaged over three shores, was nearly 40 times higher in 1997 than 1998.

Analysis of the level of recruitment allowed examination of variation at all three spatial scales — location, shore and site. Data for this analysis showed significant heterogeneity and thus results must be viewed with caution (see above). There was a
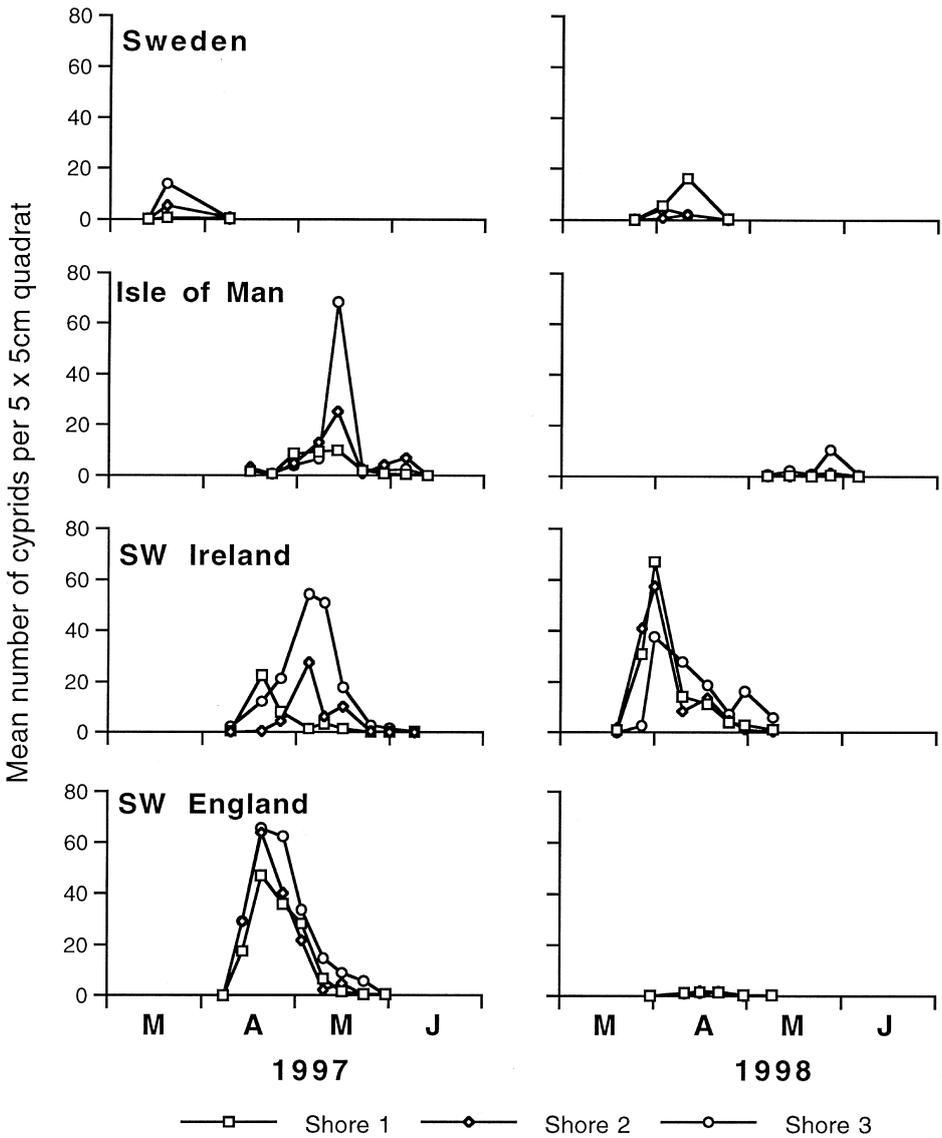
Fig. 2. Mean number of cyprids per quadrat on each weekly sampling occasion. Values are averaged for the three shores at each location. Shore names are as follows: Sweden (1) Svartskär, (2) Ramsö, (3) Krugglö; Isle of Man (1) Port St. Mary, (2) Derbyhaven, (3) Niarbyl; SW Ireland (1) Crosshaven, (2) Castlepark, (3) Castlefreke; SW England (1) Wembury, (2) Heybrook, (3) Prawle.

significant effect of the spatial scales, shore and site. For the largest scale location there was a significant interaction with year, indicating that the effect of this spatial scale varied between 1997 and 1998 (Table 3). SNK tests on the location with year interaction shows recruitment was highest in SW Ireland in both 1997 and 1998. However, the
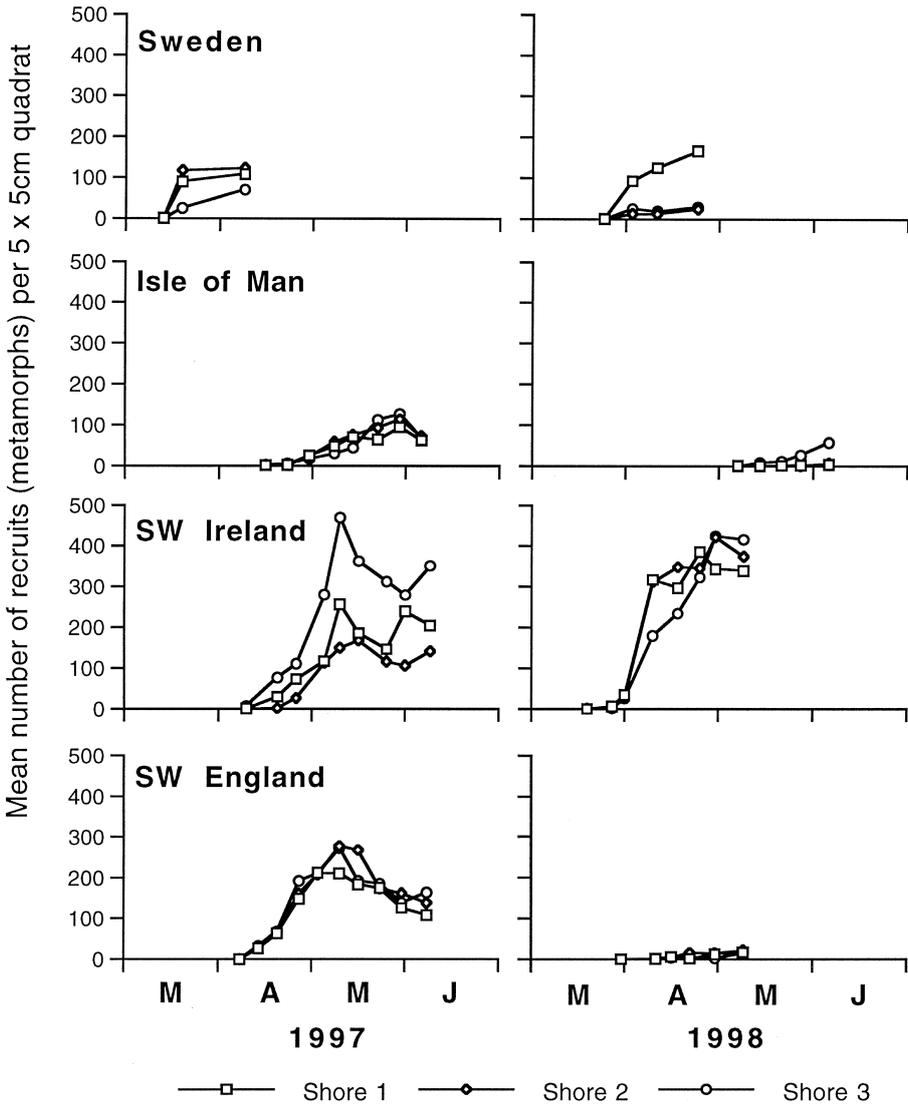
Fig. 3. Mean number of metamorphosed recruits per quadrat on each weekly sampling occasion. Values are averaged for the three shores at each location. For shore names, see Fig. 2.

effect of year within each location was inconsistent, with recruitment higher in 1998 in SW Ireland and in 1997 in SW England. These results contrast with those for total settlement, indicating that the relationship between settlement and recruitment varies at different locations and years. This is clearly demonstrated by comparing Sweden and SW England in 1997. Settlement in Sweden was 25-fold less than in SW England (SNK tests significant, Table 2), whilst recruitment was equal (SNK tests not significant, Table
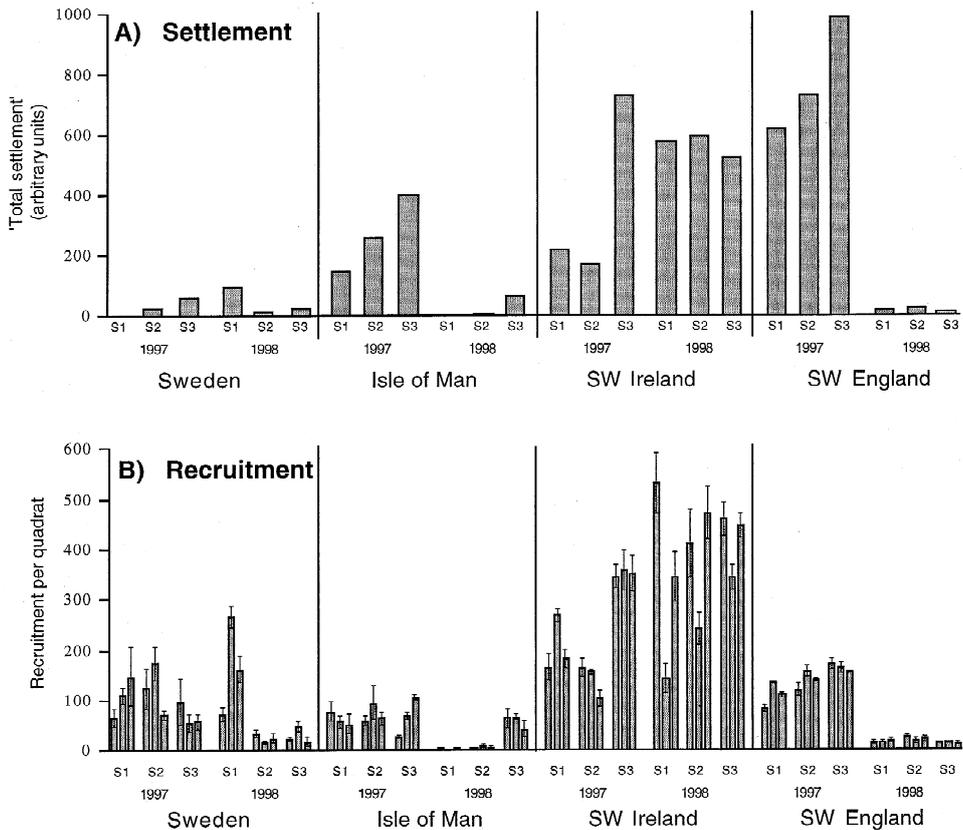
Fig. 4. Levels of settlement and recruitment of *Semibalanus balanoides* at four locations throughout Europe in 1997 and 1998. (A) Relative 'total settlement' per shore in arbitrary units, calculated as the area under the curve of weekly cyprid number against time. (B) Mean recruitment per site calculated as the number of metamorphosed individuals at the end of the settlement season. For shore names, see Fig. 2.

3). Clearly, the total input of settlers is not the only determinant of the number of individuals at the end of the settlement season.

There was a significant relationship between end of season recruitment per shore and 'total settlement' at all locations except Sweden (Fig. 5). The level of variability in recruitment which could be explained by the level of settlement was 60, 71 and 99% in the Isle of Man, SW Ireland and SW England, respectively. In Sweden, this value was only 29%. The relationship between settlement and recruitment differed substantially between SW Ireland and England. For a given level of settlement there was consistently higher end of season recruitment in SW Ireland than in SW England, indicating considerable differences in post-settlement survival (Fig. 5).

Analysis of recruitment levels separately in each year allows the partitioning of variance components associated with the spatial scales shore, site and replicate which in turn allows determination of the percentage contribution of each scale to overall

Table 2
ANOVA of 'total settlement' (area under curve of cyprid number per quadrat plotted against time). Transformation: ln(x). Cochran's test, $C = 0.3395$, $P > 0.05$

Source	df	MS	F	P
Location	3	8.44	11.61	<0.001
Year	1	11.19	15.38	<0.01
Location×Year	3	7.59	10.44	<0.001
Residual	16	0.73		
Total	23			

SNK test of Location×Year, SE=0.4924

Year	Location	Location	Year
1997	IOM=SW Ireland= SW England>Sweden	Sweden	1997=1998
1998	Ireland>IOM= Sweden=SW England	IOM SW Ireland SW England	1997>1998 1997=1998 1997>1998

variation. It should be noted that in 1997 data were significantly heterogeneous and thus results should be viewed with caution. In both years nested ANOVA revealed significant variability at all spatial scales (Table 4). There was no consistent pattern in the contribution of each scale to overall variation between the two years. Of note is the large

Table 3
ANOVA of recruitment (number of metamorphosed individuals at the end of the settlement season). Due to missing values all sites reduced randomly to four replicate quadrats. Transformation: None. Cochran's test, $C = 0.1104$, $P < 0.01$

Source	df	MS	F	P	F ratio versus
Location	3	1 092 749	26.76	<0.0005	Sh(Lo)
Shore (Location)	8	40 834	2.84	<0.02	Si(Sh(Lo)×Ye)
Year	1	8649	0.31	>0.55	Sh(Lo)×Ye
Location×Year	3	256 717	9.15	<0.01	Sh(Lo)×Ye
Shore (Location) ×Year	8	28 062	1.95	>0.05	Si(Sh(Lo)×Ye)
Site (Shore(Location) ×Year)	48	14 372	5.51	<0.0001	Res
Residual	216	2609			
Total	287				

SNK test of Location×Year, SE=27.92

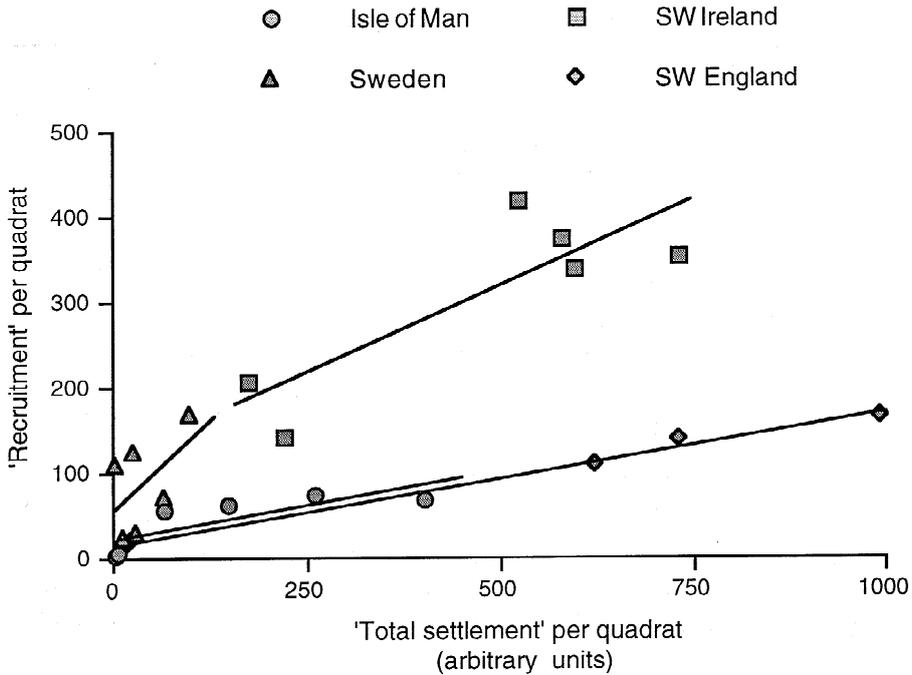| Year	Location	Location	Year
1997	Ireland>IOM= Sweden=SW England	Sweden	1997=1998
1998	Ireland>IOM= Sweden=SW England	IOM Ireland SW England	1997=1998 1997<1998 1997>1998

Fig. 5. Relationship between settlement (calculated as the area under the curve of weekly cyprid number against time and expressed in arbitrary units) and recruitment (calculated as the number of metamorphosed individuals at the end of the settlement season). Each point represents the mean value for a single shore.

variance component for the residual in 1997 (48%), indicating large variation among replicates within sites. However, in 1998 differences between replicates contributed least to overall variation. The percentage contribution of the largest scale, location, was not

Table 4
ANOVA of recruitment (number of metamorphosed individuals at the end of the settlement season) carried out separately in each year. Due to missing values all sites reduced randomly to four replicate quadrats. Transformation: square root. Variance components calculated only for random factors

	Source	df	MS	F	P	Variance component	% variance component
1997	Location	3	309.92	5.91	<0.02		
$C = 0.1955$	Shore (Location)	8	52.45	5.47	<0.001	3.57	38.2
$P < 0.01$	Site (Shore (Location))	24	9.58	2.13	<0.01	1.27	13.6
	Residual	108	4.51			4.51	48.2
	Total	143					
1998	Location	3	1942.21	23.23	<0.001		
$C = 0.1383$	Shore (Location)	8	83.61	3.78	<0.01	5.12	39.9
$P > 0.05$	Site (Shore (Location))	24	22.14	7.63	<0.0001	4.81	37.5
	Residual	108	2.90			2.90	22.6
	Total	143					

calculated owing to the problems of comparing fixed and random factors in this way. However, for both years there were clearly large effects. For example, 1998 was characterised by high settlement in SW Ireland, but virtual failure of settlement on the shores studied in SW England and on the east coast of the Isle of Man.

4. Discussion

This study examined the scales at which variation occurred in settlement and recruitment of *Semibalanus balanoides*, a dominant component of the intertidal zone throughout NW Europe. Such information does not determine the causes of patterns. However, with such information, experiments to test competing hypotheses regarding causal mechanisms can be designed at the appropriate scales (Underwood and Petraitis, 1993).

The method adopted to estimate levels of settlement and recruitment can have significant implications for the results and consequent conclusions of any study (e.g., Minchinton and Scheibling, 1993). We attempted to provide an estimate of total settlement input by making weekly counts of unmetamorphosed cyprids. In *S. balanoides* available evidence suggests that metamorphosis takes place on average 1.5 days after settlement (Connell, 1961, west Scotland; Jenkins, unpublished observations, Isle of Man). Hence, counts of settled cyprids give an estimate of settlement over the previous three high water periods. It should be noted that the level of settlement recorded will be an under-estimate owing to losses of cyprids between settlement and census. Owing to the difficulty in measuring true settlement in any benthic species (i.e. the number of larvae which irreversibly attach to the substratum) any comparison of settlement over large spatial scales will be potentially confounded by factors which affect the relationship between true and estimated settlement. However, observed differences in settlement input among locations were large and thus conclusions regarding large scale variability in settlement (see below) are dependable.

Recruitment was measured as the total accumulated number of recruits at the end of the discrete settlement season. It should be noted that, owing to the variation in length and timing of the settlement season among locations, recruits will vary slightly in age at the time of census at the different locations. However, at all locations, the number of recruits represents the end result of settlement and the total number of individuals upon which post-settlement processes can act to shape the adult population.

Sampling of settlement and recruitment in this study was undertaken on natural substrata. Obviously, over large spatial scales, substratum type will vary and indeed among locations there was a variety of rock types (Sweden, granite; Isle of Man, limestone, slate; Ireland, sandstone; SW England, sandstone). Caffey (1982) performed a large scale field experiment to determine whether large scale variation among shores in New South Wales, Australia, in the settlement and recruitment of the intertidal barnacle *Tesseropora rosea* could be explained by differences in rock type. Results indicated no effect of rock type on either settlement or survival. One option in studies of recruitment in benthic invertebrates is to use artificial settlement surfaces. However, these lack the specific settlement cues provided by a natural microalgal film (e.g., Strathmann et al.,

1981) and by conspecifics (e.g., Knight Jones, 1953). Observations suggest *S. balanoides* behaves differently toward artificial settlement surfaces in different locations (Jenkins, 1997). Given these arguments, the use of natural substrata dominated by an adult population of *S. balanoides* provides the most appropriate means of examining spatial variation in recruitment. However, it should be appreciated that differences in rock type among locations could be an additional source of variation.

The settlement rate of benthic organisms is dependent on the rate of arrival of larvae at the adult habitat combined with active selection of settlement sites by individual larvae. The level of recruitment depends not only on factors which influence settlement, but also on the level of post-settlement survival. A number of studies (e.g., Connell, 1985; Minchinton and Scheibling, 1991) have demonstrated a significant relationship between settlement input and recruitment. We found a clear relationship at three of the four locations, indicating that variation in recruitment may at least be explained partly by processes occurring prior to settlement. However, attention must also be given to processes affecting early post-settlement mortality. It should be noted that the problems associated with demonstrating a relationship between settlement and recruitment, present in the analysis of Connell (1985) and a number of later studies, and highlighted by McGuinness and Davis (1989), are not present in our study.

The level of recruitment of *S. balanoides* showed significant variation at all three spatial scales investigated, from 10s of metres to 100s of kilometres. A similar study carried out in Australia by Caffey (1985) into recruitment variation in the intertidal barnacle *Tesseropora rosea* revealed similar results; there was significant variation in the density of settlers and recruits among shores (11–555 km), sites (20–50 m) and within sites. Both Caffey's study and ours showed a high degree of variation at the largest scale.

Physical transport processes can generate variation in recruitment of benthic invertebrates over very large scales. For example, on the west coast of North America a latitudinal gradient in the degree of upwelling and a consequent gradient in the degree of offshore transport results in large scale differences in recruitment of intertidal barnacles (Roughgarden et al., 1987, 1988). Wind induced larval transport may cause large (100s kilometres) to medium scale (kilometres) variation in recruitment. Kendall et al. (1982, 1985) proposed that differences in recruitment between NW Scotland and NE England were a result of differences in the orientation of coastlines relative to the prevailing wind. As well as transport processes, factors which affect the size of the larval pool are likely to be important over large spatial scales. In 1998, variation among locations accounted for the majority of the total variation in recruitment. This was a direct result of an almost total failure in settlement in SW England. Such 'failure years' in the recruitment of barnacles have been recognised by a number of authors including Barnes (1956), Hawkins and Hartnoll (1982) and Kendall et al. (1985). Kendall et al. (1985) found adult abundance and fecundity varied little between 'success' and 'failure' years and thus attributed inter-annual variability to events occurring during the planktonic phase. Monitoring of barnacle larval populations by Barnes (1956) over a 10 year period provided evidence that 'failure years' coincided with failure or irregularities in development of the spring diatom bloom. Phytoplankton provides an important food source for developing larvae (Walker et al., 1987) and it seems likely that inter-annual

variability in the spring bloom regulates the size of the larval pool and so determines the availability of cyprids at the shore. Hawkins and Hartnoll (1982) also attributed a failure year to this cause.

It is interesting to compare the outcome of this study of recruitment variation in an open system with that in a closed system. In an open system there is a de-coupling of recruitment from local reproductive success; locally produced juveniles are transported elsewhere. In a closed system adults produce progeny that contribute to growth of the same local population. Åberg and Pavia (1997) investigated the variation in abundance of new recruits of the macroalga *Ascophyllum nodosum* over a range of spatial scales from 100s of kilometres to centimetres. Although algal propagules may be transported over large distances (e.g., Searles, 1980) the vast majority, especially those of perennial long lived species, are dispersed over short distances of the order of a few metres (Santelices, 1990). *Ascophyllum* populations may be considered closed systems relative to populations of barnacles where dispersal of larvae is very wide. Åberg and Pavia (1997) showed variation in recruit abundance at small but not large spatial scales, in contrast to our results. It is not clear whether such differences between open and closed systems are general. Variation in environmental conditions such as ice cover (e.g., Åberg, 1992; McCook and Chapman, 1997) operating over large temporal and spatial scales, can affect the reproductive output and hence local recruitment in closed systems. However, failure of recruitment in any particular year is probably less likely where progeny are produced locally and dispersal is over a short distance than where dispersal is wide and the chance of larvae encountering the adult habitat is subject to varying hydrographic conditions.

The temporal scale investigated — between-year variation — showed a significant interaction with location for both settlement and recruitment. There was no consistent ranking of locations for either settlement or recruitment between the two years investigated. For recruitment there was no consistency in the rankings of shore at any location between 1997 and 1998. A period of two years is too short to draw general conclusions about inter-annual variability, but the results clearly demonstrate a lack of consistency between years in the ranking of different spatial scales. In contrast, a number of previous studies have shown consistency among years in ranking sites by recruitment density (Kendall et al., 1985; Victor, 1986; Raimondi, 1990; Sutherland, 1990; Carroll, 1996). Such consistency may reflect the influence of different orientations of coastlines relative to prevailing winds and currents, although factors occurring post-settlement cannot be ruled out. At the level of location, lack of consistency of ranking may indicate variation in the degree to which larval development coincides with the spring phytoplankton bloom (see Barnes, 1956).

Although recruitment was a positive function of settlement input at three of the four locations, not all of the variation in recruitment could be explained by variation in settlement. The strength of the relationship between settlement and recruitment will depend upon the degree of variation in post-settlement mortality among replicate areas. Caffey (1985) showed variation in mortality of settlers on all spatial and temporal scales monitored, but found no obvious patterns. Analysis of the settler–recruit relationship in our study showed distinct differences in post-settlement mortality between two locations, SW England and SW Ireland. At equivalent levels of settlement, recruitment was far

lower in SW England, indicating higher levels of post-settlement mortality. Over large spatial scales there may be predictable and possibly consistent differences in the level of post-settlement mortality and hence in the settler–recruit relationship. Such differences may be caused by large scale differences in factors such as physical stress and predator density (see Gosselin and Qian, 1997, for a review of factors influencing early post-settlement mortality in benthic invertebrates).

Acknowledgements

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