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## Population resistance to climate change: modelling the effects of low recruitment in open populations

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**Abstract** Isolated populations or those at the edge of their distribution are usually more sensitive to changes in the environment, such as climate change. For the barnacle *Semibalanus balanoides* (L.), one possible effect of climate change is that unpredictable spring weather could lead to the mismatching of larval release with spring phytoplankton bloom, hence reducing the recruitment. In this paper, model simulations of a variable open population with space limited recruitment were used to investigate the effects of low and zero recruitment on population abundance in *S. balanoides*. Data for model parameters was taken from an isolated population in the Isle of Man, British Isles. Model simulations with observed frequencies of years with low recruitment showed only small changes in population dynamics. Increased frequencies of low recruitment had large effects on the variation in population growth rate and free space and on population structure. Furthermore, populations with intermediate to high frequencies of low recruitment appeared more sensitive to additional changes in recruitment. Exchanging low recruitment with zero recruitment severely increased the risk of local extinctions. Simulations with consecutive years of low recruitment showed a substantial increase in free space and an increase in the time taken to recover to normal densities. In conclusion, model simulations indicate that variable populations can be well buffered to changes in the demography caused by introduced environmental noise, but also, that intermediate to high frequencies of disturbance can lead to a swift change in population dynamics, which in turn, may affect the dynamics of whole communities.

**Keywords** Environmental variability · Temperature increase · Phytoplankton bloom · Free space · Community structure

### Introduction

Global changes in climate are occurring and will impinge on the distribution and abundance of species (Vitousek 1994; Hodkinson 1999; Reid et al. 2001; Tilman and Lehman 2001; Parmesan and Yohe 2003; Thomas et al. 2004; Clarke and Harris 2003, and many more). Although climate is changing globally, the effects are expected to be stronger at the edge of species' ranges and consequently, in a given area, some organisms will be more susceptible to these threats. For marine species, most studies concerning the effects of climate change have been done for species where there exist long time series of both demographic data and measurements of climate indices, such as the North Atlantic Oscillation (NAO) (Fromentin and Planque 1996; Dippner 1997; Belgrano et al. 1998; Kröncke et al. 1998; Tunberg and Nelson 1998; Reid et al. 2001; Edwards et al. 2002; Beaugrand et al. 2002; Lindley and Reid 2002; Beaugrand and Reid 2003). Many of these studies have revealed significant correlations between NAO and different population variables. While these results are restricted to a few species, they nevertheless indicate a direct link between regional climate change and changes in species abundance and variation.

In addition to general warming of air and sea temperatures, forecasts for the North East Atlantic suggest greater variability in climate, including higher frequency of extreme events (Weaver et al. 2001). Increased frequency of the positive index of the NAO is also likely and will lead to more unpredictable spring weather and hence timing and quality of the spring phytoplankton bloom (Southward 1991; Edwards et al. 2002). Boreal species will be particularly susceptible to such climate changes since these species often spawn or release larvae in single pulses, synchronized with spring or autumn phytoplankton blooms (Thorson 1950). Such effects will

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be compounded by warmer temperatures, which will lead to a reduced reproductive output and more frequent low recruitments for those species. Also, the predicted increase in frequency of extreme environmental events, especially hot summers, may have significant negative effects on post recruitment survival of boreal species (Thorson 1950; Southward 1991).

Populations of marine intertidal animals at the edge of their geographical range are typified by occasional recruitment events and population structures dominated by older individuals (Lewis et al. 1982; Kendall et al. 1982, 1985). For these populations the right environmental conditions are crucial to a successful completion of their life cycle (Barnes 1953, 1956, 1962, 1963; Crisp and Clegg 1960). This is particularly true for animals that reproduce during a single defined season where matching of larvae with planktonic food is critical to recruitment success (Cushing 1990; Barnes 1956, 1957b, 1962). Furthermore, these processes are likely to set the ultimate geographic limits of a species distribution, although this is partly governed by other near-shore processes, such as hydrographic barriers and availability of habitat (Crisp and Southward 1958).

*Semibalanus balanoides* (L.) is an excellent model organism to explore responses to climate at the edge of its range. It is a boreal cold temperate species ranging from the Arctic to the English Channel, reaching its absolute southern limit in northern Spain (see Barnes 1957a, 1958, for details on distribution). It has a requirement for temperatures below 12°C for successful gonad and brood development and breeding occurs during late autumn or winter (Crisp and Clegg 1960; Barnes 1963). The release of nauplii is induced by local environmental conditions (Barnes 1962; Barnes and Barnes 1965; King et al. 1993) but successful recruitment depends on matching larval release with the spring bloom (Crisp and Clegg 1960; Barnes 1957b, 1962, 1963; Hawkins and Hartnoll 1982; Connell 1961). The survival of cyprids and new recruits is also likely to be susceptible to warmer spring weather (Barnes 1956; Southward 1967, 1991). Furthermore, *S. balanoides* has been extensively studied with regards to its general biology, population dynamics and role in intertidal communities where it is the major space occupier on many

exposed shores (e.g. Hawkins 1983; Hartnoll and Hawkins 1985; Jenkins et al. 2000).

Southward (1991) showed that the abundance of *S. balanoides* within its southern range is strongly negatively correlated with sea surface temperature (SST), which through a 2-year lag may explain over 40% of the variance in abundance. Furthermore, it was shown that a part of the variance is explained by settlement and recruitment. This infers, as suggested earlier, that settlement and hence recruitment is climate dependent and that future changes in climate (i.e. increase in SST) are likely to have strong effects on the regeneration of *S. balanoides* at their range end. Given that recent global circulation models (GCMs) suggests that much of the warming due to current greenhouse gas emission is still to be realized (Wetherald et al. 2001), it is likely that many southern *Semibalanus* populations will experience a future scenario of continuously low recruitment, eventually contracting the southern margin of the species range. Climate change has been shown to have such an effect on Atlantic copepod (Beaugrand et al. 2002). However, gradual changes in population variables and their variance are generally hard to detect and track, especially in highly variable populations (Lundberg et al. 2000; Kaitala and Ranta 2001), mainly as a result of existing environmental stochasticity blurring the effects. Still, environmental variability may have a strong influence on population viability via recruitment (Ripa and Lundberg 2000) and it would be interesting to find out at what frequency of occurrence a lowered recruitment would be visible in the population dynamics. Also, most studies concerning the effects of climate change have been made on expanding terrestrial populations (see Parmesan and Yohe 2003 for some good examples) and it is therefore important to perform similar studies on marine populations. Inferences could then be made on future climate induced changes in marine community dynamics.

Matrix based models enable the linking of mechanisms acting at the individual level through to population level processes (see Tuljapurkar and Caswell 1997; Caswell 2000 for a general review). Structured matrix models have therefore previously proven to be useful for investigating the demography of many marine plants and animals (e.g.

**Table 1** Subjective assessment of the timing and strength of *S. balanoides* recruitment in the south of the Isle of Man during the periods 1977–1981, 1992–1994 and 1996–1998. (S.R. Jenkins, S.J. Hawkins, personal observations), followed by the measured mean SST(°C) in the region at that particular time. Average recruitment refers to the number of recruits of *S. balanoides* at mid shore level at the end of the settlement season

Year	Start of settlement	Relative strength	Average recruitment (No. recruits per cm <sup>2</sup> )	Mean temperature (°C)
1977	June	Poor	0.8	10.7
1978	April	Good	2.6	7.4
1979	March	Good	2	5.5
1980	April	Good	3	8.3
1981	March	Very good	5	7.4
1992	April	Good	≈2.5	8.5
1993	April	Good	≈2.5	8.2
1994	May	Poor	≈1	8.9
1996	April	Very good	4.3	8.2
1997	April	Good	2.7	8.9
1998	May	Very poor	0.2	11.7

Åberg 1992; Nakaoka 1996; Hyder et al. 2001; Muko et al. 2001; Svensson et al. 2004). Svensson et al. (2004) used demographic data of the barnacle *S. balanoides* from three spatially separated locations across Europe (The Isle of Man, South West Ireland and West Sweden, Jenkins et al. 2000), to build a structured matrix model of open populations with space-limited recruitment in stochastic environments. Through repeated model runs over time, the spatial variation in population dynamics (i.e. growth rate, population size, structure and free space) of this species was investigated for each location. Although not included in these model runs, it is known that barnacle populations, especially those at the edge of their range or those situated on isolated islands in a dispersive environment can experience occasional years of low recruitment. Observations in the Isle of Man and South West England suggest that extremely low levels of recruitment can occur quite frequently (Southward 1967, 1991; Jenkins et al. 2000, Table 1) and although too few data points exist for recruitment to examine a potential correlation between recruitment and SST, low recruitment appears to be associated with high temperatures (Table 1). Given the frequency of low recruitment events today and the potential for SST to increase in the future, we believe that the incorporation of low recruitment into population models is necessary to fully understand the density dynamics of this species.

This study aimed to test the effects of increased frequency of low recruitment, linked to climate change, on population size, population structure, available free space, zero density events and variation in population growth rate for a population of *S. balanoides*. We were interested in the direction and size of the effects at different model perturbation levels. The analysis was performed with four types of matrix model simulations (scenario 1–4). First, we modified the model from Svensson et al. (2004) to include the measured frequency of low recruitment years, observed in a dispersive environment in the Isle of Man. Through model simulations, new estimates of population variables were attained and compared with former results. Secondly, an artificial scenario of increased frequency of low recruitment was created in the model, making it possible to evaluate the effects of increased frequency on the population dynamics of this species. Also, to estimate the impact of low recruitment in relation to recruitment failure (zero recruits) the second analysis was repeated, this time with zero recruitment. Eventually the effect of low recruitment on local population demography may result in local extinction (zero density). Intuitively, this is more likely to occur where low recruitment occurs in consecutive years, since this would affect the ability of the barnacle population to recover. To address this question, the third analysis comprised testing the effects of consecutive years of low recruitment on population size and free space. Both the area of larval origin and settling are affected by low recruitment, which make recruitment one year somewhat dependent on the recruitment situation 2 or 3 years earlier. In the fourth analysis, we therefore included a linear

negative relationship between the frequency of normal recruitment and the number of years with low recruitment during earlier years. By varying the strength of the correlation, we could estimate the strength of the correlation between consecutive recruitment that was necessary for the population to succumb to continuous low recruitment. The collected results from all analyzes are then discussed in relation to ecological consequences of climate change in the context of species persistence, environmental variability and community structure.

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## Materials and methods

### Study sites

Demographic data for *S. balanoides* were collected at two randomly selected shores (Niarbyl N 54°10', W 4°45' and Derbyhaven N 54°5', W 4°37') in the Isle of Man (British Isles). Both shores are semi-exposed and have abundant barnacle populations. A detailed physical and biological description of the selected shores in the Isle of Man can be found in Southward (1953).

### Data collection

At each shore, two sites, at least 10 m apart, were chosen at random and at each site, two randomly located quadrats were sampled. Each quadrat was 5×5 cm in size. Photographs were taken of each quadrat, at the beginning and end of two 6-month periods. New quadrats were selected for the second time interval. Shores were sampled for periods June 1997–December 1997 and December 1997–June 1998. The photographs were digitally analyzed using Image Pro Plus (Media Cybernetics 1996). All barnacles were counted and measured for opercula length at the start and end of each 6-month period, producing measurements of growth, mortality and recruitment for each quadrat. These data were then used for the parameterisation of the model. The percent cover of bare space was recorded. An additional 250 barnacle individuals were collected and measured to parameterize a conversion function between opercula length of an individual and its occupied space.

### The matrix models and size-categories

The models used in this study are extensions of the model developed by Svensson et al. (2004). This is a size-structured matrix population model that describes the demography of an open population with space-limited recruitment in stochastic environments. For a general review of the theory behind this type of model see Caswell (2000) and for extensive reviews see Cohen (1987), Tuljapurkar (1990), Tuljapurkar and Caswell (1997). The original model will be referred to as Model-1. A brief description of this model and more specific descriptions of

the modified versions used in this study are given below. For more detailed information on basal model structure and built-in equations, see Svensson et al. (2004).

In the model, each individual in the barnacle population was initially placed into one out of three possible size-categories, expressed as series of occupied space ( $\text{mm}^2$ ) per individual intervals ( $0 \leq 1 \leq 26.0$ ;  $26.1 \leq 2 \leq 38.8$ ,  $38.8 < 3$ , from Svensson et al. 2004). From this division of individuals, the model was created based on a number of biologically derived and tested assumptions. These were;

1. Individuals of *S. balanoides* could only survive in their current size category, increase in size to any of the next categories or die.
2. Populations were considered open and all new individuals recruited into the first size category.
3. Mortality was size specific (Jenkins et al. 2001) and independent of other vital rates.
4. There was no spatial co-variation between mortality and recruitment.
5. Recruitment was partly limited by space.

Hence, the number of recruits was limited by the free space available and in model-runs free space (F) was incorporated into the recruitment process.

Data-sets of individuals divided into three size-categories were used to produce sixteen independent survival and growth matrices (eight matrices for each period). In addition, recruitment data from 1997 produced eight estimates of normal recruitment and recruitment data from 1998 eight estimates of low recruitment (see Svensson et al. (2004) for a detailed description of the procedure). This judgment was based on the experience of two of the co-authors Jenkins and Hawkins who have studied barnacle recruitment processes in the Isle of Man over a combined period of 11 years. Low recruitment had a magnitude of about 3.5% of normal recruitment. A mean transition matrix for each period and mean recruitment functions, including standard deviations, are presented in Table 2.

## Model simulations

In the model stochastic variation in growth and survival was applied. The procedure included the use of a finite state ergodic Markov chain (i.e. stochastic sample path) (Cohen 1987) to generate a sequence of environmental

states and associated matrices describing the environment (Caswell 2000). Each of these was randomly selected for the two periods out of the sixteen independent environmental states (matrices) derived from data. This produced a stochastic variation within each of the two periods resulting in  $8 \times 8$  (=64) possible combinations of annual periodic growth and survival rates.

Recruitment occurred during late spring and the recruitment process was limited to the winter–summer period (period 2) only. The simulation procedure for recruitment was a stochastic process, extracting the recruitment state and associated recruitment per area function for period 2 every time interval. The functions were randomly selected out of the eight independent recruitment states derived either from 1997 (normal recruitment) or 1998 (low recruitment) data. In the original model from Svensson et al. (2004) (Model-1), the frequency of normal recruitment was 1.

Part of the aim was to study the effects of a possible autocorrelation between years of low recruitment on the population dynamics. For this we chose a simple approach using a linear function, since there is no empirical data describing the real structure of the correlation. Hence, the model included a discrete linear negative relationship between the occurrence of normal recruitment and the number of years with low recruitment during earlier years. The procedure was described by the following equation:

$$Y = 0.75 - C_c X \rightarrow X \in Z, 0 \leq X \leq 3 \quad (1)$$

where  $Y$  is the probability of normal recruitment,  $C_c$  is a constant deciding the strength of the correlation and  $X$  is the number of consecutive years of low recruitment during the previous 3 years. We used 3 years since we believe this to be the maximum lag for the adult response to low recruitment. Initially,  $C_c$  was set at 0, meaning that no correlation was included.

In model runs, the generated sequence of projection matrices and recruitment states were applied to an initial population vector  $N(0)$  to produce a sequence of population vectors ( $N(1)$ ,  $N(2)$ ,  $N(3)$  ... etc). Each of these represented the population state at a particular time. The stochastic growth rate ( $\lambda_s$ ), that is the average growth rate, was then calculated numerically by averaging a number of one-step estimates of  $\lambda_s$  over 10,000 time units. From this, the average logarithmic population growth rate could be

**Table 2** Mean projection matrices ( $\pm$ SD) and recruitment state functions ( $\pm$  SD) ( $R$  for normal recruitment and  $LR$  for low recruitment) during summer to winter (period 1) and winter to summer (period 2) for the population in the Isle of Man

Isle of Man	To	From		
		1	2	3
Period 1	1	0.60 $\pm$ 0.14	0	0
	2	0.010 $\pm$ 0.0093	0.41 $\pm$ 0.33	0
	3	0	0.27 $\pm$ 0.33	0.50 $\pm$ 0.53
Period 2			$R = 14.11 \pm 12.65 \text{ (cm}^{-2}\text{)}$	
	1	0.74 $\pm$ 0.17	$LR = 0.59 \pm 0.58 \text{ (cm}^{-2}\text{)}$	
	2	0.044 $\pm$ 0.080	0.57 $\pm$ 0.33	0
	3	0	0.056 $\pm$ 0.12	0.47 $\pm$ 0.47

calculated (see Heyde and Cohen 1985 or Caswell 2000 for details).

Total area ( $A$ ) simulated in the model was equivalent to the size of one sampled quadrat (25 cm<sup>2</sup>). Model runs generally spanned over 10,000 time units (years). The initial 1,000 time units were disregarded from analysis to exclude any form of transient behaviour in demography and allow the population to reach its stochastic steady state.

### Scenario 1

In the first modification of Model-1, the probability of normal recruitment was changed from 1 to a normal distribution around a mean, initially set at 0.75 (estimated from Table 1) with a standard deviation (SD) set at 0.1. We call this model Model-2, as it will form the model base for some of the other scenarios. Model-2 simulation results were compared with results from Model-1 simulations.

### Scenario 2

To test the possible scenario of increased frequency of low recruitment and recruitment failure, Model-1 was modified anew. In the model, the frequency of either low recruitment or recruitment failure was set flexibly, which allowed us to introduce any desired frequency into the model. Then, to evaluate the effects of a gradual increase in low recruitment or recruitment failure on population dynamics, an appropriate scale of increase was introduced. First, one hundred different discrete frequencies of low recruitment, spanning between 0 and 1 (0, 0.01, 0.02, ... , 1), was simulated. The procedure was then repeated for recruitment failure.

### Scenario 3

To test the effects of and recovery after consecutive years of low recruitment, Model-2 (see scenario 1) was further modified. In this model, zero up to twenty (0,1, 2, ... , 20) consecutive years of low recruitment can be simulated separately. In the procedure, the population was first simulated under normal Model-2 conditions for 1000 time steps to enable the population to reach a “normal” state. This state was used as a starting point in all simulations. The barnacle population was then introduced into the modified version for  $\alpha$  (1,2, ... ,20) number of years, followed by another 50 years of normal conditions. During this time ( $\alpha + 50$  time-units) the population was monitored. Due to the stochastic environment, the procedure was repeated 50 times for each  $\alpha$ .

### Scenario 4

Using Model-2 and through iteration of the correlation constant  $C_c$  (from Eq. 1) we estimated the strength of the correlation between consecutive recruitment events that was necessary for the population to succumb to continuous low recruitment. This was done by increasing  $C_c$  in steps of 0.01 from 0 to 1 and then for each value measure the simulated mean recruitment over time. Mean recruitment was then plotted against increasing values of  $C_c$ .

For the simulations of scenario 1, 2 and 4, the average population growth rate ( $\lambda_s$ ), population size ( $N$ ), population structure, recruitment ( $R$ ), available free space ( $F$ ) and zero density events and their variance were calculated and analyzed. For the simulations of scenario 3, we followed the average development of density and free space, during and after consecutive low recruitment years.

## Results

Model construction with space as a limiting factor produces a population in stochastic steady state, that is, although population density varies it can only attain values within certain boundaries. Therefore the mean population growth rate was consistently fixed at 1 even with the introduction of low recruitment years. As expected, the introduction of low recruitment as a naturally occurring event in the model (Model-2) caused an increase of the variation in stochastic growth rate and population size (Table 3). However, the decrease in population size and subsequent increase of the average amount of free space were relatively small and the variation in free space was hardly affected (Table 3). These results indicate that frequencies of low recruitment currently observed on the Isle of Man mainly affect internal population variables and only slightly affect free space.

A gradually increasing frequency of low recruitment had large effects on the variation in population growth rate. The variation grew logarithmically up to a frequency of about 0.7 and then dropped off (Fig. 1). There was also an exponential increase of the proportion of free space (Fig. 2), but no drastic changes related to a particular

**Table 3** Results from model runs of barnacle (*S. Balanoides*) populations in the Isle of Man. Mean population growth rate ( $\lambda$ ) and its variance ( $V$ ) and mean population size ( $N$ ) and average percentage of free space ( $F$ ) per 25 cm<sup>2</sup> and their corresponding coefficients of variation ( $CV$ ), before recruitment ( $BR$ ) and after recruitment ( $AR$ ), are presented for simulations with “regular” recruitment and low recruitment

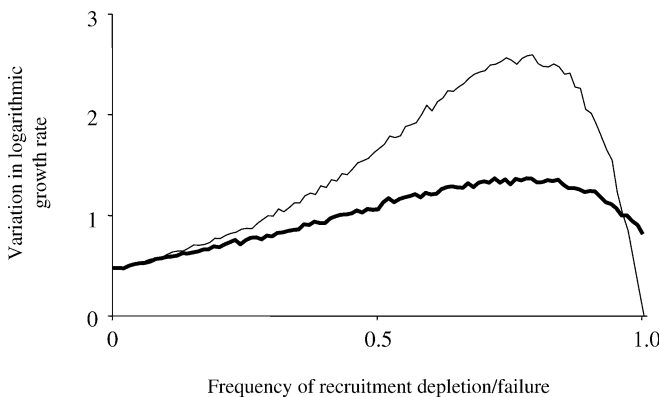
	$\lambda$	$V(\lambda)$	$N$	$CV(N)$	$F(\%)$	$CV(F)$
Excluding low recruitment						
$BR$	1.00	0.46	167	60.5	44.6	53.0
$AR$	1.00	0.37	280	56.5	21.8	96.4
Including low recruitment						
$BR$	1.00	0.79	147	76.0	51.5	51.6
$AR$	1.00	0.72	242	71.9	32.7	85.6

frequency. Simulations of recruitment failure produced a much steeper and exponential increase of the variation in growth rate but showed a similar pattern for the development of free space (Figs. 1 and 2).

Increased frequencies of low recruitment years did not impact much on the proportion of zero density events (Fig. 3), which reached a maximum value of only 3% when low recruitment occurred every year. In comparison, increased frequency of recruitment failure induced very high proportions of zero density events (Fig. 3), diverging exponentially from the low recruitment pattern at a frequency of about 0.6. These results primarily reveal two patterns: One, that local extinctions are unlikely regardless of increased frequency of low recruitment, even at a small scale, and two that at frequencies of 0.6 and higher, retained low recruitment years (compared to recruitment failure), become important for the renewal and persistence of the adult population.

Population structure changed gradually with increased low recruitment. However, even in simulations with 100% low recruitment, the population remained dominated by size category one individuals ( $\approx 77\%$ ), although the dominance was slightly reduced (compare with  $\approx 92\%$  at 0 frequency of low recruitment). In the same comparison, the proportion of size category two individuals was reduced from 5% to 2%. There was instead a great increase in the proportion of larger individuals (i.e. size category three), which at most comprised  $\approx 21\%$  of the population compared to  $\approx 3\%$  at 0 frequency of low recruitment.

Simulations of consecutive years of low recruitment revealed a clear pattern. Between 1 and 4 years (median = 2) of consecutive low recruitment years were acquired for the proportion of free space to reach and remain on a high level. Also, there was a negative relationship between the number of consecutive low recruitments and the subsequent recovery of the population to its original density (Fig. 4). After 20 years of consecutive low recruitments, the population required up to 5 years of regular recruitment dynamics to reach normal density and reoccupy empty space.



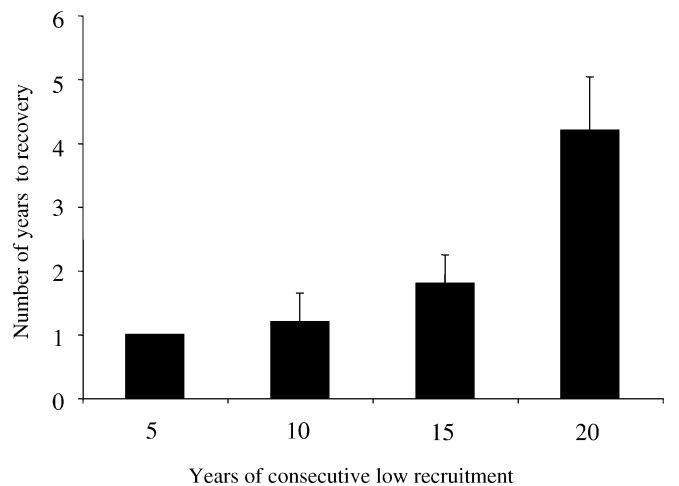
**Fig. 1** Model run variation in stochastic growth rate ( $\lambda_s$ ) for different frequencies of low recruitment and recruitment failure for the barnacle population in the Isle of Man (*thick line* low recruitment, *thin line* recruitment failure)



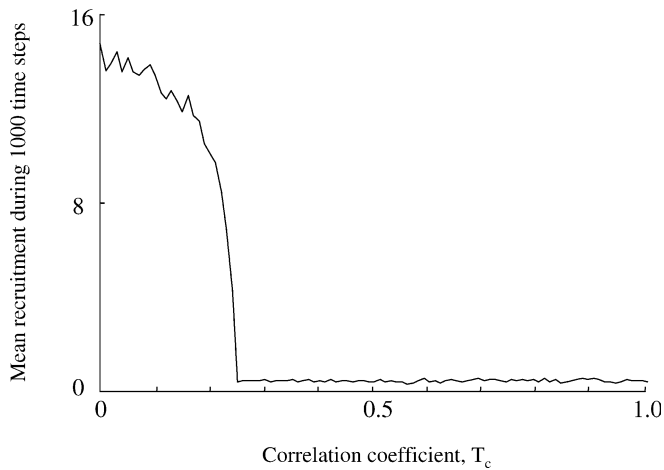
**Fig. 2** Model run proportion of free space for different frequencies of low recruitment and recruitment failure for the barnacle population in the Isle of Man (*thick line* low recruitment, *thin line* recruitment failure)



**Fig. 3** Proportion of zero density events for different frequencies of low recruitment and recruitment failure for the barnacle population in the Isle of Man (*filled circle* low recruitment, *filled triangle* recruitment failure)



**Fig. 4** Mean number of years ( $\pm$ SD) to recovery to normal densities and corresponding proportions of free space after 5, 10, 15 and 20 consecutive years of low recruitment for the barnacle population in the Isle of Man



**Fig. 5** Mean recruitment (recruits/cm<sup>2</sup>) over time ( $t=10,000$ ) for simulations of values between 0 and 1 (in steps of 0.01) of the correlation constant  $C_c$  (from Eq. 1)

An autocorrelation constant ( $C_c$  from Eq. 1) of 0.26 was required for simulated mean recruitment over time to be equivalent to mean low recruitment (Fig. 5). Thus, at this strength of the correlation, the population concedes to continuous low recruitment. Furthermore, simulations indicate a threshold value of  $C_c$  at 0.18 where weak effects of the autocorrelation rapidly turn to strong effects.

## Discussion

A combination of mainly temperature, wind and isolation determines the timing and formation of the spring phytoplankton bloom and hence recruitment of *S. balanoides*. Therefore, the development of *S. balanoides* over time is likely to be associated with winter/spring SSTs and these processes may explain a large proportion of the observed variation in adult densities (Minchinton and Scheibling 1991; Southward 1991; Menge 2000). Hence changes in climate (i.e. increased sea surface and air temperatures) could cause significant changes in the population dynamics of this species. However, inclusion of low recruitment years to the previous model developed by Svensson et al. (2004) at a rate consistent with that observed over the last 20 years had relatively little effect on the models output for the population dynamics of *S. balanoides* on the Isle of Man. Thus low recruitment, which occurs on average once every fourth year, has only limited effect on average population dynamics. Density dependence in post recruitment mortality (Lundberg et al. 2000) and the ability of variable populations which experience ‘noisy’ environments to exhibit certain buffering qualities that blur the visible effects of perturbations (Ripa and Lundberg 1996; Kaitala and Ranta 2001) are factors which may limit the effects of low recruitment years. However the extent to which such factors can negate the effect of limited input to the adult population are not boundless. Increasing the frequency of low recruitment and simulating recruitment failure (zero

recruits) obviously affected both external and internal barnacle population dynamics. Also by artificially including an autocorrelation between years of low recruitment, density was severely reduced. This demonstrates an increased sensitivity of population dynamics to disturbances in populations that are or have been subjected to changes in demographic parameters.

Increased variance of the population growth rate, reduced density and increased frequency of catastrophic events are likely to end in extinction for any population (Lande 1993; Ripa and Lundberg 2000). Hence, increased frequencies of low recruitment in an isolated population or in a population at its end range should therefore ultimately lead to local extinctions, at least at a small scale. However, this study revealed that for *S. balanoides*, very low recruitment is not equivalent to recruitment failure and that the importance of recruitment may vary drastically from year to year, partially depending on recruitment history. Comparing the effects of low recruitment and recruitment failure it was clear that at a frequencies of about 0.6 and higher, surviving adult individuals from previous years can no longer buffer for high frequencies of zero recruitment, making low recruitment at this stage essential for population persistence. Chiefly, this shows that even low recruitment can maintain a population at viable levels, indicating a certain degree of density dependent survival of recruits. But it also shows that if low recruitment occurs at frequencies of 0.6 and above, the population is likely to become more sensitive to further disturbances in recruitment. Hence, even though increased temperatures, or other changes in climate for that matter, induce population changes that are hard to detect due to existing environmental noise (Kaitala and Ranta 2001), there might be an unseen development towards populations that are more sensitive to additional changes in the environment.

The relationship between adult abundance and the size of the larval pool is exceedingly complex. However, repeated low recruitments on a large scale ought to affect the size of the larval pool in subsequent years for the entire region, especially for isolated populations, such as the one in the Isle of Man (Hughes et al. 2000). Simulations of consecutive years of low recruitment suggested that 4 or more years are necessary to drastically change and maintain free space at a higher level. For 4 consecutive years of low recruitment to occur around the Isle of Man, it would require a positive autocorrelation between low recruitment and the chances of low recruitment during subsequent years. At present, the extent to which this is the case is not clear. Using an artificial linear function, it appears that a fairly strong correlation was required to continuously reduce recruitment, though that shift to low recruitment was swift. Hence, even though model simulations predicts weak to moderate effects of low recruitment on free space, the frequency of low recruitment may eventually exceed a threshold that could drastically change the proportion of free space.

The model clearly predicts relatively mild changes in barnacle population dynamics as a result of moderate levels of low recruitment and recruitment failure but there

are a number of biological factors that are difficult to include in the present model. Most important of these is the gregarious nature of *S. balanoides* settlement. Both laboratory (e.g. Knight-Jones 1953) and field experiments (e.g., Hawkins 1983; Hills et al. 1998; Jenkins et al. 1999) have shown conclusively that planktonic cyprids of this species settle more readily on surfaces bearing adult conspecifics. The model simulated patterns at small scales where larval choice has been shown to be important. However, the general premise, which motivated the modelling, was based on the potential for increased frequency of low recruitment over large spatial scales. The key question in considering the role of gregarious settlement in population dynamics under these circumstances is whether loss of cover of *S. balanoides* over large scales due to low recruitment further reduces settlement when larvae become available. Observations on sheltered fucoid dominated rocky shores in the Isle of Man where barnacles are rare suggest that lack of an adult stimulus over scales of 100s of metres can severely limit settlement even when larvae are abundant (Hawkins and Hartnoll 1982; Hawkins 1983; Jenkins et al. 2000; Jenkins and Hawkins 2003). Thus it is likely that the model predictions of population variables somewhat underestimate the reduction in population size and increase in free space following an increase in the frequency of low recruitment.

According to model simulations, low to intermediate frequencies of low recruitment have relatively little impact on free space. However, even a small increase of the proportion and variation in free space would potentially create a change in the wider community, owing to the major role that *S. balanoides* plays in community dynamics (Hawkins and Hartnoll 1982). Dense barnacle cover promotes the development of macroalgae on exposed shores by providing a suitable settlement surface for algal propagules. In addition barnacle cover reduces grazing of propagules by the dominant patellid grazers on exposed rocky shores (Lewis and Bowman 1975; Hawkins and Hartnoll 1982). Thus a decrease in barnacle cover and a change in internal population structure caused by increased frequency of low recruitment is likely to reduce fucoid development and increase the homogeneity of the mid shore community (see Hawkins et al. 1992 for a review). It is also possible that vacant niches could appear, open for invasion by external species (Tilman and Lehman 2001). In Northern Ireland for example, Southward (1991) and Burrows (personal communication) found that during warmer time periods, the more southerly barnacle species *Chtamalus montagui* (more common higher up on the shore) were dominating areas on the shore that were otherwise covered with *S. balanoides*. Such a shift in species composition may further decrease the possibilities of re-colonisation by a suppressed species, and at the edge of a species range cause a contraction of the species margin.

Similar to the findings of Southward (1991), there was in model simulations a mean time lag of about 2 years between recruitment and the response of the adult population, although the time lag varied considerably

between simulations. Then, modelling consecutive years of low recruitment showed that about 3–5 years were required to eliminate traces of past settlement, indicating a mean life span of about 4 years. As a result we saw a change towards increased domination of older and larger individuals in the population. From these results it is evident that it takes some time before low recruitment impacts on the population dynamics and hence, ultimately determines adult density. This reveals that post recruitment processes are important factors in determining the population response to recruitment disturbances, even at low densities. Minchinton and Scheibling (1991) and Menge (2000) found similar results for populations with high densities. Therefore, instability in post recruitment processes acting at the adult level, for example due to climate change, could probably produce a more explicit population response than do fluctuations in recruitment. The relative effects of recruitment and post recruitment processes on population dynamics are known to vary also within a species (Caley et al. 1996; Svensson et al. 2004). However, such a scenario is complicated to evaluate, since it would require a measured correlation between a climate variable with survival. To date, no such data exist for *S. balanoides*.

In conclusion, the use of matrix model techniques seems to be a valid approach for this type of analysis. However, several issues regarding model structure were raised in the discussion and there is always a need to be cautious when interpreting model results. Still, given the possible effects of gregariousness and interaction with other species, we can be quite certain that the model does not exaggerate but rather understates the effects of climate change on population dynamics. According to model output, the population of *S. balanoides* on the Isle of Man was quite resistant to relatively high frequencies of low recruitment and recruitment failure, indicating a general tolerance to changes in climate. One explanation could be that this population even when subjected to normal recruitment is regulated by density dependent survival and fecundity or other mechanisms (Hills and Thomason 2003) and that the low recruitment is not low enough to severely affect population size. Another explanation would be that the impacts of low recruitment are made invisible by already existing variability (Kaitala and Ranta 2001). Yet, we did see an increase in the variation of stochastic growth rate and a substantial increase of free space during simulations of high frequencies and consecutive years of low recruitment. Furthermore, at intermediate to high frequencies, the population dynamics became more sensitive to further changes in recruitment and the overall population structure was altered. This shows that the ability of a variable population to buffer changes in demography is not unlimited. Such information is important to consider for management of species in isolated areas or with a contracting margin.



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