

# Population dynamics of *Mytilus edulis* along environmental gradients: density-dependent changes in adult mussel numbers

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**ABSTRACT:** The densities of each age class of adult (>1 yr old) mussels *Mytilus edulis* were measured in autumn and spring over 8 yr on each of 12 intertidal mussel beds in the Exe estuary, southwest England. The possibility that density-dependent changes in adult numbers in each of 9 yearly age classes occurred over the summer and winter periods was explored directly on individual beds and indirectly by combining data from all beds. There was direct evidence of density-dependent changes in both seasons in some age classes on some beds. The indirect tests suggested, however, that density-dependence was much more widespread over beds, age classes and seasons than had been suggested by the direct tests. The critical density above which density-dependent losses occurred, and to which the density-dependence tended to return numbers irrespective of the abundance of the mussels at the start of summer or winter, varied considerably among beds in several age classes. These critical densities were correlated most closely with the time for which a bed was exposed over low tide but were also influenced by the distance of a bed from the estuary mouth and the softness of its substrate. Between them, these 3 variables defined the environmental gradient of intertidal mussels in the Exe estuary. The residual, density-independent variations in the changes in numbers of several age classes of adult mussels about the density-dependent relationships were correlated with weather variables (temperature, gales and rainfall) in several cases and in both seasons. Surprisingly, there was evidence of widespread density-dependent immigration of adult mussels, especially in summer and in the younger age classes. While the passive movement by adult mussels in storms is well established, it is not known whether active movements occur in these older mussels. Although much of the density-dependence was due to mortality, immigration was therefore often an important component of the density-dependent relationships detected on individual beds. However, immigration on some beds countered losses on others. Perhaps because of this, density-dependence was often masked, and thus not detected, at the estuary scale in all but the youngest mussels whose estuary-wide abundance was dominated by 2 large mussel beds, where their numbers tended to co-vary. Thus, strong density-dependence at one scale may not be detected at a higher scale.

**KEY WORDS:** Mortality · Immigration · Scale · Sub-population · Stability

## INTRODUCTION

Logistical constraints frequently limit studies of population dynamics to the organisms living within a conveniently worked area, even though it is known that their population densities vary at several spatial scales and along environmental gradients and that processes operate at multiple spatial scales. Organisms in such sub-populations are unlikely to be totally

isolated and their population dynamics may depend as much on processes occurring elsewhere as on those within the study area itself. Many benthic marine invertebrates, including the mussel *Mytilus edulis* L., have a wide geographical distribution (Seed 1976) and their free-living planktonic larvae allow a great potential for dispersal. It has not yet been possible to study such species at a sufficiently large scale for dispersal to be unimportant and the dynamics to be determined mainly by birth and death rates within the study area itself. Even so, the combined 'meta-population' dynamics of groups of such sub-populations

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will still be affected by processes occurring within each, as well as on the interactions among them (Connell 1985, Roughgarden et al. 1985, Roughgarden & Iwassa 1986, Hastings & Wolin 1989, Hughes 1990, Sutherland 1990, Taylor 1990). In marine organisms, such processes include spatial and temporal variations in settlement and recruitment (Caffey 1985), density-dependent mortality (Hancock 1973, Beukema 1982), self-thinning (Hughes & Griffiths 1988), emigration (Ambrose 1986, Underwood 1988) and density-limited growth (Okamura 1986, Morrissey 1987, Peterson & Black 1987). Studies in one place are therefore still important, although their value will be enhanced by considering more than one spatial scale and by relating variations in sub-population dynamics to environmental gradients. In this study, insights have been gained into the dynamics of the *Mytilus edulis* population in the whole Exe estuary, southwest England (McGrorty et al. 1990) by studying individual mussel beds, or sub-populations, that occupy different positions along the species' intertidal environmental gradient (McGrorty & Goss-Custard 1991, 1993, McGrorty et al. 1993).

At the estuary scale (McGrorty et al. 1990), regulation of the mussel population was principally the result of a very strong density-dependent mortality of spat (0 yr) during their first winter after settling on the adult beds. Thereafter, as adults, densities were remarkably stable varying annually by only 1.5-fold over the 8 yr study, and there was little evidence of further density-dependent regulation despite some mussels surviving up to 10 yr. However, the population did not consist of a single uniform patch, but of 12 separate sub-populations, or mussel beds, scattered throughout the seaward half of the estuary. At this finer scale there were large (1 to 3 orders of magnitude) differences among beds in the densities of the various age classes of mussels (McGrorty & Goss-Custard 1991). Also, though there was little evidence to suggest that the rates of mortality differed among beds, the 'critical' (Hassell 1975) density, above which the 1st winter density-dependent mortality operated (McGrorty & Goss-Custard 1993), varied widely according to the position of the bed along the environmental gradient. Despite this variation among beds, the 1st winter density-dependence acted in the same direction on all beds and the combined effect was detected at the larger estuarine scale as a strong density-dependent regulation of the whole population. There are, however, examples of terrestrial insects in which strong density-dependence at one scale, e.g. the leaf (Hassell et al. 1987), was not detected at a larger scale, e.g. the bush (Southwood & Reader 1976). The main aim of this paper is, therefore, to investigate whether, despite the paucity of evidence for density-dependent losses

of adult age classes at the estuary scale, density-dependent regulation nevertheless operated at the smaller bed scale at some or all ages in summer or winter.

It is well known that on open coasts mussel beds may be wholly or partially destroyed by annually varying weather factors, such as ice or storms (Dare 1976). Even though this seemed unlikely in the small, sheltered Exe estuary, we nevertheless investigated whether weather variables might explain some of the residual density-independent variation in mortality after the effect of density-dependent losses had been taken into account. Finally, the analyses revealed that 37% of the seasonal 'mortality' estimates across all adult age classes and beds were negative, that is to say, involved gains rather than losses. We therefore investigated whether all of these values were due to sampling errors, or whether, despite their sessile habit and the apparent stability of the mussel beds, some might have been real increases in density due to the migration of adults.

## METHODS

**Study area and field methods.** In the sheltered estuary of the river Exe, southwest England, most adults (91%) and most 0 yr mussels (95%), or spat, occurred in September 1976 on the 12 largest of the 31 intertidal beds (Fig. 1), which together made up the whole intertidal mussel population. The remaining 19 beds were either very small or consisted of widely scattered small clumps and all declined to extinction within 2 yr. Beds were defined as geographically discrete areas of mussels, separated by areas of bare sand or mud. However, in 3 cases (Beds 3/4, 30/31 and 26/27), areas of mussels separated only by a stream or gully were given separate bed status because there were marked differences in mussel density and cover, or in substrate, elevation or topography, all factors which were thought likely to affect or result from differences in population dynamics. Each bed was sampled in March and September, from September 1976 to September 1983. The methods for sampling, measuring and ageing mussels are detailed in McGrorty et al. (1990). In brief, 600 samples  $0.04 \text{ m}^2$  in area were collected from the 12 main beds using a stratified random procedure. Eight beds were each divided into 2 strata on the basis of clearly visible differences in mussel density; the other 4 beds were each regarded as a single stratum. Samples were allocated to each stratum in proportion to its area and the standard deviation of the density estimate of the most abundant year class. Mussels were counted, measured and aged from external growth

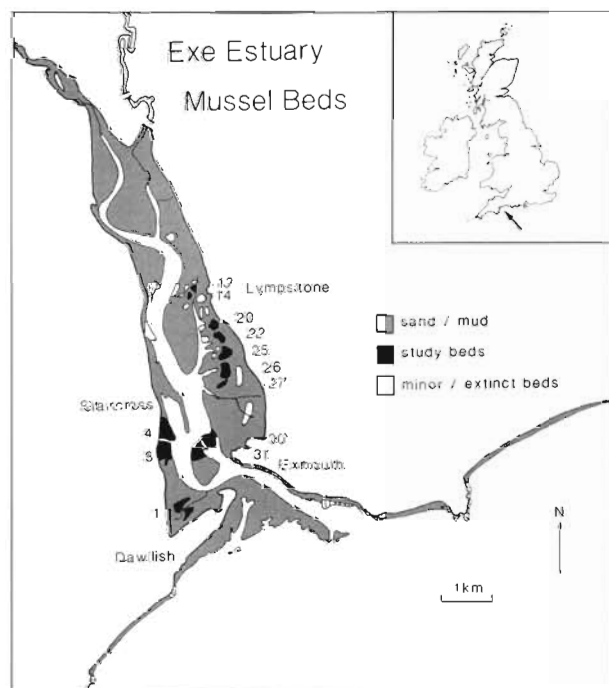


Fig. 1. Map of the Exe estuary, Devon, England, showing mussel bed locations. The 12 study beds are numbered

rings. Ageing of all mussels in this way was only possible after the pattern of winter, and other, disturbance rings had been established by following the growth of individually marked mussels (cutting the byssus threads each time the mussel was measured to create disturbance rings), by sectioning shells and hinge ligaments and by conducting blind tests on mussels of known age (>95% aged correctly, authors' unpubl. data).

**Environmental variables.** The methods used to measure the environmental variables are detailed in McGrorty & Goss-Custard (1991). In brief, tidal level could affect the time available for spat to settle and established mussels to feed, as well as their vulnerability to different predators and adverse weather. Tidal level was measured as mean aerial exposure time, the proportion of the tidal cycle for which the beds were exposed, averaged over 3 representative tides with predicted heights at high water of 3.1, 3.6 and 4.0 m. Tidal heights varied between 2.5 and 4.3 m; however, plotting a frequency histogram of the predicted tidal heights in the Exe estuary for the year (data from Admiralty Tide Tables 1978) revealed 3 peaks at the values indicated, which were therefore the most common heights of neap, medium and spring tides respectively. Aerial exposure of the 12 beds varied between 17.2 and 45.1%. The distance from the sea could affect salinity and the supply of both settling plantigrade lar-

vae and planktonic food from outside the estuary. The distance measured from maps varied between 0.78 and 3.93 km. The softness of the sediments between established mussels could affect the attractiveness of a bed to settling larvae and the chances of their being subsequently smothered by mud. It was measured as the mean penetration depth of a standard cylindrical steel rod (900 g in weight, 90 cm long, 1.33 cm<sup>2</sup> cross-section and end area) dropped between mussels from a height of 1 m at 20 randomly selected sites on each bed, and varied between 3.8 and 17.4 cm.

Weather data for the study period were extracted from monthly reports, published by the Meteorological Office (Bracknell, Berkshire, England), which summarise daily observations made at Starcross, adjacent to the estuary, for the appropriate period of year (summer: 16 March to 15 September; winter: 16 September to 15 March). Mean daily temperature was expressed as the deviation from the 30 yr (1931 to 1960) average. The incidence of gales was measured as the number of days when wind speeds exceeded 34 knots (force 8) irrespective of direction. Mean daily rainfall was expressed as a percentage of the 30 yr average.

**Data analysis.** Mussel larvae settled in late winter (February to March) and summer (McGrorty et al. 1990) and developed a recognisable gonad (by eye) at a length of ca 10 mm in autumn or winter. Therefore, regardless of their precise age, they were classed in the following March as 1 yr old adults capable of breeding. Adult mortalities were calculated from density estimates derived from the biannual surveys for each year class from 1 to 9+ yr old and expressed as  $k$ -values ( $k = \log_{10}$  initial density -  $\log_{10}$  final density; Varley & Gradwell 1960);  $k_{2s}$ , ...,  $k_{10s}$  and  $k_{2w}$ , ...,  $k_{9w}$  denoted mortalities during the 2nd to 10th summers and 2nd to 9th winters respectively.

**Tests for density-dependence on single beds:** A preliminary examination of the data was made by plotting annual stage (age and season) mortalities ( $k$ ) for each bed against the logarithm<sub>10</sub> (log) of the density at the beginning of the stage (see Fig. 3 for examples). Slopes greater than zero suggest possible density-dependent mortalities. However, there are several well-known difficulties associated with statistical testing of relationships expressed in this way, including non-independence of the  $x$  and  $y$  variables, which are discussed in the present context in McGrorty et al. (1990). Any autocorrelation between the variables will tend to change the slope of the relationship, thus indicating density-dependence whether it is present or not. To avoid these problems, Bartlett's (1949), reversed axes (Varley & Gradwell 1968, Slade 1977) and major axis tests (Smith 1973) on log initial density against log final density were used on each bed at each age and season. In these tests

slopes significantly different from 1 at  $p < 0.05$  indicated density-dependent mortality. Pollard et al. (1987) suggested a different approach using a randomisation procedure to avoid autocorrelation problems. However, these authors devised their test specifically to detect density-dependence from a series of annual censuses of the density of animals at one stage (usually adults), not from stage to stage within year classes. The method also assumes that there are no errors in the estimated density values. The 'classical' methods that we used may have less power than the randomisation test, but do allow for error in the density estimates.

In addition to its own density, the density of other ages or sizes could also affect mortality at a particular age. Though the variables were not entirely independent in this case, the age class whose mortality ( $y$  variable) was being considered contributed only a small part of the total initial density ( $x$  variable), and the 3 tests related each stage mortality to the combined densities of (1) young adults in their 2nd to 5th, (2) old adults in their 6th to 10th year and (3) all adults, and slopes significantly different from zero at  $p < 0.05$  indicated density-dependence. Nonetheless, the densities of each age class were in general positively correlated with the densities of these combined age groups, for example, 94% of the correlations ( $r$ ) between the densities of individual age classes and the densities of all adults, across all beds and seasons, were positive and 59% were significant at the 5% level of probability. Accordingly, only analyses based on mortality ( $k$ ) against the initial density of the particular age class in question are presented in this paper

**Tests for density-dependence across all beds combined:** Significant results from the single bed tests were regarded as direct evidence of density-dependence at a particular stage on a particular bed. However, these commonly used tests have either low statistical power (Holyoak 1993) or fail to detect density-dependence when the variation in the data is small or the time series is short (Hassell et al. 1989). Thus, in the present study, the range of initial densities may have been too narrow for individual bed density-dependent relationships to be expressed, especially where sampling errors in the  $y$  variate (the  $k$ -values) were large. Further tests were therefore required to determine whether density-dependence was more widespread across beds and ages than indicated by the single bed analyses.

This was done by plotting mortality against initial density for all 12 beds together at each stage and testing 3 regression models based on different assumptions about the density-dependence occurring at each age (Fig. 2). Model 1 assumed that all beds shared

a common relationship, and so had the same slope and intercept. Model 2 assumed that beds shared a common slope, but had separate intercepts. Model 3 assumed that the beds had both separate slopes and intercepts.  $F$ -tests were used to select the model, if any, that best explained the variation across beds in mortality against density.

## RESULTS

### Density-dependence in stage mortalities

#### Direct evidence of density-dependence on individual beds

Only 12% (290/2448) of the individual tests were significant at the 5% level of probability, but this still represented more than twice the number expected by chance. Likewise, adult density-dependent mortality was supported by 1 or more of the 3 tests at  $p < 0.05$  in only 21% (169/816) of all the possible combinations of initial density, bed, year group and season (Table 1), but this represents 4 times the number that would be expected by chance (41/816). In 96% of the significant relationships the effect of the initial density on the mortality was positive; that is, the greater the initial density the greater the mortality in the following summer or winter period. The effect was negative in only 6 cases, fewer than expected by chance at  $p < 0.05$ . Clearly, negative density-dependence was rare and overall density generally had a positive effect on mortality.

Summing the significant relationships from Table 1 reveals that in 38 cases density-dependent mortality was related to the initial density of the particular age class, in

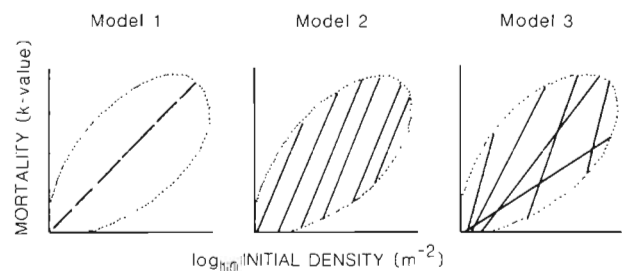


Fig. 2. Tests for density-dependence across all beds combined: diagrammatic representation of the 3 regression models applied. Model 1 calculated a common relationship across all beds, to which the data from each contributed only a small part. Model 2 calculated a common slope but a separate intercept for each bed, resulting in parallel lines. Model 3 calculated separate slopes and intercepts for each bed. (.....) Boundary of the data points for all beds combined, (—) individual bed relationships

49 cases to the density of young adults (2 to 4 yr), in 34 cases to the density of old adults (5+ yr) and in 48 cases to the density of all adults. These results suggest that mortalities of particular age classes are more often related to the combined densities of young or all adults than simply to their own initial density. However, at most ages and on most beds where density-dependence was supported by tests, there were significant relationships between mortality and more than 1 of the 4 measures of initial density. As we needed to identify the best overall measure of initial density for later analyses and each explained a different proportion of the variance in the mortality, only the measure which explained the greatest proportion of the variance in each case was considered further. Summing again across all beds and stages, in contrast to the earlier finding, mortality was then shown to be related more often to the initial density of the particular age class (30 cases) than to combined densities of all adults (18 cases) or other combinations of densities (22 and 15 cases for young and old adults respectively). These results support the earlier decision to present in this paper only those analyses based on the relationship between mortality at each age and its own initial density.

At each age (1 to 9 yr old) significant relationships ( $p < 0.05$ ) were indicated by the 3 tests for at least 3, and up to 9, of the 12 beds in each season (Table 1). Although no clear pattern to the distribution of significant relationships across beds and age classes occurred, density-dependence may have been more widespread in young adults than in old, and on the large muddy beds (26 and 20) in summer and on beds near the sea (31, 27, 26 and 4) in winter. Density-dependent mortality in adults was thus widespread across ages and beds, but may not have occurred at all ages on all beds.

The slopes ( $b$ ) of the individual bed density-dependent relationships, based on the initial densities of the particular age classes and supported by the tests ( $p < 0.05$ ), varied between 0.50 and 2.40. In other words, for every additional mussel beyond the critical density (intercept on the  $x$  axis) at the beginning of the period, on average 0.5 to 2.4 mussels died during the period. However, the slope was significantly  $>1$  (major axis and reversed axes tests of log survivors on log

Table 1 Tests for density-dependent mortality in adult mussels on single beds. 2S, ..., 9W: the 2nd summer to 9th winter periods. +: 1 or more of the 3 tests for density-dependence gave a significant result ( $t$ -test,  $p < 0.05$ ) for each of 4 relationships:  $k$  on  $\log_{10}$  initial density (ID) of the particular age class (upper left),  $k$  on  $\log_{10}$  ID of young adults (2 to 4 yr, upper right),  $k$  on  $\log_{10}$  ID of old adults (5 yr+, lower left) and  $k$  on  $\log_{10}$  ID of all adults (lower right). + and -: positive and negative density-dependence respectively

Age	Bed no.											
	1	3	4	13	14	20	22	25	26	27	30	31
2S	++ +	++		++ ++	++	+		++	+	+	+	
3S	++	+		+	++	++ +	++		++	+	+	
4S	+				++	++ +			+	+	+	
5S			+		+	+					+	+
6S		+				++ +		+	+	+	++	
7S		++ ++				+	+	+	+		+	
8S		+			+	+		+	++	++		
9S		+	+		+			+				-
10S					+			+	+-			
2W			+							+	++	++
3W			+							+	++	++
4W			+						+		++	+
5W			+			+			+	+		+
6W						-	+		++			+
7W				++ ++					+			++
8W							++ ++		+	+	-	+
9W							++		+	+		

initial densities;  $b < 0$ ,  $p < 0.05$ ) in only 3 cases, the 6th and 7th summer and 7th winter on Bed 26, suggesting that overcompensating ( $>1$  died for each additional mussel) density-dependence was uncommon. Most slopes were close to and not significantly different from unity, implying strong to near perfectly compensating density-dependence (Varley et al. 1973). Three examples chosen to illustrate the range of significant relationships are presented in Fig. 3; the near perfectly compensating density-dependence ( $b = 0.98$ ) in the 2nd summer on Bed 3, the strong density-dependence ( $b = 0.80$ ) in the 3rd summer on Bed 9

and the overcompensating density-dependence ( $b = 2.40$ ) in the 7th summer on Bed 26. The relationships also illustrate that not all  $k$ -values were positive (i.e. losses), indeed the 3rd summer 'mortality' ( $k_{3s}$ ) on Bed 20 was negative (i.e. gains) in 6/7 years. Overall 37% of  $k$ -values were negative, due either to sampling error or immigration.

#### Indirect evidence of density-dependence across all beds

The failure to establish density-dependent mortality in most cases (Table 1) may reflect a failure of detection more than an absence of density-dependence. Many of the individual relationships consisted of tight clusters of points, as Fig. 3 also illustrates. Had the range of initial densities been greater, density-dependence might have been detected more widely.

The analyses, based on 3 different assumptions (Fig. 2), of the data from all 12 beds combined provided indirect evidence for more widespread density-dependence across age classes, beds and seasons. As would be expected, the proportions of the total variance explained by the 3 models increased as the model assumptions changed from a common relationship across all beds (Model 1), to a common slope but different intercepts (Model 2), to different slopes and intercepts (Model 3) (Fig. 4), but the increase was not always statistically significant ( $F$ -tests,  $p < 0.05$ ). However, at each age, in both summer and winter, at least one of the models explained a significant proportion of the variance in mortality, suggesting that mussels were indeed subject widely to density-dependent mortality.

The model that best described the density-dependence varied between age classes and seasons. Although a common relationship across all beds (Model 1) explained only a small ( $r^2 = 16\%$ ) but significant ( $F = 14.72$ ,  $p < 0.0001$ ) proportion of the variance in 5th summer mortality, neither Model 2 nor 3 explained significantly more (Model 2:  $F = 1.30$ ,  $p = 0.25$ ; Model 3:  $F = 0.96$ ,  $p = 0.49$ ; Fig. 4a). At this age, therefore, there is insufficient evidence to reject the hypothesis that a common relationship applied across all 12 beds. But at all other ages in the summer, Model 2 explained a significantly ( $p < 0.05$ ) greater proportion of the variance in the total mortality than Model 1 and in some cases Model 3 explained a significantly greater proportion than Model 2, indicating that different relationships applied on the different beds.

The details of these different relationships are as follows. In the 2nd to 4th summers, Model 2 explained a significantly greater proportion of the

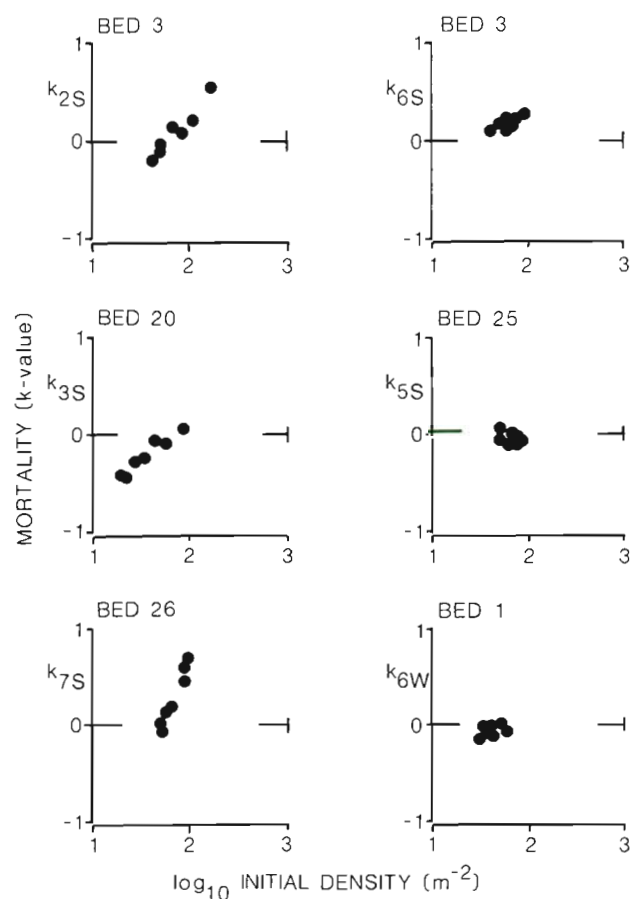


Fig. 3. Density-dependence on single beds: 6 of the 204 combinations of bed, age and season selected to illustrate the range of relationships found between the mortality ( $k$ ) and the  $\log_{10}$  of the initial density for the period over which the mortality acted (2S: 2nd summer; 6W: 6th winter). Slopes ( $b$ ) of the left-hand graphs suggest near perfect (Bed 3,  $k_{2s}$ ,  $b = 0.98$ ), strong (Bed 20,  $k_{3s}$ ,  $b = 0.80$ ) and overcompensating (Bed 26,  $k_{7s}$ ,  $b = 2.40$ ) density-dependence. Right-hand graphs are examples of relationships for which the range of values on both axes was small and the data formed tight clusters of points. Note that many  $k$ -values were negative, which could have been due to sampling error or immigration.

variance than Model 1, but there was no significant improvement in fit when Model 3 was used. Density-dependence in young adults in summer is, therefore, best described by a series of relationships with different intercepts, but with a common slope. Mortality occurred in these mussels at the same rate on all beds, but the process began to operate only when density exceeded different critical values on each bed. Many beds had intercepts significantly different from each other ( $t$ -tests,  $p < 0.05$ ) as implied by Model 2 giving the best fit to the data. For each age class we therefore took the estimates of the critical



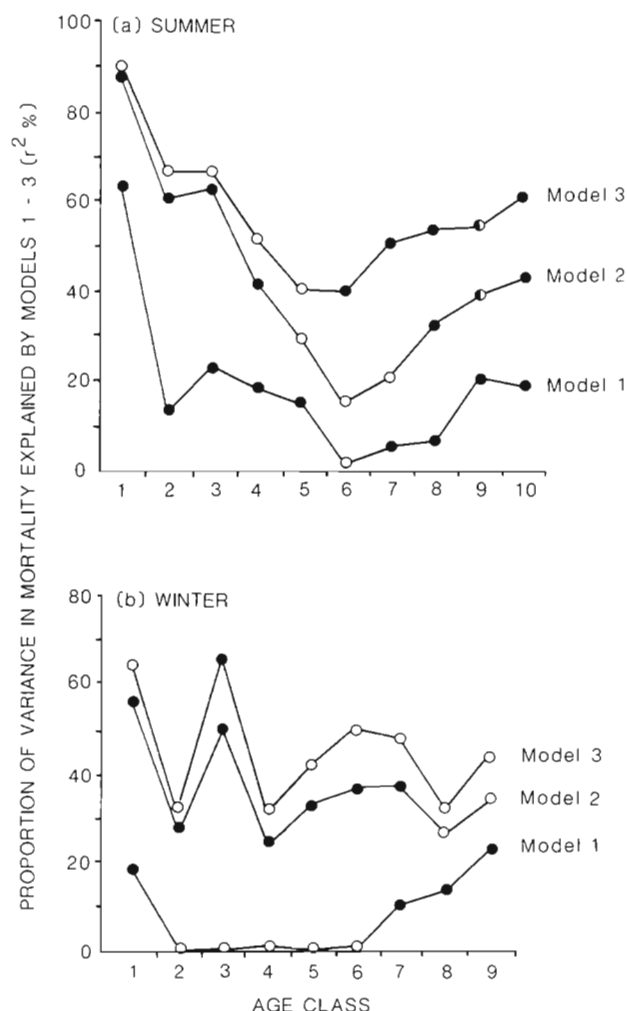


Fig. 4. Tests for density-dependence across all beds: proportion of the variance in mortality ( $r^2$  %) at each age in summer and winter explained by the 3 regression models of mortality ( $k$ ) on  $\log_{10}$  initial density for all beds combined. (●) Model 1 explained a statistically significant proportion of the variance in mortality ( $F$ -tests,  $p < 0.05$ ) and Models 2 and 3 explained, in turn, a significantly greater proportion ( $F$ -tests,  $p < 0.05$ ). (◐) Probabilities for  $F$ -tests  $> 0.05$ , but  $< 0.1$ ; (○)  $p > 0.1$ .

densities for the 12 beds as our dependent variable in further analyses. For the 6th to 10th summers, by contrast, Model 3 gave the best fit, suggesting that both separate slopes and intercepts were appropriate for each bed in these older adults. As well as providing indirect evidence of density-dependent mortality at each age in summer across all beds, this analysis suggested that a common relationship of mortality with density was shared by some age classes in summer but not by others.

In winter, Model 1 gave the best fit to the data in only the 8th and 9th winters, implying that a common rela-

tionship across all beds occurred only at these 2 ages (Fig. 4b). At all other ages, Model 2 gave a significantly better fit than Model 1. In contrast, Model 3 further improved the fit only in the 3rd winter. Hence, at most ages in winter, the rate of increase of mortality with density was the same on all beds, but the mortality operated above different critical densities. As in summer, there was thus indirect evidence of density-dependent mortality occurring in all age classes on all beds, with a common relationship between mortality and density being shared by some beds but not by others.

To place these variations in adult density-dependence in perspective, the adult stages may be compared with spat in which very strong density-dependence occurred in both summer and winter (McGrorty & Goss-Custard 1993). In summer, across adult age classes as a whole (Fig. 4a), less (15 to 62%) of the total variance was explained by the most appropriate model for density-dependence than in spat (1st summer, 89%). However, a greater proportion of the variance in mortality was explained by density-dependence in the 2nd and 3rd summers (60 and 62%, Model 2) than in later years. This indicates that variations in the mortality during the first 3 summers of life were dominated by density-dependence. The variation explained by density-dependence then declined up to the 5th summer before increasing again, indicating only a weak influence of density-dependence in the middle years, but a stronger influence thereafter. The variation in mortality accounted for by density-dependence showed no such clear trends with age in winter, however (Fig. 4b). Density-dependence explained only 57% of the variation in mortality rates in spat and between 14 and 66% in adults.

There were similar differences between winter and summer in how the strength of the density-dependence, measured as the slope ( $b$ ) of mortality against density, changed with age. In winter (Fig. 5b), the density-dependence was moderately strong at most ages, with the values for  $b$  varying between 0.35 (Age 5) and 0.79 (Age 9). In contrast, the strength of the density-dependence in summer (Fig. 5a) was very high in the early years, with rates of mortality ( $b$ , Model 2) of 0.89, 0.83 and 0.94 for spat, 2nd and 3rd year mussels respectively. Likewise, values were high in later years ( $b = 0.60$  to  $0.74$ , Ages 8 to 10), but were very low during the middle years. Nonetheless, although the strength of the density-dependence and the proportion of the variation in mortality it explained varied among ages, and the pattern of variation with age differed between seasons, the results do indicate that, throughout most of their life, mussels were frequently subject to strong density-dependent mortalities.

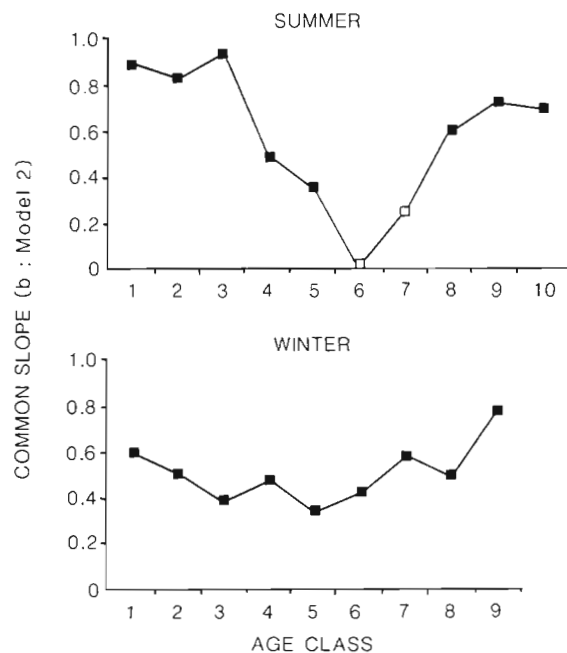


Fig. 5. Tests for density-dependence across all beds: common slopes ( $b$ ) derived from Model 2 regressions of mortality ( $k$ ) on  $\log_{10}$  initial density at each age in summer and winter (■) Slopes significantly  $>0$  ( $t$ -tests,  $p < 0.05$ ); magnitude of each indicates the strength of the density-dependent relationship. (□) Slopes not significantly different from zero, suggesting mortalities at these ages were independent of density

### Environmental correlates of critical densities

Despite there being some evidence in some age classes that mortality increased with density at different rates on some beds, in most stages the beds shared a common slope. In general the rate of increase in mortality with density did not vary along the environmental gradient. However, in all but 3 cases (5th summer and 8th and 9th winters), the critical densities at which the density-dependent mortality began to take effect, measured as the intercept with the  $x$  axis, did vary among beds (Fig. 6). In this strongly regulated population, these critical densities represented both the densities above which the density-dependent mortality operated and the densities to which numbers tended to return at the end of each stage, regardless of the numbers present at the beginning. It is important therefore to determine why these levels, and hence the abundance of each adult stage, differed among beds.

The variation in critical densities that occurred among adult stages on one bed and among beds at one age is illustrated in Fig. 6. On Bed 31, the critical density in summer declined steadily with age

while, in winter, it declined only in the older stages (Fig. 6a). Critical densities in the 2nd year increased with exposure time (distance up-shore) up to a limit (Fig. 6b). These patterns are typical of most ages and beds, although the actual values of the critical densities varied between them.

Fig. 6b shows how the variation among beds in critical densities might be related to factors that, amongst them, define the species' environmental gradient. The critical densities on each bed at each age and season were measured as the  $x$  intercepts of the density-dependent mortality function in those ages and seasons for which there was good evidence that bed differences in intercept did, in fact, occur. This was done by applying to each bed, age and season the common slope that had been estimated from Model 2 and calculating the resulting intercept on the  $x$  axis. The critical densities for different beds at each age and season were then regressed against bed exposure time, distance up the Exe and substrate softness. Fig. 7 plots the resulting partial regression coefficients, standardized by multiplying each by the standard deviation of the parameter values. In both summer and

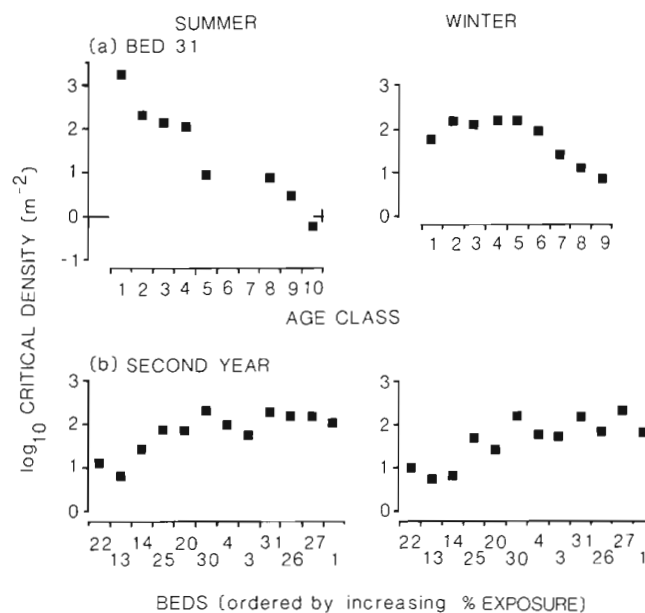


Fig. 6. Critical densities of mussels above which density-dependent mortalities operated; examples chosen to illustrate the variation in critical densities with age, season and bed. (a) Critical densities at each age in summer and winter for Bed 31; (b) critical densities on each bed, ordered by increasing distance upshore or % exposure time, in summer and winter for 2nd year mussels. No values are given for mussels in their 6th and 7th summers on Bed 31, as the slopes of the Model 2 relationships were not significantly different from zero (see Fig. 5)



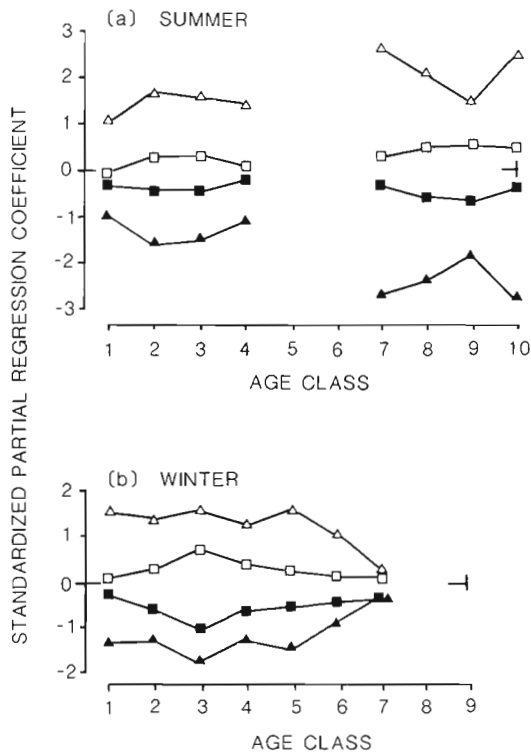


Fig. 7. Environmental correlates of critical densities: standardized partial regression coefficients ( $sprc = b \times SD$ ) for the 3 environmental variables: distance upshore [as the quadratic in exposure, exposure ( $\Delta$ ) – exposure<sup>2</sup> ( $\blacktriangle$ )],  $\log_{10}$  distance up-estuary ( $\blacksquare$ ) and  $\log_{10}$  substratum softness or muddiness ( $\square$ ) are plotted for mussels of each age class in (a) summer and (b) winter. Partial regression coefficients were derived from multiple regression analyses using critical densities calculated from Model 2; hence the missing data for periods when only Models 1 or 3 applied (see Fig. 4). Magnitude of the sprcs indicates the relative size of the effects of the 3 variables on the critical densities at each age

winter (Fig. 7a, b), the quadratic in exposure (exposure – exposure<sup>2</sup>) had the largest standardized coefficients, and therefore the largest effect on the critical densities, and was significant at almost all ages. Distance up the Exe had small negative values and substrate softness small positive values, but these variables had a significant effect only at some ages, which varied between summer and winter. These patterns were generally repeated when critical densities were calculated as the initial densities of all adults combined, rather than of just the age class in question; the only difference was that substrate softness failed to reach the 5% significance level at any age in summer. Hence, in both summer and winter and at most ages, critical densities were highest on those beds lying within the middle of the range of exposure time. At some ages, critical densities were also higher on beds near the sea with softer, muddier substrates.

While providing evidence that critical densities varied with environmental factors, these tests do not enable us to easily visualise how the critical density at each age varied with each of the factors which, between them, defined the environmental gradient across the 12 beds. This can be done from the multiple regression equations by inserting values of 1 variable across its observed range while holding constant the values of the other 2 at their mean level. The predicted critical densities at each age and season show the shape and direction of density changes across the range of each environmental variable as well as the relative magnitudes of the densities at each age and season.

Critical densities bore a curvilinear relationship with exposure time in both summer (Fig. 8) and winter (Fig. 9) and, in general, decreased with increasing age. The location of the peak along the exposure time axis also varied among stages. For example, the critical densities of spat and adult mussels, up to their 6th winter, peaked on beds lying just above 30% exposure time, while those of older mussels peaked at a lower shore level. Critical densities declined linearly with distance up the Exe estuary, but the trend was significant ( $p < 0.05$ ) only in the youngest and oldest mussels in summer and in young adults in winter (Figs. 7, 8 & 9). Critical densities also increased linearly as the substrate became softer, but again only significantly so in some age classes. Exposure time was thus the most important component of the environmental gradient that determined the critical densities above which density-dependent mortalities operated, although at some ages its effect was modified by the distance of the mussel bed from the estuary mouth and by the softness of its substrate.

#### Weather correlates of density-independent mortalities

The residual variations about the density-dependent mortality relationships defined by Models 1 to 3 certainly included error fluctuations. They may also have included additional density-independent mortalities associated with annually varying environmental variables, particularly the weather. If so, the residual mortalities would be expected to co-vary across all, or most, beds. In fact, only 57% of between-bed correlations of residuals were positive and very few (7%) were significant, at  $p < 0.05$ . Either groups of beds were affected differently by the weather, or the pattern of variation in the residuals was determined mainly by error fluctuations. This was tested by analysing groups of beds separately. We expected, for example, that the beds lying at the lowest levels of the shore (Beds 13, 14 and 22), or those furthest up the estuary (Beds 13, 14,

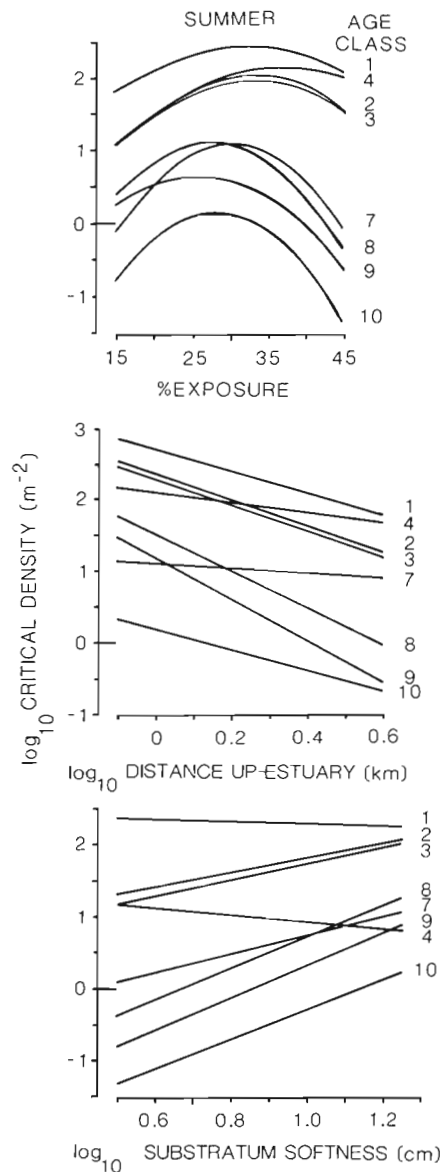


Fig. 8. Variation in critical densities at each age in relation to each of the environmental factors which, between them, define the environmental gradient across the 12 beds in summer. Critical densities were predicted from multiple regression equations by inserting values of one variable across its observed range, while holding constant the values of the other two at their mean level

20 and 22), might be less affected by the weather than those lying at higher levels, or nearer to the sea. Principal Components Analyses revealed that the first 3 axes, according to age and season, explained 74 to 86% of the variation in the residual mortality. However, plotting the 3 axes against each other produced, in most cases a wide scatter of points, there being no consistent pattern of outliers across all mortalities. Any density-independent losses of adult mussels due to

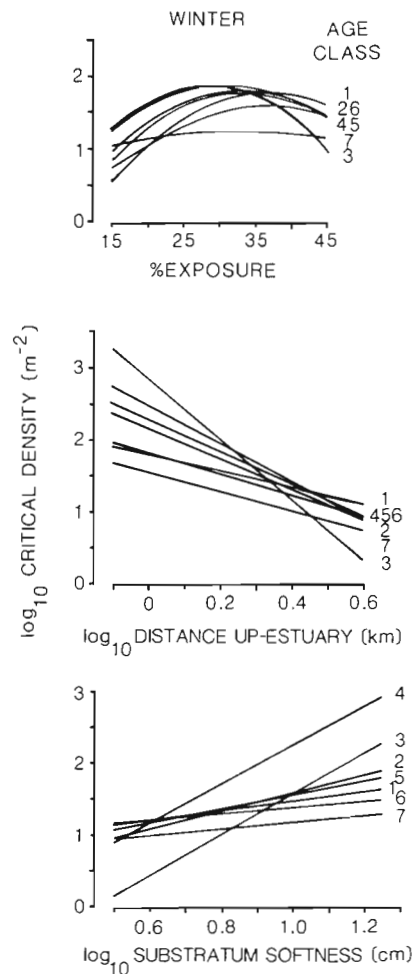


Fig. 9. Variation in critical densities at each age in relation to each of the environmental factors which between them define the environmental gradient across the 12 beds in winter.

weather factors seemed likely only to explain a small proportion of the residual variance.

This was tested by multiple regression of the residual mortalities for each age, across all beds combined, against air temperature, wind strength and rainfall for the appropriate season. There were no significant inter-correlations between these weather variables for the 8 yr of the study (all values of  $r < r_{p0.05} = 0.7$ , for  $df = 6$ ). As expected, the analysis explained little (<25%) of the residual variance. Nonetheless, as plotting the standardised partial regression coefficients against age shows, there were some significant effects ( $t$ -tests,  $p < 0.05$ ) at some ages and seasons (Fig. 10). Temperature was correlated with residual mortalities in young mussels up to their 5th year in summer and winter, but not in older mussels. However, the sign of the relationship varied. In summer, 4th and 5th year mussels showed a significant negative relationship with temperature, indicat-

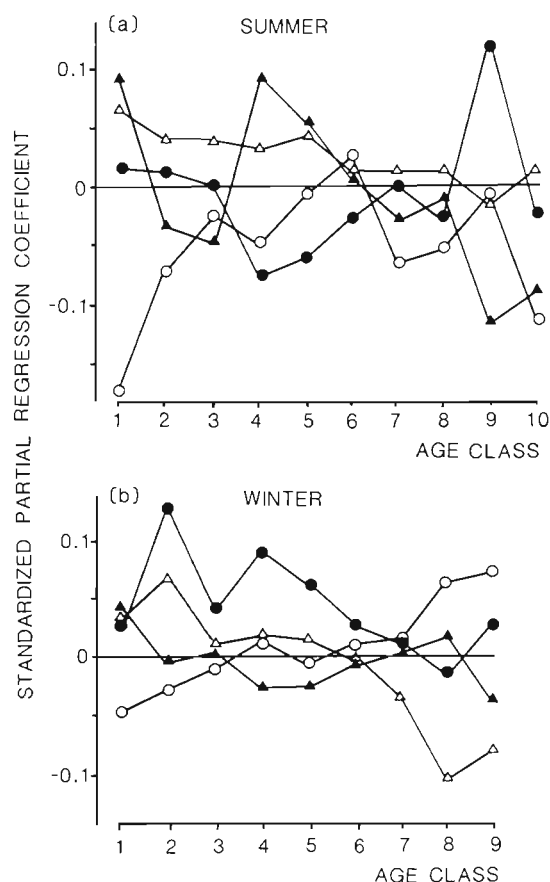


Fig. 10. Weather correlates of density-independent mortalities: standardized partial regression coefficients ( $sprc = b \times SD$ ), derived from multiple regression analyses of the residual variations about the density-dependent mortality relationships across all beds combined (defined by Models 1 to 3 as appropriate, see Fig. 4) against the quadratic in air temperature [ $^{\circ}C$  (●) +  $^{\circ}C^2$  (○)], wind strength expressed as frequency of gales (▲) and rainfall (Δ) plotted for each age between the 1st (spat) and 10th years of life in (a) summer and (b) winter periods. Magnitude of the sprc of each of the 3 weather variables indicates the relative size of their effects on density-independent mortality at each age

ing more died in years when temperatures were unusually low. First and 2nd year mussels also showed a significant negative relationship, but only in the quadratic, indicating that more died in years when temperatures were unusually low or high. In winter, the residual mortalities of 2nd to 5th year mussels showed a positive relationship with temperature, indicating that more young adults died in years when temperatures were unusually high. Rainfall also had significant effects on residual mortality but again with a varying sign. It had a positive effect in the 1st and 5th summer and the 2nd winter, suggesting that more young mussels died in years with higher than average rainfall. In contrast, it had a negative effect in the 8th winter, implying that more of these older

mussels died in years with less than average rainfall. The incidence of gales had a significant and always positive effect on the residual mortality in the 1st summer and winter and 4th summer, indicating that more died in years when gales were more frequent. There is therefore some evidence that the density-independent fluctuations around the underlying density-dependent relationships, particularly in young mussels up to their 5th year, were related to annual variations in the weather to which they were exposed over the low water period.

### Immigration

The many (37%) negative adult  $k$ -values (Fig. 3) could have been due to errors in estimation or to the immigration of adult mussels. Although sampling errors were undoubtedly large, especially on small beds where few samples were taken (McGrorty et al. 1990), frequent small changes in bed shapes occurred and we occasionally observed small clumps of mussels being washed onto some of them, suggesting that at least passive movements occurred. At first sight, there was little direct evidence of significant seasonal increases in density attributable to adult immigration. Mean density estimates of particular age classes were significantly higher ( $t$ -tests,  $p < 0.05$ ) at the end of summer or winter than at the beginning in only 62 cases. This is equivalent to only 4% of all bed/age/seasonal combinations available, though significantly higher than the 2.5% that would be expected for a 2-tailed  $t$ -test on the basis of chance alone.

Detailed examination suggests, however, that immigration might have occurred on many occasions. Fig. 11 shows, for each bed and age class in summer and winter, the number of years out of the 7 studied when the  $k$ -value was negative. In the absence of mortality, immigration or emigration, unbiased sampling errors alone would be expected to result in an equal number ( $7/2 = 3.5$ ) of apparent increases and decreases in density over the summer or the winter period. But as mussels die in both summer and winter, the null hypothesis is not that  $k$ -values should be negative in half the years, but in less than half the years, although by an unknown amount for each age class. Increases in density in more than half of the years, therefore, provide evidence for immigration. Visual inspection of Fig. 11 reveals that densities of 1 to 9 age classes on all 12 beds in summer and of 1 to 5 age classes on 9/12 beds in winter increased in more than half of the years (Fig. 11, ▲). This suggests that immigration was more common than indicated by the much smaller number of occasions (Fig. 11, Δ) when the comparison between the densities present at the start

and end of a period showed a significant increase ( $t$ -tests,  $p < 0.05$ ). Immigration was apparently more common among younger (2 to 5 yr) than older mussels and occurred widely in both summer and winter. It was, however, especially common in summer on the large, muddy, up-estuary beds (Beds 20, 25 and 26)

and in winter on the 3 beds nearest the sea (Beds 1, 30 and 31), when mainly older mussels were involved. Immigration of mussels is therefore not just a first year phenomenon associated with recruitment but, in the Exe, also occurs in adults. Without independent measures of adult migration rates, their  $k$ -values

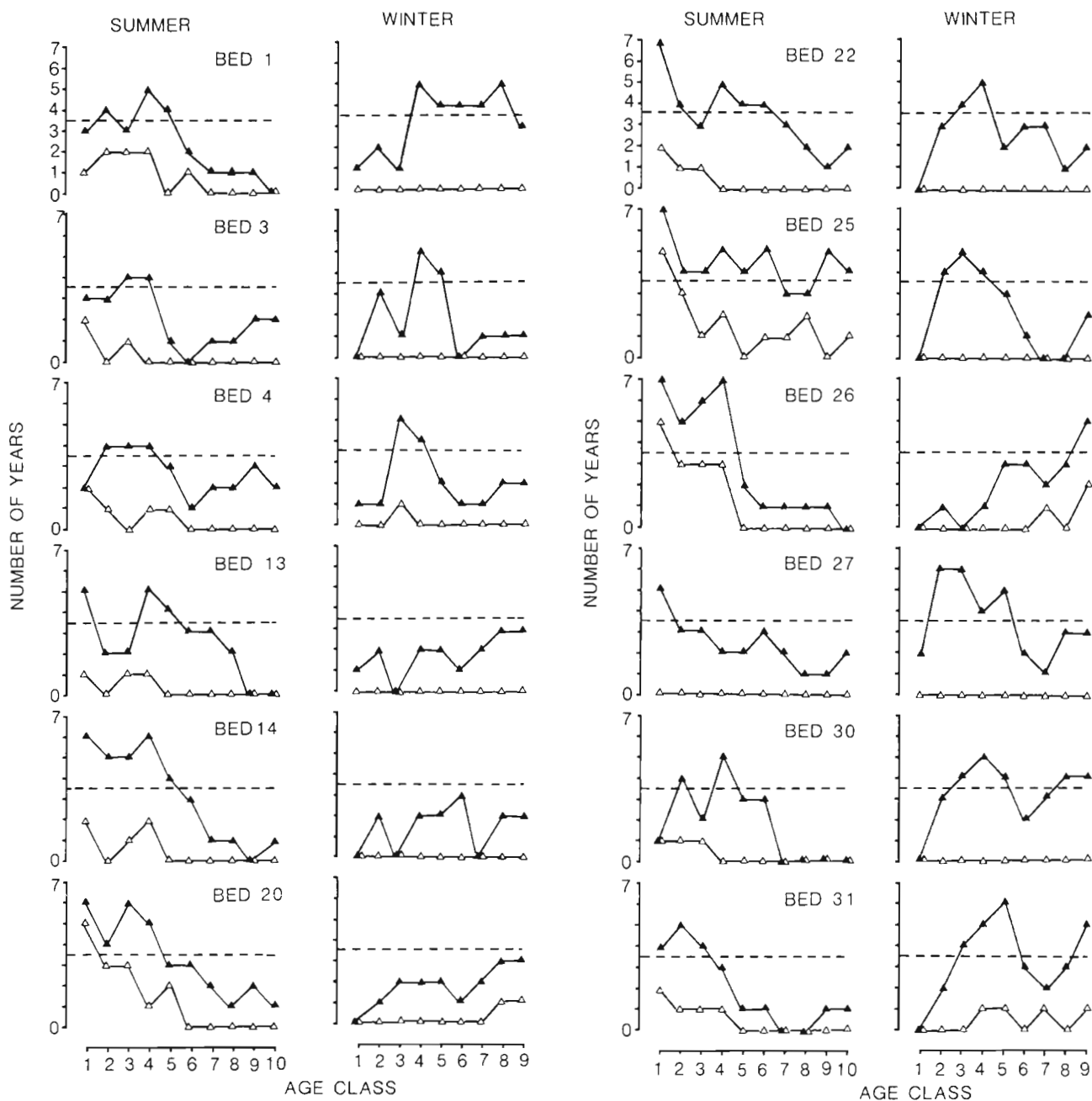


Fig. 11. Immigration: for each bed and age class the number of years out of the 7 studied ( $\Delta$ ), is plotted for which there was a significant increase in density ( $t$ -tests,  $p < 0.05$ ) over summer and winter periods. Also plotted is the number of years ( $\blacktriangle$ ) for which the estimated population density increased during a season, regardless of whether the increase was statistically significant. Values above the dashed line, indicating half of the years, support the hypothesis of adult immigration onto the beds

should perhaps be regarded more as net losses than mortalities in the strict sense.

## DISCUSSION

### Density-dependent mortality and the initial density problem

There are a number of well-known mortality agents of mussels which occurred in the Exe estuary (McGrorty et al. 1990). Mussels were smothered by mud after river floods, buried by storm-driven sand and torn from the beds and cast ashore during gales, but such events were sporadic and unpredictable. In summer, many older adults died after spawning, possibly as a result of acute physiological stress (Worrall & Widdows 1984), while younger (smaller) adults were eaten by shore crabs *Carcinus maenas*. In winter, the main predator of adult mussels was the oystercatcher *Haematopus ostralegus*, though shore crabs remained inshore if the weather was mild (Beukema 1991). No humans fished for mussels from these beds during the study, and other common predators of mussels, e.g. dogwhelks and starfish, were rarely found in the estuary. We have no data on mortality caused by parasites or disease organisms, but we also have no reason to suspect that they were important. The most likely agents of density-dependent mortality in adult mussels were the 2 common predators mentioned above, *C. maenas* and *H. ostralegus*.

The question that we must ask, however, is not just what the mortality agents were, but why in a mixed age population was the mortality of a particular age class more often only related to its own initial density than to the density of other or all adults? In other words, as the density of a particular age class increased above its critical density, why should individuals of that age class have died as opposed to individuals of other age classes, younger or older? Intuitively, one would expect mussels to interact with their immediate neighbours in the clump or patch, irrespective of age or size; for example, in competing for food (as filter feeders), space or other resources. Indeed, mussels at high densities and in the centre of clumps grow slower than those at low densities and the edges of clumps (Bertness & Grosholz 1985, Okamura 1986, Lin 1989) and there was much variation in length at each age within and among beds in the Exe (S. McGrorty unpubl.). However, competition for food was unlikely to lead to mortality, except perhaps in the summer after spawning. Examination of dense mussel clumps showed that small mussels live within the matrix of spaces between larger mussels and may therefore, for example, feed from water at different levels within the bed, perhaps thereby reducing

competition among different size and age classes, but at the same time increasing competition for suitably sized spaces among individuals of the same size and age class.

Okamura (1986) also showed that mussels at the edge of a clump were more susceptible to predation than those at the centre, while Boulding & Hay (1984) showed that crabs preferentially forage in areas of higher prey density. However, another aspect of selective feeding by their predators may also be important in explaining which mussels were more likely to die when the density of a particular age class increased. Crabs of all sizes will eat mussels, but the size of prey is closely linked to the size of the crab (Walne & Dean 1972). Each crab preferentially selects only a narrow range of sizes of prey, thereby optimising intake, but will eat suboptimal prey. However, each encounter with the preferred size reinforces its preference and more suboptimal prey will be rejected before another prey is chosen (Elner & Hughes 1978). Likewise oystercatchers could eat almost any adult mussel, but are selective. In winter they prey mainly on 4 to 6 cm mussels, but in spring take smaller mussels (>2 cm) as larger ones begin to spawn and become less profitable (Cayford & Goss-Custard 1990). Furthermore, depending upon the method used to open a mussel, individuals may select from only a part of the potential prey population available to them. For example, those oystercatchers that break the shell ('hammerers') as opposed to 'stabbing' between the valves select only those mussels with thinner than average shells (Durell & Goss-Custard 1984). If, as seems likely, these are predominantly young, fast-growing individuals and old individuals with highly eroded shells, then the actual prey eaten by these oystercatchers may be derived predominantly from only a limited number of year classes.

This hypothesis of selective predation by groups of predators distinguished by size or feeding technique is realistic, and if true, points to a sharply focused mortality of preferred prey, that is, single age classes or small groups of age classes with overlapping size distributions rather than mortality acting generally across all adults. The finding that those significant density-dependent relationships that explained the greatest proportion of the variance in mortality occurred more often among the mortalities of particular age classes and their own initial densities than against the combined densities of all adults is therefore reasonable, if at first surprising, in a highly aggregated mixed age population. In reality, the mortality of a particular age class is probably related to its own density plus some fraction of younger and older age classes, but we do not know what these fractions are and are therefore unable to calculate the true initial density. Clearly, however, the initial density of the particular age class was a better measure in most

cases than the total density of adults and we used these relationships in further analyses. In practice, there was actually little difference in the conclusions of those analyses, whichever initial density was used.

### Regulation of the adult mussel population

Large annual fluctuations in mussel spat settlement in the Exe estuary were severely dampened by a powerful 1st winter density-dependent mortality (McGrorty et al. 1990), and the total adult population was remarkably stable throughout the study. However, the densities of the various components of the adult population did vary, for example by up to  $\pm 25\%$  among years in young adults < 5 yr old, so it was surprising that the only evidence of density-dependence at the estuary scale was in the 2nd winter and 10th summer. The first aim of this paper, therefore, was to test whether density-dependence was more common among adults at the smaller scale of individual beds than appeared to be the case at the estuary scale. Evidence of density-dependent mortality was indeed widespread across beds at all ages. There was direct evidence of strong density-dependence in 44% of the adult year class/mussel bed combinations in summer and in 33% in winter. Combining the data from all beds provided further, indirect evidence of widespread density-dependence in adult mussels. Particular age classes either shared a common density-dependent relationship across all beds (Model 1, 4 cases), or shared a common slope but separate intercepts (Model 2, 8 cases), or had separate slopes and intercepts for each bed (Model 3, 5 cases). There was therefore some evidence of density-dependent mortality across all of the beds at each adult stage.

Except in the 4 cases of a common relationship across all beds, there was considerable variation among beds in the critical densities at which mortality began to be density-dependent. Since the critical density is both that above which the strong density-dependent mortality operates and the value to which density will tend to return after the mortality has acted, variation in critical densities was an important factor in determining the wide variation in the average abundance of adult mussels on each bed within the Exe estuary (McGrorty & Goss-Custard 1991). Critical densities varied mainly in relation to tidal inundation, or the distance upshore, with peak densities occurring at between 25 and 38% exposure time. Though varying with age and season, in general the highest critical densities of spat and young adults occurred on beds lying above 30% exposure, while those of older adults peaked at lower levels. Since up-estuary beds tended to be exposed for a shorter time than beds near the sea

(distance up the Exe vs exposure,  $r = -0.65$ ,  $p < 0.05$ ), the spatial variation in critical densities along the environmental gradient also explains the net displacement of mussels up the estuary with increasing age (McGrorty & Goss-Custard 1991). It is clear that an earlier conclusion (McGrorty & Goss-Custard 1993) that the spatial variation in adult mussel densities was due to the powerful 1st winter density-dependent mortality and the variation in the critical densities of recruits along the environmental gradient was only partially correct. Adult densities are themselves also regulated by strong density-dependence throughout life and the critical densities of adults also vary along the same environmental gradient, principally in relation to exposure time.

At the scale of 1 bed, mussels were thus subject to density-dependent mortality throughout their life. At each age, the density-dependence was moderately strong to near perfect [slopes ( $b$ ) = 0.36 to 0.94] in at least 1 season. However, at the estuary scale, it was only detected in the 1st and 2nd winters and 10th summer (McGrorty et al. 1990). This pattern may be common among populations with patchy distributions. Jones et al. (1987) found little evidence of density-dependent mortality in the cabbage butterfly *Pieris rapae* L. at the field scale, but found strong evidence within some patches of plants. Likewise, although Southwood & Reader (1976) failed to detect density-dependence in the viburnum whitefly *Aleurotrachelus jelinekii* (Frauenf.) on 3 bushes, it was later discovered at the scale of individual leaves (Hassell et al. 1987, Southwood et al. 1989). Clearly, density-dependence may occur in some sub-populations but not in others and, despite its detection at a small scale, may not be detected at a larger one.

Nonetheless, it is still surprising that, in the Exe, density-dependence was not more widely detected at the estuary scale when it was detected so widely at the bed scale. Its detection at both scales in the 10th summer can be easily understood, since so few individuals survived until autumn, regardless of the densities in spring, so that there was inevitably a close association between the mortality and initial density ( $k_{10s}$ ,  $\log N$ ;  $b = 1.09$ ,  $r = 0.71$ ). This does not apply in the 1st and 2nd winters, however. At the beginning of their 1st winter, an average 68% of the spat that had successfully settled in the estuary during summer occurred in just 2 beds (30 and 31) and were then subject to a near perfect, density-dependent, over-winter mortality ( $b = 0.96$  and  $0.74$ ; McGrorty & Goss-Custard 1993). The density of spat on these 2 beds also varied in a very similar manner among years ( $r = 0.88$ ,  $p < 0.01$ ). The large, over-winter, density-dependent mortalities on these 2 beds swamped any contrary temporal variation in the mortality on the



remaining beds, thus dominating spat dynamics at the larger estuary scale.

Though the dominance of Beds 30 and 31 declined during adulthood, it still had an important influence during the 2nd winter; an average 45% of 2nd-winter adults occurred on these 2 beds and densities co-varied in 6 of the 7 yr. During the 4 winters when densities were highest (1979/80 to 1982/83), mortalities on these 2 beds and on another large, seaward bed (26) were sufficiently large enough to counter increases in density elsewhere in the estuary; the 2nd-winter mortality was thus significantly density-dependent ( $t$ -tests,  $p < 0.05$ ) at the estuary level. Again, the detection of density-dependence at the estuary scale was due to the dominating influence of a few large and dense beds.

In later years, the dominance of Beds 30 and 31 declined further as the percentage of each age class occurring on them declined to 32%. In addition, density changes on them as well as on other beds were also frequently of opposite sign (Fig. 12). As a result, for most ages and seasons, adult mortalities on the

different beds did not follow the same pattern among years; for example, 22 of the 66 correlations between the 2nd summer mortalities ( $k_{2S}$ ) on all combinations of pairs of beds were negative, as were 30 for the 3rd winter mortality ( $k_{3W}$ ). Thus, mortalities on some beds were countered by immigrations on others, reducing the range of variation in density at the estuary level compared to that on individual beds; for example, compare the 1.8-fold variation at the estuary scale for 4 yr old mussels with the 2.3- to 21.3-fold variations found on individual beds. This buffering undoubtedly prevented density-dependence at the estuary scale from being detected.

At least a third of the increases in density that occurred in individual beds could have been the result of immigration rather than of sampling errors. Interestingly, immigration often had opposite effects at the 2 scales considered. While masking density-dependence at the estuary scale, it was an important element of the relationships found on many individual beds and may have contributed significantly to population stability (Lomnicki 1980, Ambrose 1986).

However, while the movement of mussel clumps by storms is well known (Seed 1976), it is not known whether adult mussels can deliberately detach themselves and move elsewhere. Whatever the process involved, the importance of migration can only be accurately assessed by direct measures of emigration and immigration rates.

### Density-independent mortality

The second aim of the study was to test whether, with the influence of density-dependent losses taken into account, there were residual density-independent losses from year to year whose magnitudes were related to variations in the weather. Evidence for this was found in mussels up to their 5th year. The greater losses of young mussels in years with more gales and higher rainfall were probably due to the direct effects of dislodgement or burial by river-borne silts (liquid mud). The greater losses of mussels in their 1st and 2nd summers in warmer than average years could have been a direct result of the weather or an indirect result of increased predation. The greater losses in warm winters were also probably due to epibenthic predators, such as crabs (Beukema 1991, 1992, McGrorty & Goss-Custard 1993) that migrate offshore in winter but remain inshore

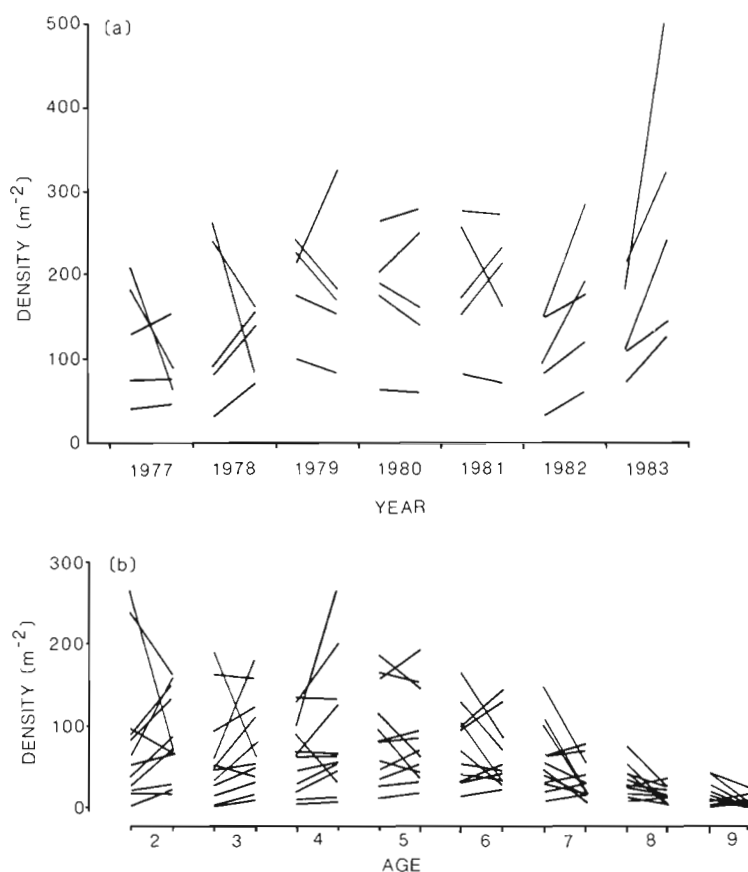


Fig. 12. Changes in density (a) of second year mussels over the summer on 5 large/dense beds in 7 successive years and (b) of adult mussels of all ages between their 2nd and 9th years on all beds during summer 1978

longer and return earlier in mild winters. On the other hand, there is no obvious explanation for the greater losses of young mussels in cool summers, unless food supplies are reduced and competition between mussels within clumps (Okamura 1986, Svane & Ompi 1993) is increased. Whatever the mechanisms involved, there was evidence of weather-related, density-independent losses of young adult mussels, in addition to the density-dependent losses occurring at the bed scale, throughout the estuary.

In conclusion, there was evidence of strong density-dependent regulation of the adult mussel numbers at all ages and on all beds, but this was rarely detected at the estuary scale. Although much of the density-dependence was due to mortality, probably by crabs and oystercatchers, immigration was an important component of the relationships on many individual beds. However, immigration on some beds countered losses on others, so that density-dependence was masked, and thus not detected, at the estuary scale.

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