Experimental Demography of the Sand-Dune Annual, *Cakile Edentula*, Growing Along an Environmental Gradient in Nova Scotia

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**SUMMARY**

1. A method of analysis is proposed to test whether differences in survivorship of a given species among two or more habitats are the result of variation among the habitats in environmental factors (density-independent effects), or in species density (density-dependent effects).

2. The method requires that a range of seed densities of the species be sown in a given habitat, and survivorship and reproductive output measured for each sowing density. If a straight line with negative slope can be fitted to the survivorship vs. sowing density relationship, then the survivorship y-intercept of the line is an estimate of density-independent mortality, and the slope is an estimate of the density dependence of mortality.

3. If this analysis is carried out for the species growing in several habitats, it is possible to test whether intercepts or slopes (and consequently density-independent or density-dependent effects) differ among habitats. A similar analysis can be carried out for reproductive output.

4. The annual plant *Cakile edentula*, a common species on sand dunes in eastern North America, is used as an example. Three experimental sites along a sand-dune gradient were each sown with seeds at a range of densities and survivorship and reproductive output measured for each density at each site.

5. The density dependence of survivorship changed significantly ($P < 0.001$) along the gradient (among habitats), whereas density-independent mortality stayed constant.

6. Significant differences ($P < 0.001$) were observed for both density-independent and density-dependent effects on reproductive output.

7. The effects of density on survivorship were greatest at the landward end of the gradient, whereas the effects of density on reproductive output were greatest at the seaward end.

**INTRODUCTION**

The problem of determining the relative importance of density-dependent and density-independent factors in regulating population size in plants and animals remains a central issue in autecological studies. It has been noted (e.g. Harper 1960, 1967) that plants respond to increased density either by phenotypic plasticity or mortality. A mortality response implies density-dependent mortality; a plastic response implies density-dependent reproductive output. Thus a plant population may, in theory, be regulated by either density-independent or density-dependent effects, acting on either mortality or reproduction. Watkinson & Harper (1978) concluded that in the sand dune annual *Fulvia fasciculata*, population dynamics could be described in terms of density-independent mortality and density-dependent reproduction. In species of *Papaver* (Harper & McNaughton 1962) and *Bromus* (Wu & Jain 1979), both density-dependent mortality and density-dependent reproduction were observed. Putwain, Machin & Harper (1968)

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concluded that *Rumex acetosella* populations were regulated mainly by a density-dependent reduction in vegetative reproduction.

The degree of density dependence may vary with both biotic and abiotic environmental conditions. Pemadasa & Lovell (1974b) showed that the effects of density on seedling establishment and tiller production in four dune annuals (*Aira caryophyllea, A. praecox, Cerastium atrovirens* and *Vulpia membranacea*) vary with both soil nutrient status and interspecific crowding. Keddy (1980) found that *Cakile edentula* plants growing on open shingle beaches exhibited density-dependent reproductive output but density-independent mortality (as in *Vulpia fasciculata*). When the shingle was covered by thick mats of decaying *Zostera marina*, however, both mortality and reproductive output varied with density. In their study of *Papaver* spp, Harper & McNaughton (1962) found that experimental plots of different exposure produced different density responses for both mortality and reproductive output.

Similarly, the degree of density dependence may differ among species. Harper & McNaughton (1962) found that density-independent and density-dependent effects on survivorship were not significantly different among the five *Papaver* species examined: reproductive output (as measured by number of capsules per plant) differed among species, but the degree of density dependence of reproductive output did not. Wu & Jain (1979) also found between-species differences in density-dependent effects: *Bromus rubens* showed greater density-dependent mortality and less density dependence of reproductive output than did *B. mollis*. Pemadasa & Lovell (1974b) observed among-species differences in the effects of density on both seedling establishment and tiller production of four dune annuals.

Thus, among species, there appears to be considerable variation in the importance of environmental factors and of density in determining reproductive output. Moreover, the degree of density dependence appears to vary with environmental conditions such as nutrient status, interspecific crowding, exposure and the presence of decaying organic matter. It may be difficult to separate these effects in field studies. It may be that variation in density among habitats is correlated with variation in environmental factors, making it impossible to separate density-dependent and density-independent effects on survivorship and reproductive output. Precisely this problem was encountered in an autecological study of *Cakile edentula* (Bigel.) Hook. This annual member of the Brassicaceae is common on sand dunes along the eastern coast of North America (Rodman 1974). The species is well-suited to studies on demography, as it is a short-lived annual, seedlings germinate synchronously in the spring, individual plants are discrete, and they produce large easily-counted fruits. Plants can be found growing in a wide range of habitats, and these habitats are arranged along an environmental gradient stretching from open sandy beach (seaward) to densely-vegetated dunes (landward). A 2-year study of naturally-occurring populations (Keddy 1978) showed that the density of *C. edentula* plants varied along this gradient and that there were also significant differences in survivorship and reproductive output. Density was highest near the middle of the gradient; survivorship and reproductive output were both highest on the open sand and decreased significantly landward. This finding raised the question: how much of the observed variation in survivorship and reproductive output was the result of variation in population density, and how much was the result of environmental factors?

For example, mortality caused by large pieces of debris tossed about by storm waves might be expected to be independent of plant density, and to be of decreasing importance landward. Damping-off disease is density-dependent (Burdon & Chilvers 1975a, b, 1976), and mortality might, therefore, be highest near the centre of the gradient where seedling
densities were the highest. The degree of density dependence might also differ among habitats, however, if (for example) soil moisture differed, and the rate of spread of damping-off disease were correlated with soil moisture. Dry habitats with high seedling density might have far less density-dependent mortality than would moist habitats with much lower seedling density. Similarly, differences in nutrient supply among habitats might affect plant size. In high-nutrient habitats, large plants would interact at low density (with a density-dependent effect on seed production), whereas in low-nutrient habitats, small plants at similar density might not interact at all (no density-dependent effect on seed production). Thus, in the study of *Cakile edentula*, correlations between density and survivorship or reproductive output were confounded by the marked heterogeneity in habitat which occurred along the gradient. Plotting mortality and seed production against density, as was done by Watkinson & Harper (1978), implicitly assumes that there is no strong correlation between density and environmental conditions. This may rarely be true.

The relative importance of density-independent and density-dependent population regulation has become important in another area of ecology: the evolution of life-history traits. Theory predicts that organisms exposed to high density-independent mortality will be selected for earlier maturity, larger broods, higher reproductive efforts and shorter life-spans than will organisms exposed to density-dependent mortality (MacArthur & Wilson 1967; Pianka 1970; Stearns 1977). The two extremes are known, respectively, as r- and K-selection.

In a recent review, Stearns (1977) examined published studies on the evolution of life-history traits, and assessed each study according to six criteria of reliability. One criterion was whether the author attempted to measure the degree of density-dependent or density-independent regulation. Stearns concluded that only one out of the fifty-two studies met this criterion, and even suggested that the requirement that the degree of density dependence be measured 'seems to have been asking too much'.

To study the role of density in population regulation, curvilinear regression has been used. Harper & McNaughton (1962) fitted a quadratic equation to relate the number of plants produced to sowing density; they pointed out that the linear term in their quadratic fit was 'a measure of the chance that a seed will produce a plant irrespective of sowing density', and the squared term represented 'a measure of the role of density in affecting establishment'. Putwain, Machin & Harper (1968) used a more complex regression model to examine yearly changes in population size, but concluded: 'it is relatively easy to derive regression equations that relate population sizes at different sampling times, but it is much more difficult to assign firm biological meaning to the individual regression coefficients'.

In the present paper a different (although related) method is proposed to make analysis and interpretation more straightforward. It measures and tests for among-habitat differences in the relative importance of density-independent and density-dependent factors affecting survivorship and reproductive output. The method is then applied to the sand dune population of *Cakile edentula* described above. In addition, the analysis is extended by experimentally modifying one environmental variable (nitrogen supply) and testing whether this modification affects survivorship and reproductive output in a density-independent or density-dependent manner.

**METHOD OF ANALYSIS**

*A simple model*

A small homogeneous area is selected, divided into plots, and sown with seeds at a different density in each plot. The densities range from very low to very high, and for each
the proportion of plants surviving (to produce seeds) is measured. If it is assumed that the proportion of plants surviving shows a linear decrease with increasing density (Fig. 1), then

$$p = i_p - s_p N \quad \text{(for } s_p > 0)$$

(1)

where $p =$ proportion surviving and $N =$ sowing density. The y-intercept, $i_p$, measures the proportion of plants which would survive at zero (optimum) density, that is, the proportion of plants which would survive in the absence of any density-dependent effects. The slope, $s_p$, is related to the intensity of intraspecific competition: the greater the magnitude of $s_p$, the greater the reduction in the proportion of plants surviving as density increases.

![Diagram](image)

**Fig. 1.** The results of a conceptual experiment: proportion of plants surviving ($p$) plotted against sowing density ($N$). The proportion dying at any given sowing density ($m_{tot}$) is equal to the sum of the proportion dying irrespective of sowing density ($m_l$) plus the proportion dying from density-dependent effects ($m_d$).

As Fig. 1 shows, total mortality at a given density, $m_{tot}$, can be divided into two components, $m_l$ and $m_d$. These are determined by the intercept and slope of the line. The component $m_l$, which is independent of sowing density, is the proportion of plants which die in the absence of intraspecific competition: its magnitude depends entirely upon environmental properties, and not upon sowing density. The component $m_d$, which is a linear function of $N$, the sowing density, measures the proportion of plants which will fail to survive due to competition at a given density.

Now assume that some measure of reproductive output is obtained for the adult plants produced at each sowing density; and that reproductive output, $b$, is also a decreasing linear function of density:

$$b = i_b - s_b N \quad \text{(for } s_b > 0).$$

(2)

In a manner analogous to the preceding analysis of the proportion of plants surviving, it is possible to determine for a given habitat both the reproductive output in the absence of competition, $i_b$, and the density-dependent factor for reproductive output, $s_b$.

Unless the maximum possible reproductive output for a plant is known, however, (which in practice it never is), it is impossible to proceed further and to determine the actual reduction in reproductive output caused by density-independent and density-dependent factors. This contrasts with survivorship, where the maximum possible value is known to be 1-0, when all the seeds sown survive.
Among-habitat comparisons

Assume that the previous conceptual experiment is carried out in each of three different habitats, and that the proportion of plants surviving is a linear function of sowing density in each habitat. Comparison of the values of the slopes and intercepts derived for each habitat will show whether the three habitats differ from each other in density-independent and density-dependent factors. Figure 2 shows four possible outcomes of this conceptual experiment.

(a) Intercepts and slopes identical (the three lines are coincident): no difference among habitats in density-independent mortality and no difference in degree of density dependence.

(b) Intercepts the same, slopes different: no difference in density-independent mortality, but the degree of density dependence differs among habitats.

(c) Intercepts different, slopes the same: density-independent mortality differs among habitats, but there is no difference in degree of density dependence.

(d) Intercepts and slopes different: both density-independent mortality and degree of density dependence differ among habitats.

![Figure 2](image)

**Fig. 2.** Proportion of plants surviving plotted against sowing density: four possible outcomes, (a)–(d), of comparisons among three habitats (see text for details).

There are straightforward statistical tests for determining whether slopes or intercepts for a family of lines differ significantly (Graybill 1976).

Again, if some measure of reproductive output was obtained for the adult plants at each sowing density, an analogous procedure could be applied to reproductive output.

Now consider the relationship between the results that might be obtained from natural, as opposed to experimentally sown, populations. Assume that for several populations (each in a different habitat) proportion of plants surviving, reproductive output and initial density of seeds are known. Then, as noted in the Introduction, observed differences in the proportion of plants surviving could be due to differences among habitats in (1) density-independent mortality, (2) density dependence, or (3) initial seed density. Even if factors (1) and (2) were identical for the habitats concerned—that is, in terms of the graphic representation in Fig. 2(a), even if the same line described all habitats studied—each natural population might be represented by a different point on that line, determined by
its initial seed density. Thus, on the basis of single observations of natural populations, it would be impossible to discern which of the above three factors is responsible for the observed differences in demography.

Problems in the application of the model to experimental results

The ultimate aim is to take data describing the relationship between proportion of plants surviving and sowing density for each of several habitats, and to test whether the $y$-intercept and the slope of the lines fitted to the data are different. There are two basic problems in doing so: both are related to difficulties with non-linearity. Extreme non-linearity may render the entire approach invalid, while a smaller problem is that estimation of $y$-intercepts may be difficult.

The use of a linear model to represent density-independent and density-dependent factors is not new: thus Smith (1935), Andrewartha & Birch (1954, Chap. 9) and Wilson & Bossert (1971, Chap. 3) have all represented density-independent and density-dependent factors in a similar graphical manner. The possible problem with this approach is that density dependence may often be non-linear. In fact, Andrewartha & Birch (1954) criticized Smith (1935) for using a linear model to separate density-independent and density-dependent effects (Chap. 2), although they too found it a convenient assumption later in the same book (Chap. 9). Appropriate transformations, such as the logarithm of density, may often reduce this problem, but there is a more basic difficulty, the severity of which will vary from experiment to experiment. In any experiment using a range of sowing densities, at the lower end of the range plants may be too widely spaced to be affected by competition; as density increases, intraspecific competition eventually occurs, and a point of inflection is reached (Fig. 3, middle line). Harper (1977, Fig. 6/3) gives an example of such a relationship in *Trifolium subterraneum*. This critical density, corresponding to the point of inflection, may differ among habitats if plant sizes are very different.

By choosing increasingly complex equations, it will be possible to obtain lines which more closely describe such curvilinearity. Harper (1977) has reviewed some of this work relating yield, survivorship and reproduction to plant density. While curve-fitting is a useful...
tool for summarizing data or describing relationships, as equations become increasingly complex their interpretation becomes more difficult (cf. the earlier-quoted remarks of Putwain, Machin & Harper (1968) on the difficulty of assigning biological meaning to regression coefficients). Simple linear models may sometimes appear less realistic, but, as Fig. 2 shows, they provide a restricted number of possibilities, each with a different biological interpretation. In addition, their statistical properties are well-understood. Thus they provide a powerful tool for hypothesis-testing.

Therefore, with regard to the first problem, limited amounts of curvilinearity may be reduced by using appropriate transformations of density. The fundamental problem—of low non-interactive densities producing a point of inflection—will depend upon the range of densities chosen for the experiment and upon the phenotypic plasticity of the plants involved. Where marked curvilinearity is observed, the above method is inappropriate; curvilinear regression (e.g. Harper & McNaughton 1962) remains an alternative in such cases.

Now consider the problem of estimating y-intercepts. Figure 3 shows several possible relationships in experimentally-sown populations between proportion of plants surviving and initial density. In all cases the y-intercept of the line, \( p(0) \), corresponds to zero sowing density, which is impossible to observe experimentally. Therefore, estimating the y-intercept involves extrapolation beyond the measured results, and, as Fig. 3 shows, the accuracy (and precision) of the value of \( p(0) \) may be low. (An equivalent diagram can be drawn relating some measure of reproductive output to sowing density.)

An alternative to extrapolation is to test whether the lines intersect at the minimum density used in the experiment. In practice, \( p(N_{\min}) \) will presumably approximate the limiting value of \( p(N) \) as \( N \) becomes vanishingly small, especially if \( N_{\min} \) is one plant per experimental plot, and the plot is large enough that the plant grows in the absence of intraspecific competition. There are no mathematical difficulties with this approach; it is possible to test whether a family of lines share a common intercept on any arbitrary y-axis.

Thus the possible options are: (1) to extrapolate each line directly to \( p(0) \), and then to test whether the intercepts differ; or (2) to test whether the lines intersect at \( p(N_{\min}) \), and then to extrapolate from these results to those that might be obtained at zero density.

In the following study of *Cakile edentula*, the latter approach has been used. In this particular study, a log transformation of sowing density provided the best linear fit to the data: the minimum density of one plant per plot therefore became zero on the x-axis.

**APPLICATION TO CAKILE EDENTULA**

The problem was outlined in the Introduction: the survivorship and reproductive output of *C. edentula* decline significantly to landward along an environmental gradient. Density also changes landward, rising to a maximum near the centre of the *C. edentula* distribution (Keddy 1978). Some of this variation in survivorship and reproductive output may be the result of changes in environmental factors. For example, the density of culms of *Ammophila breviligulata* Fern., and the general species-richness of the vegetation, increase landward along the gradient from open sandy beach to densely vegetated dune (Keddy 1978). The findings of Pemadasa & Lovell (1974a) and of preliminary field trials (Keddy 1978) also suggest lowered nitrogen availability inland. From the observation of natural populations alone, however, it was not possible to separate the effects of changes in environmental factors from the effects of changes in density.
Demography of Cakile edentula

METHODS

The study area (Keddy 1978) was on Martinique Beach in Halifax County, Nova Scotia, Canada (44°41’N, 63°7’W). Figure 4 shows a cross-section of this barrier beach.

Mature distal fruit segments were collected at Martinique Beach in autumn 1976, and stored during the winter in mesh bags buried outside in moist sand. These distal fruit segments normally each contain a single seed (Rodman 1974).

The following spring, experimental sites were chosen at three positions along the barrier beach: (1) open sandy beach at the seaward extremity of naturally-occurring C. edentula populations; (2) densely-vegetated dunes at the landward extremity of naturally-occurring C. edentula populations; and (3) a middle region where the density of C. edentula seedlings is normally highest (Keddy 1978). The positions of these three sites are shown in Fig. 4. The section of beach used had only a very small C. edentula population in the preceding autumn.

![Dune profile](image_url)

**Fig. 4.** The dune profile in the study area, and the location of the three study sites.

At each site, 135 plots, each 20 x 20 cm in size, were marked out in a strip 1 x 5.4 m, with the long axis of this strip at right angles to the gradient. Sowing densities were randomly assigned to the plots. The following number of seeds was sown in different plots: 1, 5, 10, 25, 50, 100 and 200; the number of replicate plots for each number of seeds was (respectively): 100, 10, 10, 4, 2, 2 and 2. Five plots were left without additional seeds. No seedlings germinated in any of these control plots.

In addition, on the landward site, a replicate set of plots was sown as above. These replicate plots received ammonium nitrate at 2.9 g m⁻² (N at 1.0 g m⁻²) on five occasions during the peak of the growing season: on 10, 17 and 24 June, and 8 and 22 July. The object of this treatment was to modify experimentally one environmental factor which possibly changed along the gradient.

The seeds were sown on 15 April 1977, while still within the distal fruit segment. The plots were examined weekly during the period of peak germination (late May and early June) and once every 2 weeks thereafter. For each plot at each site, the number of seedlings observed, the total number of plants surviving to produce mature fruits, and the number of distal fruit segments produced per survivor were recorded. Final observations were made on 29 September, at which time all but a few stunted plants had died; these few plants were killed by autumn storms.

Survivorship was defined as

\[
\frac{\text{Number of plants surviving to produce mature fruits}}{\text{Number of seeds sown}}
\]
Reproductive output was defined as the number of mature distal fruit segments produced by a plant. It was measured individually: as each plant ceased flowering, the fruits were counted and the plant marked but left in place, in order to ensure that density remained constant except for natural mortality.

For each site, the results from all plots of a given sowing density were combined for analysis. The method of Graybill (1976) was then used to calculate F-statistics to test for differences in slope and intercept of lines fitted to the data. The survivorship data were transformed by arcsine $\sqrt{x}$ prior to statistical analysis, although untransformed data are presented in the Figures for ease of interpretation.

RESULTS

Survivorship and reproductive output

As shown in Fig. 5 and Table 1(a), there were no significant differences in density-independent effects (value of y-intercept) on survivorship among the habitats.

![Graphs showing survivorship and reproductive output](image)

**Fig. 5.** Survivorship (proportion of seeds sown which produce plants with fruits) of *Cakile edentula* plotted against sowing density (log scale) in three habitats, and the effects of nitrogen fertilization (broken line) at the landward site. Thick lines have slopes significantly different from zero at $P = 0.05$. The regressions for arcsine $\sqrt{x}$-transformed data (d.f. = 1.5) are:

<table>
<thead>
<tr>
<th>Site</th>
<th>Equation</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seaward site</td>
<td>$y = 0.36 + 0.05 \log_{10} x$</td>
<td>2.23</td>
<td>N.S.</td>
</tr>
<tr>
<td>Middle site</td>
<td>$y = 0.26 + 0.01 \log_{10} x$</td>
<td>0.10</td>
<td>N.S.</td>
</tr>
<tr>
<td>Landward site</td>
<td>$y = 0.44 - 0.22 \log_{10} x$</td>
<td>33.3</td>
<td>0.001</td>
</tr>
<tr>
<td>Landward site + N</td>
<td>$y = 0.50 - 0.20 \log_{10} x$</td>
<td>11.4</td>
<td>0.025</td>
</tr>
</tbody>
</table>

Slopes and intercepts are compared in Table 1(a), (b).
Demography of Cakile edentula

However, there were significant among-habitat differences in density dependence, caused by a significant relationship at the landward site (Fig. 5).

There were highly significant differences in density-independent effects on reproductive output among habitats. Density dependence also differed among habitats, with the seaward site showing the greatest density dependence (Fig. 6). Reproductive output is measured per surviving reproductive plant, and is plotted against sowing density. Initially, it might seem most appropriate to plot reproductive output against the number of plants surviving. There are two objections to this approach. First, many plants of *C. edentula* survive until severe frost or autumn storms, yet entirely fail to reproduce; it would therefore be necessary to plot reproductive output against the combined density of both reproductive and non-reproductive plants in the autumn fruit production period. Secondly, plotting reproductive output against final density ignores density effects which occurred earlier in

![Graphs showing reproductive output vs. sowing density for different habitats](image)

**Fig. 6.** Reproductive output of *Cakile edentula* (mean number of distal fruit segments per plant) plotted against sowing density in three habitats, and the effects of nitrogen fertilization (broken line) at the landward site. Thick lines have slopes significantly different from zero at \( p = 0.05 \). The regressions for arcsine \( \sqrt{x} \)-transformed data (d.f. = 1.5 except landward + N, where d.f. = 1.4) are:

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Regression Equation</th>
<th>( F )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Seaward</td>
<td>( y = 21.6 - 7.01 \log_{10}x )</td>
<td>23.4</td>
<td>0.001</td>
</tr>
<tr>
<td>(b) Middle site</td>
<td>( y = 2.00 - 0.30 \log_{10}x )</td>
<td>1.66</td>
<td>N.S.</td>
</tr>
<tr>
<td>(c) Landward</td>
<td>( y = 1.81 - 0.31 \log_{10}x )</td>
<td>7.87</td>
<td>0.05</td>
</tr>
<tr>
<td>(d) Landward + N</td>
<td>( y = 6.24 - 1.79 \log_{10}x )</td>
<td>13.7</td>
<td>0.25</td>
</tr>
</tbody>
</table>

Slopes and intercepts are compared in Table 1(a), (b).
the growing season; autumn density may be a poor estimate of the density which actually affected reproductive output. To avoid these problems, reproductive output is expressed as a function of sowing density. An added advantage of this is that at any given density, the product of survivorship and reproductive output yields the total number of distal fruit segments produced by fruits sown at that density.

Nitrogen addition to the landward site had no significant effects on survivorship (Fig. 5 and Table 1(b)), but it did affect reproductive output (Fig. 6 and Table 1(b)). At low sowing densities it significantly increased reproductive output (that is, it reduced the density-independent depression of reproductive output), but it also increased the density dependence of reproductive output.

<table>
<thead>
<tr>
<th>Table 1. F-values for tests of the hypothesis that the intercepts and slopes of lines are the same: * = P &lt; 0.025; *** = P &lt; 0.001. All comparisons v. sowing density.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density-independent (intercepts)</td>
</tr>
<tr>
<td>---------------------------------</td>
</tr>
<tr>
<td>(a) Among-habitat variation (d.f. 2,15)</td>
</tr>
<tr>
<td>Survivorship (Fig. 5)</td>
</tr>
<tr>
<td>Reproductive output (Fig. 6)</td>
</tr>
<tr>
<td>(b) Variation with nitrogen fertilization (d.f. 1,10)</td>
</tr>
<tr>
<td>Survivorship (Fig. 5)</td>
</tr>
<tr>
<td>Reproductive output (Fig. 6)</td>
</tr>
<tr>
<td>(c) Among-habitat variation (d.f. 2,15)</td>
</tr>
<tr>
<td>Seedlings/seeds sown (Fig. 7)</td>
</tr>
<tr>
<td>Reproductive plants/seedlings (Fig. 8)</td>
</tr>
</tbody>
</table>

† At the landward site: d.f. 1.9 for reproductive output.

Plants grown at the lowest density on the landward site with added nitrogen were significantly taller (64 v. 28 mm) and had significantly longer leaves (29 v. 8 mm) than had the unfertilized controls (Mann–Whitney U-Test of these: U_{15,15} = 11 and 1 respectively; P < 0.001 for both).

Further investigation of survivorship

It is possible to extend the above approach to provide additional information on survivorship in *Cakile edentula*. The mortality which occurred can be apportioned between two time-periods: (1) before seedlings emerged above the surface of the substrate (including seeds which failed to germinate during the year of the experiment); and (2) after the seedlings emerged, but before they managed to reproduce. The overall proportion surviving is given by:

\[
\text{No. of seedlings observed} \times \frac{\text{No. of plants surviving to produce fruits}}{\text{No. of seeds sown}} \times \frac{\text{No. of seedlings observed}}{\text{No. of seeds sown}}
\]

Using this analysis, we can test whether there are differences in survivorship between these two stages (pre-emergence and post-emergence) in the life-history of *Cakile edentula*.

Figures 7 and 8 and Table 1(c) show the results of subdividing survival in this manner. A comparison among the three non-fertilized habitats for both stages of mortality shows that in neither time-period were there significant among-habitat differences in density-independent effects, whereas in both there were significant among-habitat differences in density dependence (Table 1(c)). Within the landward site there was some evidence of density dependence in survivorship for both time-periods.
Demography of Cakile edentula

![Graphs showing proportion of seeds producing seedlings against sowing density in different habitats.](image)

**Fig. 7.** Number of seedlings of *Cakile edentula* per seed sown plotted against sowing density in three habitats (nitrogen fertilizer had not yet been added, so (d) is a replicate of (c)). Thick lines have slopes significantly different from zero at $P = 0.05$ level. The regressions for arcsine $\sqrt{x}$-transformed data (d.f. = 1,5) are:

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Equation</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Seaward site</td>
<td>$y = 0.81 + 0.05 \log_{10}x$</td>
<td>5.96</td>
<td>N.S. (0.10)</td>
</tr>
<tr>
<td>(b) Middle site</td>
<td>$y = 0.82 + 0.04 \log_{10}x$</td>
<td>0.31</td>
<td>N.S.</td>
</tr>
<tr>
<td>(c) Landward site (1)</td>
<td>$y = 1.02 - 0.21 \log_{10}x$</td>
<td>6.09</td>
<td>N.S. (0.10)</td>
</tr>
<tr>
<td>(d) Landward site (2)</td>
<td>$y = 1.03 - 0.27 \log_{10}x$</td>
<td>8.64</td>
<td>0.05</td>
</tr>
</tbody>
</table>

Slopes and intercepts are compared among the three unfertilized sites in Table 1(c).

**Relationship between experimental and natural populations**

Figure 9 is constructed from the data in Figs 5 and 6 to show the observed variation in survivorship and reproductive output with sowing density along the gradient. The shaded area shows the densities which commonly occur in natural populations (Keddy 1978). As these are low at the extremes of the gradient, the strong density dependence shown at the extremes might not be observed in most natural populations.

**DISCUSSION**

**Factors affecting reproductive output**

It appears that nitrogen is one critical factor determining adult plant size and reproductive output of *C. edentula*. Plants fertilized with ammonium nitrate were larger and had a higher reproductive output than had the controls. Pemadasa & Lovell (1974a), in a study of the effects of major nutrients on the growth of four dune annuals, concluded...
that growth was limited by nutrient deficiency, particularly of nitrogen. The large amounts of wrack (mostly dead *Zostera marina*) which wash up on the beach in late summer may be an important source of nutrients. Reproductive output was positively related to the abundance of *Zostera* along the gradient (Keddy 1978).

Variation in the density of *Ammophila breviligulata* along the gradient may be another factor contributing to the observed variation in reproductive output. Pemadasa & Lovell (1974b) found that the presence of *Festuca rubra* reduced tiller production in *Aira caryophyllea*, *A. praecox* and *Vulpia membranacea*.

Shortages of nitrogen and increased competition from *Ammophila breviligulata* are two factors which could explain the observed landward decrease in reproductive output of *Cakile edentula*.

**Factors affecting survivorship**

Damping-off disease was observed to be a major cause of mortality in *C. edentula* in
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years prior to that of the experiments (Keddy 1978). The disease caused rapid death of seedlings, and was observed to be strongly density-dependent. There was no evidence of damping-off in the year of the experiment however.

The most important cause of death appeared to be severe stunting. Large numbers of severely-stunted seedlings occurred inland; they neither flowered nor produced fruits before dying. As they did not reproduce, they were not included in the survivorship data. These plants were much smaller than those that reproduced; many consisted of a stem less than 1-cm tall with a single pair of tiny yellowed leaves. Holt (1972) noted that the probability of flowering is often related to plant size, and Werner (1975) has clearly demonstrated the positive relationship between plant size and the probability of reproducing in a given year. Thus, while the proximate cause of death of a stunted plant may be any one of many physical factors (such as blown sand, storms, or frost), the ultimate cause is the factor which initially caused the stunting. As noted earlier, lack of nitrogen and competition by Ammophila breviligulata may both be responsible for reduced plant size.

When one compares survivorship in the pre-emergence (seed to seedling, Fig. 7) with that in the post-emergence (seedling to adult, Fig. 8) stage, similar patterns are observed. One might expect different causes of death, and therefore different patterns, in these two stages. This situation would appear to be worth investigating for other species. It is possible, for example, that different habitats could all exhibit high density-independent mortality, but that the time when it occurs could differ.

Density, survivorship and reproductive output

It may now be possible to relate the above information to the observed variation in density-independent and density dependent effects on survivorship and reproductive output (Fig. 9). Consider survivorship first. One possible cause of the among-habitat variation in density dependence is variation in the intensity of damping-off disease. However, there was no evidence of damping-off in 1977. Instead, the pattern in survivorship may be directly related to the pattern in reproductive output. At the seaward end of the gradient, increased density resulted in decreased reproductive output, but had no effects on survivorship (Fig. 9); however, at the landward end of the gradient, increased density had little effect on reproductive output, but a significant effect on survivorship. Harper (1960, 1967) noted that increased density may result in either a decrease in survivorship, or a phenotypic reduction in plant size and reproductive output, or both. The variation in survivorship shown in Fig. 9 may therefore be causally related to the variation in reproductive output, in the manner shown in Fig. 10. At the seaward end of the gradient, where plants are large and have a high density-independent reproductive output, increased density results in phenotypically smaller plants with lower reproductive output, although reproduction is not entirely inhibited. At the landward end, density-independent effects reduce size and reproductive output; here, where tiny plants produce only one or two fruits each in the absence of intraspecific effects, increased density inhibits reproduction entirely. The result is decreased survivorship—that is, a smaller proportion of plants surviving to produce mature fruits—with increasing density.

It is also possible that the observed changes in survivorship and reproductive output are completely unrelated (rather than causally related as illustrated in Fig. 10). Each may be independently affected by one or more physical or biotic factors.

In conclusion, the among-habitat differences in survivorship and reproductive output observed in natural populations of Cakile edentula result from variation in both density-independent and density-dependent effects. This illustrates two considerations
FIG. 9. Variation in survivorship and reproductive output of Cakile edentula with density along an environmental gradient (based on Figs 5 and 6). Densities of C. edentula that occurred naturally are represented by the shaded area.

FIG. 10. Possible relationship between reproductive output and density of Cakile edentula with increasing density-independent limitations. At the seaward end of the gradient, increasing density results in reduced reproductive output; while at the landward end of the gradient, increasing density results in an increased proportion of plants which are below the critical minimum size for reproduction.

which may be overlooked in planning and interpreting autecological studies. (1) In studies of natural populations, among-habitat differences in survivorship and reproductive output cannot be solely attributed to differences in physical factors when density also differs among these habitats (or to density, when physical factors differ). (2) An autecological study of a species should attempt to identify which physical factors affect survivorship and reproductive output, and should determine whether they act in a density-independent or density-dependent manner.
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REFERENCES


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