Population ecology in an environmental mosaic: *Cakile edentula* on a gravel bar

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The population ecology of the annual plant *Cakile edentula* was studied on a gravel bar in Halifax County, Nova Scotia, where it grows in a two phase mosaic consisting of (1) open shingle or gravel and (2) thick mats of dead *Zostera marina* wrack. Cohorts of seedlings were marked and regularly counted in both habitats. Reproductive output and seed dispersal were also studied.

There were marked differences in *C. edentula* ecology between the two habitats. In general, survivorship and reproductive output were both greater in shingle. However, caterpillar grazing in late summer was concentrated on shingle plants, with the eventual result that net reproductive output was greater in wrack. There was no evidence of seed movement between wrack and shingle.

Seedlings of *C. edentula* often grew in dense clusters around the remains of the previous year's parent(s). In both habitats, *C. edentula* seedling density declined with distance from the centre of clusters. Reproductive output increased with distance in both habitats; survivorship increased with distance only in wrack. Distal fruit segments were dispersed further than proximal segments; thus seedlings derived from distal segments tended to grow further from the previous year's parent, and in turn had higher survivorship and reproductive output. Distal fruit segments are normally thought to function primarily for long-distance dispersal; on shingle beaches "long-distance dispersal" of less than a metre could significantly improve the reproductive success of a seedling.

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L'écologie des populations de la plante annuelle *Cakile edentula* a été étudiée sur une barre de gravier dans le comté d'Halifax en Nouvelle-Ecosse. Les populations de *C. edentula* y croissent sous la forme d'une mosaïque à deux phases, l'une consistant en galets ou graviers ouverts et l'autre, en tapis de matériel mort de *Zostera marina*. Des cohortes de plantules ont été marquées et comptées régulièrement dans les deux habitats. Le rendement reproducteur et la dissémination des graines ont aussi été étudiés.

Il y a des différences marquées entre les deux habitats dans l'écologie de *C. edentula*. En général, la survie et le rendement reproducteur sont plus élevés sur les galets. Cependant, le broutage par les chenilles à la fin de l'été est concentré sur les plantes des galets, avec le résultat que le rendement reproducteur net est plus élevé sur les tapis de zostère. Il n'y a pas de mouvement de graines entre les tapis de zostères et les galets.

Les plantules de *C. edentula* croissent souvent en groupes denses autour des restes des parents de l'année précédente. Dans les deux habitats, la densité des plantules de *C. edentula* diminue avec l'augmentation de la distance à partir du centre des groupes de plantules. Le rendement reproducteur augmente avec la distance dans les deux habitats; la survie augmente avec la distance seulement sur les tapis de zostère. Les segments distaux des fruits sont disséminés plus loin que les segments proximaux; par conséquent, les plantules provenant des segments distaux ont tendance à croître plus loin de la plante-mère et à présenter une survie et un rendement reproducteur plus élevés. Les segments distaux des fruits sont normalement considérés comme responsables de la dissémination sur de longues distances; sur les plages de galets, une "dissémination sur de longues distances" de moins d'un mètre peut augmenter significativement le succès reproducteur d'une plantule.

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Introduction

There is considerable interest in the ecology of species which inhabit environmental mosaics (for example, Levins 1962, 1963; MacArthur and Wilson 1967; Horn and MacArthur 1972; and Weins 1976). *Cakile edentula* (Bigel.) Hook., an annual member of the Brassicaceae, can often be found growing in a two phase mosaic (after Pielou 1975) on gravel bars along the eastern coast of Nova Scotia. It grows in two distinct habitats: (1) open shingle or gravel, and (2) thick mats of wrack (piles of dead *Zostera marina* L. 10 cm or more thick on top of shingle). One object of this investigation was to test for differences in the population ecology of *C. edentula* between these two distinct but intimately mixed habitats. A fortuitous combination of circumstances also made it possible to test for between-habitat differences in caterpillar grazing.

Within each of these habitats, plant density can

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vary greatly; plants can be found growing in dense clusters or as widely scattered individuals. The dense clusters appear to be the result of the extremely rough surface; dispersed fruits tend to lodge in the spaces between stones, and therefore are apparently carried only a short distance from parent plants. I therefore investigated whether the distance which a seedling grew from the centre of dense clusters had any effect on survivorship or reproductive output.

Finally, observations were made on dispersal of the peculiar two-parted fruit of *C. edentula*. This fruit has attacted considerable interest (for example Barbour 1972; Rodman 1974 and references therein). The fruit has two segments each of which normally contains one seed; the distal segment is deciduous, whereas the proximal segment remains permanently attached to the parent. Thus each fruit appears to provide for two very different modes of seed dispersal. I therefore investigated fruit dispersal within and between habitats.

Methods

The study area

The study area was located on the end of a shingle bar stretching out across the mouth of Chezzetcook Inlet, Halifax County, Nova Scotia, Canada (latitude 40°40′15″ N longitude 63°13′30″ W). Chezzetcook Inlet has rich *Zostera marina* beds, and dead *Z. marina* wrack had accumulated in long bands over the surface of the shingle. Generally, these bands of wrack were about 1 m wide by many metres long. Separate patches of wind-blown wrack had built up around obstacles and in depressions in the shingle. In 1976, the shingle bar under study had two major bands of wrack running the length of the beach above the summer high tide line, and four major patches, each several metres on a side. (Plants growing in smaller patches were not used in this study.) The depth of wrack varied greatly, but usually exceeded 10 cm in the areas I studied.

Sampling methods

All experiments were set up, and cohorts identified, on 1 June, 1976, immediately following the peak of seedling emergence. Plants were censused at regular 2-week intervals until 20 October, 1976, when all plants had died.

"Scattered" plants were defined as widely spaced plants growing alone at the centre of a circle 25 cm in diameter, that is, at least 12.5 cm from other seedlings. Since most seedlings germinated in clusters, "scattered" seedlings were uncommon. I individually tagged 30 such seedlings in each habitat. Because of their rarity, I simply tagged the first 30 scattered seedlings I located in each habitat. The plants were observed each sampling interval to determine survivorship.

Most seedlings germinated in dense, circular clusters about 0.3–0.5 m in diameter. To study clustered plants, a stake was used to mark the centre of each cluster, and a series of concentric rings was centred about each stake for censusing. The rings were 10, 20, 30, and 50 cm in diameter, corresponding to maximum distances of 5, 10, 15, and 25 cm from the centre of the cluster. The number of seedlings between each two consecutive rings, and the number contained by the smallest ring, were counted every 2 weeks. The criteria for selection were that a seedling cluster must contain a minimum of 50 seedlings, be separated by at least 0.5 m from adjacent clusters, and be unobstructed by pieces of debris such as logs and lobster traps. Subject to these criteria I found 10 usable clusters (n = 1027 seedlings) in shingle, but only 3 in wrack (n = 231 seedlings).

Since individual seedlings were not tagged in the clusters, any turnover in the seedling population could be missed, resulting in underestimates of both maximum density and mortality. However, formal censusing of cohorts was not initiated until the peak germination period had passed. The few seedlings which germinated late in clusters were visually smaller, and were not counted. Thus, it seemed reasonable to treat those seedlings which had emerged before 1 June as a cohort.

Survivorship was defined as

$$\left(\frac{\text{number of plants producing mature fruits}}{\text{maximum number of seedlings observed}}\right)$$

Reproductive output was more difficult to determine. As noted earlier, *C. edentula* has a two-parted fruit. The proximal segment of the fruit is smaller and often sterile (Rodman 1974; Keddy 1978). Unfortunately, it is difficult to determine in the field whether or not each proximal segment contains a viable seed. Even with field-dissection of fruits I could not determine whether a given seed was viable, and it was necessary to count thousands of fruits. Thus, it was not possible to determine whether the degree of proximal segment sterility varied among habitats. I estimated reproductive output conservatively by counting only the number of mature distal fruit segments per plant; all mature distal fruit segments normally contain a single seed (Rodman 1974). Preliminary observations on the effects of density (unpublished) revealed that, if anything, proximal pod sterility was greatest on small plants at high densities near the centre of clusters. Thus the trends discussed later in this paper would err on the conservative side.

Reproductive output for each surviving scattered plant was counted directly. For clusters, because of the extremely large number of plants involved, I estimated reproductive output based on a sample of five plants from each distance interval in each cluster (n = 200 plants in shingle; n = 53 plants in wrack, some intervals had less than five plants). These plants were chosen based on a randomly chosen compass bearing and distance from the centre of the cluster.

All estimates of survivorship and reproductive output discussed under Effects of clustering and Effects of habitat mosaic in the Results section are based on data from the period 1 June to 9 August, 1976. By this time most plants were mature, and all observations were completed on 9 August in preparation for a predicted hurricane which had the potential to destroy the *C. edentula* population under study. The storm did not materialize, but a major outbreak of salt marsh caterpillars (*Estigmene acrea* Dru.: Arctiidae) did. By this time, many clustered plants had begun to senesce naturally; however, censusing of scattered plants was reinitiated. Reproductive output and survivorship after 9 August are treated separately (under Effects of caterpillar grazing in Results) to separate the added effects of caterpillar grazing from the effects of innate physical differences between the two habitats. The caterpillar populations were the largest I have encountered in these habitats (0.5 caterpillars per plant on scattered plants).

Survivorship curves for *C. edentula* are based upon cohorts germinating in clusters (shingle n = 1027; wrack n = 231).

The type of fruit segment from which naturally occurring seedlings originated could usually be determined by digging up the seedling. In most cases, the remains of the fruit could be located near the junction of the hypocotyl and the primary root. In approximately 10% of the cases, the fruit segment could not be relocated. This is not surprising as in some seedlings the fruit remains attached to the cotyledons, is carried above the surface, and shed there. In such cases, an individual fruit segment, even

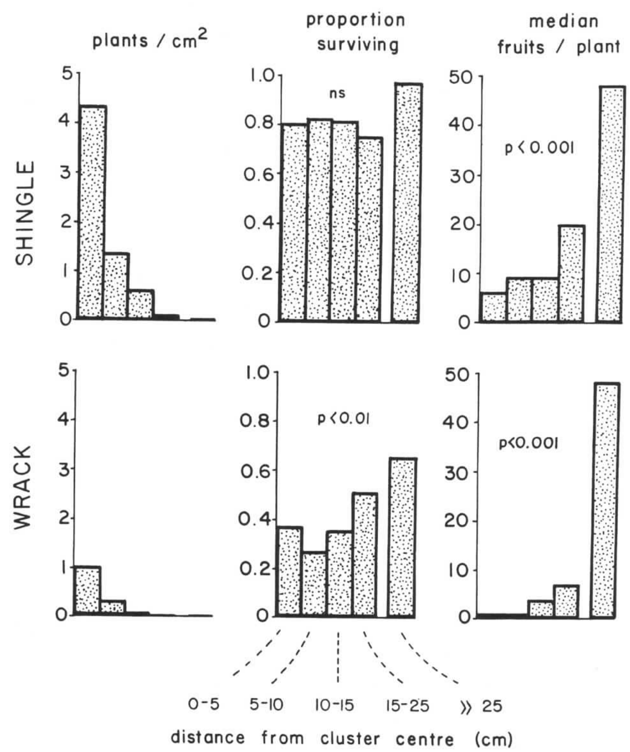

FIG. 1. Density (plants per square centimetre), survivorship (proportion surviving), and reproductive output (median number fruits per plant) plotted against distance from the centre of seedling clusters in two habitats. Plants designated as ≫25 cm from cluster centre represent the "scattered" plants discussed in the text. Survivorship: shingle, $\chi_4^2 = 8.49$, $p < 0.10$, $n = 1057$; wrack, $\chi_4^2 = 16.25$, $p < 0.01$, $n = 261$. Reproduction: the median test extended to k independent samples (Siegel 1956); shingle, $\chi_4^2 = 60.22$, $p < 0.001$, $n = 229$; wrack, $\chi_4^2 = 39.57$, $p < 0.001$, $n = 73$.

if it could be found, could not be assigned to a given seedling. To compare the types of fruit segments (whether proximal or distal) which gave rise to naturally occurring plants, I excavated both seedlings from clusters, and scattered seedlings. Because of the aforementioned shortage of suitable clusters in wrack, and the general shortage of scattered seedlings, I carried out this work in shingle only, with $n = 20$ scattered seedlings. These were virtually all that remained, for $n = 30$ had already been tagged. A remaining shingle cluster was dug up (to a depth of 10 cm) and returned to the lab, where fruit types were examined.

To determine the amount of between-habitat movement of fruits during the winter, mature fruits were spray painted in the field with one distinctive fluorescent colour for each of the two habitats. The fruits were painted while still attached to parent plants to allow for natural dispersal. Distal fruit segments were relocated the following spring by excavating in both shingle and wrack areas before germination had occurred (16 April 1977).

All chi-square test statistics with one degree of freedom were calculated using a correction for continuity (Siegel 1956). The designation ns refers to test statistics with associated probabilities $p > 0.05$.

Results

Survivorship and reproductive output

Effects of clustering

Dense clusters of germinating *C. edentula* seedlings are common on shingle beaches in Nova Scotia. In this study, densities as high as 9.5×10^5 seedlings per square metre were observed near the centre of these clusters. Excavation of three of these clusters revealed that they marked the remains of one or more buried plants from the previous year.

Figure 1 (left) shows that the density of seedlings in a cluster declined rapidly with increasing distance from the centre of the cluster. Examination of the centre and right sections of Fig. 1 shows that survivorship increased with distance from the cluster centre in wrack, and reproductive output increased with distance from the cluster centre in both habitats.

Effects of habitat mosaic

Figure 1 also shows that the effects of growing in a cluster differ between shingle and wrack; whereas survivorship changes with distance from the cluster centre in wrack, it does not significantly change over the same distance in shingle. (Note too that the changes in seedling density with distance are actually much greater in shingle.)

For further between-habitat comparisons, scattered and clustered plants will be considered separately. Table 1 shows that irrespective of density, a greater proportion of the seedlings which germinated in shingle survived to maturity (for scattered seedlings, 0.97 in shingle compared with 0.67 in wrack; for clustered seedlings, 0.80 in shingle compared with 0.36 in wrack).

In spite of these differences in survivorship (measured as proportion surviving to produce mature fruit), cohort survivorship curves for seedlings of *C. edentula* were similar in both shingle and wrack (Fig. 2). There is a slight suggestion that *C. edentula* seedlings exhibit higher early season mortality in wrack; many had wizened and blackened stems and roots, suggesting death was caused by damping-off disease. Since seeds often germinate at a depth of 10 cm or more below the substrate surface, considerable seedling mortality may occur before they emerge and are counted.

Now consider reproductive output. Table 1 shows that for scattered plants, there was no significant difference between habitats. In clusters, shingle plants performed significantly better than wrack plants, with a mean reproductive output of 15.6 distal fruits per plant versus 6.0. Thus, for both scattered and clustered plants, shingle plants had survivorship and reproductive output values greater than or equal to those for plants growing in the *Zostera marina* wrack.

TABLE 1. Comparisons of survivorship and reproductive output of *Cakile edentula* in two habitats

	Scattered	Clustered
Survivorship	Shingle > wrack[a]	Shingle > wrack[b]
Reproductive output	Shingle = wrack[c]	Shingle > wrack[d]

[a] $\chi_1^2 = 7.12$, $p < 0.01$; shingle $n = 30$, survivors = 29; wrack $n = 30$, survivors = 20.
[b] $\chi_1^2 = 174.2$, $p < 0.001$; shingle $n = 1027$, survivors = 820; wrack $n = 231$, survivors = 84.
[c] Mann–Whitney U test: U = 296, $p = 0.122$; shingle $n = 29$, (mean = 75.0); wrack $n = 20$, (mean = 85.0).
[d] Median test: $\chi_1^2 = 19.56$, $p < 0.001$; shingle $n = 200$, (mean = 15.6); wrack $n = 53$, (mean = 6.0).

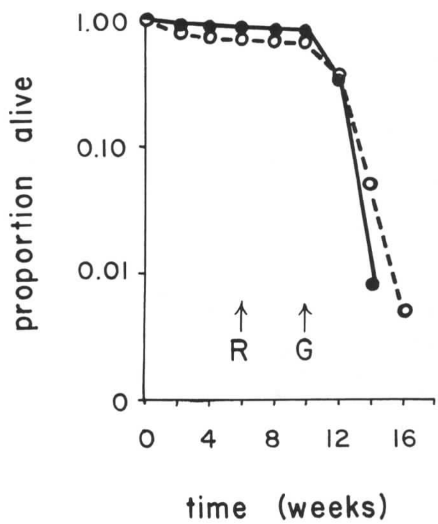

FIG. 2. Survivorship curves for emerged seedlings of *C. edentula* in two habitats (●—● shingle; ○—○ wrack). R, reproduction initiated; G, beginning of intense grazing by caterpillars, t_0, 1 June, shingle $n = 1027$ plants, wrack $n = 231$ plants. NOTE: Since natural senescence and caterpillar grazing were occurring at approximately the same time, it would be incorrect to conclude from this figure that the heavy mortality shown after 10 to 12 weeks was caused by grazing; only an estimated one quarter of the plant deaths at this time could be attributed to grazing (see text).

Effects of caterpillar grazing

A major outbreak of salt marsh caterpillars (*Estigmene acrea*) occurred in late August. In the month following the outbreak, more than one quarter of the scattered plants were stripped of leaves and killed. (Many of the clustered plants had already senesced by this time.) There was a slight suggestion that mortality was heavier in shingle ($\chi_1^2 = 2.03$, $p < 0.10$ one-tailed; shingle $n = 29$, deaths = 11; wrack $n = 20$, deaths = 3). Reproductive output was also affected. Data in Table 2 support the qualitative observation that the effect of grazing was greater in shingle than in wrack. Although initially there was no significant difference in reproductive output between the two habitats (Table 1), wrack plants had significantly more fruits than shingle plants after caterpillar grazing.

The net decline in the number of fruits per plant in shingle could be due to either (*i*) preferential destruction of large plants with many fruits, or (*ii*) grazing of fruits on all plants irrespective of plant size. The latter appears to be the case. The number

TABLE 2. Effect of caterpillar grazing on the reproductive output (mean number of distal fruit segments per plant) of "scattered" *Cakile edentula* plants in two habitats

	Habitat		
	Shingle	Wrack	Mann–Whitney U test
Before grazing	75.0	85.0	$U_{29,20} = 296$, $p = 0.122$
After grazing	49.7	78.5	$U_{18,17} = 90.5$, $p < 0.025$*

*One-tailed.

of fruits on each plant was recorded in August, just before the heavy caterpillar grazing. By subdividing shingle plants into two categories, those that were killed by caterpillars, and those that survived, it is possible to test whether, initially those that were killed had more fruits than those that survived. There is no evidence that plants bearing many fruits were selectively killed (Mann-Whitney U test: $U_{18,11} = 75$, $p > 0.05$; mean of those survived = 73.2, $n = 18$; mean of those killed = 78.0, $n = 11$).

Fruit dispersal

Excavation of seedlings usually revealed the type of fruit segment from which they germinated (see Methods for details). Table 3 shows that the scattered seedlings were more likely to have originated from distal fruit segments. Table 4 shows, however, that painted distal fruit segments were rarely dispersed from one habitat to another.

TABLE 3. The fruit segments from which scattered and clustered seedlings germinated

	Fruit segment	
	Proximal	Distal
Scattered	0	20
Clustered	133	108

$\chi_1^2 = 20.4$, $p < 0.001$.

TABLE 4. Within and between habitat dispersal of painted distal fruit segments of *Cakile edentula* (from October 1976 to April 1977)

	Habitat of recovery	
Habitat where fruit was produced	Shingle	Wrack
Shingle	245	0
Wrack	0	175

Discussion

Effects of habitat mosaic

There were significant differences in the population ecology of *C. edentula* between two habitats which occurred in a two phase mosaic. In general, *C. edentula* plants growing in shingle had higher survivorship and reproductive output than those growing in wrack. However, heavy caterpillar grazing affected shingle plants more than wrack plants. The result was that the net reproductive output of shingle plants was finally lower than that of wrack plants. (This may not be a regular occurrence, however; nowhere else have I seen densities of caterpillars as great as occurred during this 1-year study.)

These between-habitat differences are all the more interesting because of the intimate intermingling of shingle and wrack habitats. Plants may be spatially separated by only a fraction of a metre, yet be growing in very different habitats. Moreover, there is surprisingly little between-habitat seed movement. In this sense, the two *C. edentula* populations appear to be largely independent of each other. Vandermeer (1972) has defined this sort of mosaic with poor dispersal between adjacent patches (that is, a strong diagonal element in the matrix of habitat transition probabilities) as a "coarse grained habitat."

Effects of clustering

It has been hypothesized by Janzen (1970) that the wide separation between mature conspecific tropical trees is due to a combination of (*i*) a decline in the number of seeds dispersed and (*ii*) an increase in the proportion of seedlings surviving as functions of increasing distance from the parent tree. He suggests that the low probability of survival near the parent, where seedling densities are highest, is due to increased probability of attack by host-specific insects.

In this study, seedling density declined with distance from the centre of seedling clusters, which is approximately the distance from the parent plant of the previous year (Fig. 1, left). This is consistent with seed distribution patterns observed in many other species (Harper 1977; Watkinson 1978). However, survivorship changed significantly with distance from parent only in wrack, in spite of the fact that seedling densities were often much higher in shingle. As well, damping-off caused higher mortality in wrack than in shingle (Fig. 2, weeks 0 to 4).

Burdon and Chilvers (1975*a*, 1975*b*, 1976) have demonstrated that the mortality caused by damping-off disease is directly related to seedling density. It is tempting to speculate that mats of moist wrack are more suitable for fungal growth than the comparatively dry shingle. This could explain the observed relationship between mortality and density in wrack and the apparent absence of this phenomenon in shingle. In mats of eelgrass wrack, predatory fungi might play the same role as Janzen (1970) hypothesized for insects.

Fruit dispersal

It has been suggested (Barbour 1972; Rodman 1974) that the fruit dimorphism of the genus *Cakile* reflects two different modes of dispersal. The distal deciduous segments may be blown about the beach, or carried for long distances at sea. The proximal segments are presumably buried in the immediate vicinity of the parent. This difference in dispersal modes is demonstrated here. Those seedlings which grew in dense clusters originated from both proximal and distal fruit segments. Scattered seedlings occurred infrequently, but those which I examined ($n = 20$) originated exclusively from distal fruit segments.

Both Barbour (1972) and Rodman (1974) apparently view the distal pod segment as a method of ensuring that long-distance dispersal to new habitats can occur. Rodman notes that the first vascular plants discovered growing on the new island of Surtsey were *Cakile* plants. However, data presented here suggest that, at least on gravel bars, where fruit dispersal is limited, the advantage associated with distal fruit segments may in fact be "long-distance dispersal" of less than a metre. This is because there is marked variation in survivorship and reproduction over small distances. In both habitats, those seedlings which grew farthest from the centre of seedling clusters had a higher reproductive output (Fig. 1). In wrack, survivorship also increased with distance from the centre of these clusters (Fig. 1). Thus, seeds which were dispersed away from the centre of these seedling clusters produced, on the average, far more offspring than those which remained near the centre of the cluster. Thus, dispersal of less than a metre could significantly alter the reproductive success of a seedling.

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