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**Abstract**

The purpose of this study was to analyze the dispersal dynamics of the ovoviviparous bivalve Gemma gemma (hereafter referred to as Gemma) in an environment disturbed by the pit-digging activities of horseshoe crabs, Limulus polyphemus. Gemma broods its young and has no planktonic larval stage, so all dispersal is the result of juvenile and adult movement. Animal movement was measured using natural crab pits, hand-dug simulated crab pits, and cylindrical bottom traps in the intertidal zone at Tom's Cove, Virginia, USA.

This study demonstrated that horseshoe crabs create localized patches with reduced densities of Gemma, that all sizes and ages of Gemma quickly disperse into these low density patches, and that the mechanism of dispersal is passive bedload and suspended load transport. Freshly excavated natural pits had significantly lower Gemma densities than did undisturbed background sediment, but there were no significant differences in total density of other species, number of species, and species diversity (H'). Equitability (J') was greater in pits than in controls because of the reduced abundance of Gemma, the numerically dominant species. Newly dug simulated crab pits also had significantly lower Gemma densities than controls and returned to control levels by the next day. Density recovery trajectories for individually marked pits showed consistent responses in summer and fall, but not in winter when low Gemma abundance resulted in greater variability among pits.

Significant positive correlations between the volume of sediment and the number of Gemma collected per bottom trap support the hypothesis that Gemma dispersal is a passive transport phenomenon. Assuming no active, density-dependent movement, the product of the Gemma density frequency distribution in undisturbed background sediment and the frequency distribution of sediment volume collected per trap created a predicted Gemma frequency distribution in traps that matched the actual distribution. Absolute dispersal rates and relative dispersal rates (absolute dispersal rate divided by background density in undisturbed sediment) into pits and traps were greater in summer than winter. Dispersal rate results suggest that increased horseshoe crab disturbance in summer may cause an increase in Gemma transport. Because Gemma individuals are dispersed by hydrodynamic action, it was expected that small, young individuals would be most easily transported in the bedload. There was, however, little evidence that movement into pits and traps was size- or age-selective.

Most recent benthic dispersal research has focused on the large-scale movement and settlement patterns of invertebrate larvae. The results from this study illustrate that dispersal of bottom-dwelling juveniles and adults plays an important role in regulating the local distribution and abundance of Gemma. Previous workers have shown that young Gemma live in dense aggregations and that growth and fecundity are reduced at such high densities, leading to population crashes. This study demonstrated a mechanism by which Gemma disperses into low-density patches where intraspecific competition may be mitigated, possibly resulting in enhanced individual reproductive success and population fitness.

**Disciplines**
Environmental Sciences

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# DISPERSAL DYNAMICS OF THE BIVALVE
# *GEMMA GEMMA* IN A PATCHY ENVIRONMENT[1]

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*Abstract.* The purpose of this study was to analyze the dispersal dynamics of the ovoviviparous bivalve *Gemma gemma* (hereafter referred to as *Gemma*) in an environment disturbed by the pit-digging activities of horseshoe crabs, *Limulus polyphemus. Gemma* broods its young and has no planktonic larval stage, so all dispersal is the result of juvenile and adult movement. Animal movement was measured using natural crab pits, hand-dug simulated crab pits, and cylindrical bottom traps in the intertidal zone at Tom's Cove, Virginia, USA.

This study demonstrated that horseshoe crabs create localized patches with reduced densities of *Gemma,* that all sizes and ages of *Gemma* quickly disperse into these low density patches, and that the mechanism of dispersal is passive bedload and suspended load transport. Freshly excavated natural pits had significantly lower *Gemma* densities than did undisturbed background sediment, but there were no significant differences in total density of other species, number of species, and species diversity (*H'*). Equitability (*J'*) was greater in pits than in controls because of the reduced abundance of *Gemma,* the numerically dominant species. Newly dug simulated crab pits also had significantly lower *Gemma* densities than controls and returned to control levels by the next day. Density recovery trajectories for individually marked pits showed consistent responses in summer and fall, but not in winter when low *Gemma* abundance resulted in greater variability among pits.

Significant positive correlations between the volume of sediment and the number of *Gemma* collected per bottom trap support the hypothesis that *Gemma* dispersal is a passive transport phenomenon. Assuming no active, density-dependent movement, the product of the *Gemma* density frequency distribution in undisturbed background sediment and the frequency distribution of sediment volume collected per trap created a predicted *Gemma* frequency distribution in traps that matched the actual distribution. Absolute dispersal rates and relative dispersal rates (absolute dispersal rate divided by background density in undisturbed sediment) into pits and traps were greater in summer than in winter. Dispersal rate results suggest that increased horseshoe crab disturbance in summer may cause an increase in *Gemma* transport. Because *Gemma* individuals are dispersed by hydrodynamic action, it was expected that small, young individuals would be most easily transported in the bedload. There was, however, little evidence that movement into pits and traps was size- or age-selective.

Most recent benthic dispersal research has focused on the large-scale movement and settlement patterns of invertebrate larvae. The results from this study illustrate that dispersal of bottom-dwelling juveniles and adults plays an important role in regulating the local distribution and abundance of *Gemma.* Previous workers have shown that young *Gemma* live in dense aggregations and that growth and fecundity are reduced at such high densities, leading to population crashes. This study demonstrated a mechanism by which *Gemma* disperses into low-density patches where intraspecific competition may be mitigated, possibly resulting in enhanced individual reproductive success and population fitness.

*Key words: bioturbation; dispersal; disturbance;* Gemma gemma; *infauna; intertidal;* Limulus polyphemus; *patch; pit; recolonization; sediment transport; soft-bottom.*

## INTRODUCTION

Recent theoretical and empirical investigations have demonstrated the importance of dispersal in the maintenance of plant and animal populations (see reviews in Lidicker and Caldwell 1982, Pickett and White 1985, Menge and Sutherland 1987, Underwood and Fairweather 1989, Grosberg and Levitan 1992). Several studies have dealt with organisms with a sessile adult stage and mobile seeds (Pacala 1989) or larvae (Possingham and Roughgarden 1990, Gaines and Bertness 1992) that disperse over large distances. Yet even on small spatial scales, dispersal may play a crucial role in enhancing individual reproductive success and population fitness. Hamilton and May (1977) predicted that when intraspecific competition exists, selection for dispersal should always occur if propagules can move

away from existing members of a population into areas where fewer individuals reside. In disturbed, patchy environments there should be strong selection pressure for local dispersal into low density patches where competition is less intense than in the background community.

The dynamics of dispersal into low density patches have been studied in a variety of terrestrial, freshwater, and marine systems (Sousa 1984, Pickett and White 1985). They have been particularly well documented in rocky shore marine communities. Patch dynamics and dispersal in soft-bottom marine systems, however, remain poorly understood. Patches in the form of pits, mounds, and defaunated areas of sediment are created by a variety of physical and biological agents. Patches range in diameter from millimetres (teleost fish bites of sediment, Billheimer and Coull 1988, Palmer 1988*a*) to centimetres (fecal mounds, Varon and Thistle 1988; crab and ray foraging and mating pits, Woodin 1978, Reidenauer and Thistle 1981, VanBlaricom 1982, Grant 1983, Thrush 1986*a, b,* Thrush et al. 1991), metres (walrus and whale foraging pits, Nerini and Oliver 1983, Oliver and Slattery 1985, Oliver et al. 1985, Nelson and Johnson 1987; deep-sea nekton falls, Smith 1986), and kilometres (defaunation due to anoxia, Boesch et al. 1976, von Westernhagen et al. 1986; lowered salinity, Thomas and White 1969; toxic algae blooms, Simon and Dauer 1977; ice scour, Gordon and Desplanque 1983; storm-induced sediment erosion and deposition, Yeo and Risk 1979, Thistle 1988, Barry 1989). Until recently, the prevailing view was that soft-bottom disturbance patches were recolonized primarily by free-swimming larvae (Grassle and Grassle 1974, McCall 1977, Gallagher et al. 1983). An emerging paradigm, however, is that recolonization of small disturbance patches may be effected by mobile, postlarval juveniles and adults (Thistle 1981, Commito 1982, Bell and Devlin 1983, Levin 1984, Thrush 1986*a, b,* Palmer 1988*b,* Varon and Thistle 1988, Smith and Brumsickle 1989, Hall et al. 1991, Thrush et al. 1991, Armonies 1992, Gunther 1992). Yet little is known about the mechanisms of postlarval dispersal.

The purpose of this paper is to examine the dispersal dynamics of the small (<5 mm long) ovoviviparous bivalve *Gemma gemma* (hereafter referred to as *Gemma*) in a disturbed, patchy environment. This clam broods its young and releases them as benthic juveniles (Sellmer 1967). There is no free-swimming, dispersing larval stage, so *Gemma* serves as a useful model of postlarval dispersal without research complications resulting from the movement of planktonic larvae. Although adult *Gemma* often have a random spatial distribution, juveniles are clumped, possibly because they remain close to their mothers after release (Jackson 1968, Botton 1984*a*). Weinberg (1985, 1989) showed that under crowded conditions, *Gemma* individuals had reduced rates of body growth and fecundity that led to subsequent population crashes. These results suggest

that the ability to disperse actively or passively away from high density areas into recently disturbed, low density patches may be important for *Gemma.*

## STUDY SITE AND HYPOTHESES

The study site was located at Tom's Cove, Assateague Island, Virginia, USA, near the sites of Woodin (1978, 1981) and Bell and Woodin (1984); see Woodin (1978) for a detailed description. The major epibenthic disturbance agents were horseshoe crabs, *Limulus polyphemus,* and blue crabs, *Callinectes sapidus.* Crabs excavate pits to forage at high tide and to avoid desiccation at low tide. Horseshoe crabs dig pits over the entire tidal cycle to feed and mate. Many horseshoe crabs, but few blue crabs, were observed at the site during the course of this study. Pits often possessed a long, shallow groove extending away from the perimeter, a feature characteristic of horseshoe crab excavations. Thus, most pits at the time of this study were dug by horseshoe crabs. Pit formation at Tom's Cove is strongly seasonal and occurs primarily from May to October. In summer, pits cover up to 45% of the sediment surface on any given day (Woodin 1978) and generally persist for one or two days, resulting in extremely high sediment turnover rates. During the course of this study pits were generally elliptical, $\approx 18 \times 25 \times 8$ cm deep, and often surrounded by a raised rim of sediment 5 cm wide and 2 cm higher than the undisturbed sediment surface. Similar rim features have been described for ray pits (Howard et al. 1977) and are due to the removal of sediment from the pits and its subsequent deposition.

*Gemma* can be a dominant member of the infauna in intertidal and shallow subtidal sandy areas from Nova Scotia to Texas (Bradley and Cooke 1959, Sellmer 1967, Jackson 1968, Green and Hobson 1970, Bell and Woodin 1984, Botton 1984*a, b,* Weinberg 1985, Schneider and Mann 1991). *Gemma* was the most abundant macrofaunal organism at Tom's Cove in the years reported by Bell and Woodin (1984). Their field experiments demonstrated that horseshoe and blue crab disturbance played an important role in controlling community structure and that *Gemma* abundance often increased in response to crab exclusion manipulations. It is logical to infer that crab digging activities reduce the densities of small infaunal forms living close to the sediment surface. Therefore:

$H_1$:  *Gemma* density in newly dug pits at Tom's Cove is lower than the background density in undisturbed sediment.

The mechanism of *Gemma* dispersal into disturbed patches has not been determined. Jackson (1968) argued that *Gemma* movement is the result of actively directed burrowing away from high density areas. Active movement of infaunal copepods (Reidenauer and Thistle 1981, Varon and Thistle 1988) and amphipods (VanBlaricom 1982, Nerini and Oliver 1983, Dewitt

and Levinton 1985) into disturbed areas has been ob-served in soft-bottom systems. Near-bottom water flow over depressions in the sediment surface often leads to increased sedimentation due to reduced sheer stress and forces of resuspension (Nowell and Jumars 1984). Ac-cumulation of organic material in pits may increase food supplies, thus creating attractive habitats for some benthic organisms (Thistle 1981, VanBlaricom 1982, Nowell and Jumars 1984). Organisms may actively move to such areas in search of food.

However, there is little evidence for active, horizon-tal *Gemma* movement through the sediment. In labo-ratory experiments using Tom's Cove *Gemma* over a wide range of densities under static, no-flow condi-tions, most individuals placed on the sediment surface burrowed but did not move from within a 1 cm² area during 15-h test periods (J. D. Belt and J. A. Commito, *unpublished data*). Some recent studies (Chandler and Fleeger 1983, Palmer and Gust 1985, Fegley 1988, DePatra and Levin 1989) have indicated passive dis-persal due to water currents as the transport mechanism for meiofauna. Palmer (1988b) argued that passive transport should be the primary means of meiofauna dispersal in disturbed environments, such as at Tom's Cove, where there are high sediment resuspension rates. Nowell and Jumars (1984) suggested that small benthic organisms have transport characteristics simi-lar to those for sediment particles, a prediction borne out by field (Matthiessen 1960) and flume studies (Han-nan 1984, Butman et al. 1988). Savidge and Taghon (1988) reported that the influx of organisms and re-covery of disturbed populations were more rapid in depressions than in defaunated sediment plugs that were flush with the sediment surface. But they found little correlation between immigration rates and organic matter concentration in depressions. Their results sug-gested that animals were not actively choosing de-pressions rich in organic matter, but were carried pas-sively by water currents.

Large numbers of juveniles and adults of the bivalve *Mya arenaria* have been found to move across the sand-flat surface by passive bedload and suspended load transport due to wind-generated water currents (Mat-thiessen 1960, Emerson 1991, Emerson and Grant 1991). Similarly, *Gemma* have been captured in nets at the sediment–water interface (Sellmer 1967, Green and Hobson 1970), suggesting that hydrodynamic ac-tion may play a role in their dispersal. Therefore:

$H_2$:    *Gemma* dispersal is passive as individuals are moved with sediment particles as part of the bedload and suspended load. There is a positive relationship between the volume of sediment and the number of *Gemma* collected by cylin-drical bottom traps flush with the sediment sur-face.

If water currents were always rapid enough to exceed critical erosion velocities for all sizes of *Gemma*, then passive transport should not be size selective. However, current velocities in the intertidal zone are not constant. The most easily moved sediment particles in the bed are 0.18 mm in diameter (Sanders 1958). Above this size, the larger the particle, the greater is the water velocity necessary to move it, and Matthiessen (1960) demonstrated that this relationship was true for *Mya arenaria* individuals as well. *Gemma* offspring are 0.375 mm long when released (Sellmer 1967), so small individuals should be more readily dispersed than large ones if passive transport is the mechanism of dispersal. Therefore:

$H_3$:    *Gemma* dispersal is size- and age-selective. A greater proportion of small (young) individuals is collected in pits and traps than is found in undisturbed background sediment.

## METHODS

Natural crab pits, hand-dug simulated crab pits, and cylindrical bottom traps were used to test the hypoth-eses concerning *Gemma* dispersal at Tom's Cove.

### Natural crab pits

Freshly excavated crab pits $\leq$1-d-old were easy to discern because of their black color due to the exposure of anoxic sediment from below the sediment surface. On 8 October 1983 the first 15 fresh pits encountered in the mid-intertidal zone within an area 50 × 50 m on either side of a linear transect parallel to shore were sampled. Two numbered stakes were placed 1 m from the center of each pit, one on each side so that the stake–pit–stake combination formed a straight line. Be-cause the pits were marked, they could be sampled even after they filled in and were no longer distinguishable from the surrounding sediment, a process that usually took one tidal cycle. Repeated sampling of the same pit allowed the recovery of individual pits to be fol-lowed through time, assuming that the samples were sufficiently small relative to pit size not to cause sig-nificant further disruption.

Samples were taken from pits and from control lo-cations 1 m from each pit. Each sample consisted of two combined 2.6 cm diameter cores (10.6 cm² com-bined area, or 3.0% of the average pit surface area) taken to a depth of 15 cm. Core contents were placed in buffered formalin, stained with rose bengal, sieved on 0.25 mm diameter mesh, and sorted. All animals except nematodes were included in the analysis. Shell lengths of *Gemma* were measured to the nearest 0.01 mm with an ocular micrometer. Samples were taken on 8 October 1983 (day 0) when fresh pits were marked and on 22 October 1983 (day 14) and 20 January 1984 (day 104). Ten of the 15 pits and controls from each of the first two sampling dates were randomly selected for analysis. Winter ice later dislodged stakes from all but two of the marked pits, so January data consist of these two marked pits and controls, plus eight addi-

tional control samples taken haphazardly through the ice.

## Simulated pits

Natural crab pits were easy to identify at Tom's Cove, but they were not perfectly uniform in size and shape and were difficult to age precisely. In addition, locations with crab pits may have had different characteristics than undug background areas if crabs actively chose to dig where, for example, prey densities were high. To reduce variability, simulated-pit experiments were conducted. They began early in winter near the end of the crab digging season and during summer while crabs were very active. The elliptical pits were dug by hand at low tide and had dimensions of 18 × 25 × 8 cm deep with rims 5 × 2 cm (W × H), mimicking the typical size and shape of natural crab pits at the site. This procedure provided replicate pits of identical size, shape, and age. Arrays of simulated pits and cylindrical bottom traps were established and sampled during periods of light winds recorded by the United States National Weather Service at the Wallop's Island National Aeronautics and Space Administration Center, ≈10 km from the study site. There were no significant differences in wind velocity among the simulated pit and trap deployment periods when dispersal rates were calculated (Kruskal-Wallis test, $P > 0.75$; mean wind velocity = 3.1 m/s). Tidal variations in water velocity were assumed to play a minor role in dispersal at the study site because it was located at the shallow, upper end of Tom's Cove, away from areas with rapid tidal currents.

On 9 November 1985, a winter array of 20 pits and 20 controls was established in the mid-intertidal zone in four rows parallel to shore. Each row contained five pits and five controls in alternating sequence, 2 m apart. Rows were also 2 m apart and marked with stakes at the ends so that pits and controls could be located for repeated sampling. On the same day (day 0), when the returning tide water was ≈5 cm deep, a 15 cm deep core was taken from each pit and control location with a 4.0 cm diameter coring device (12.6 cm² area, or 3.6% of the pit surface area). Samples were also taken from the same positions on 10 November 1985 (day 1), 15 November 1985 (day 6), 15 December 1985 (day 36), and 10 January 1986 (day 62).

On 17 June 1986 (day 0), a summer array was established and sampled, but with three rows for a total of 15 pits and 15 controls. Samples were also taken on 18 (day 1) and 23 June 1986 (day 6). Samples from winter and summer arrays were processed as described above, except that only *Gemma* individuals were included in the analysis.

## Bottom traps

In order to examine the movement of *Gemma* more precisely than is possible by following pit recolonization, arrays of cylindrical bottom traps were estab-

lished in the winter and summer at Tom's Cove. Bottom traps of this design have been referred to as bedload traps (Emerson 1991, Emerson and Grant 1991), but they capture particles falling from the suspended load in the water column as well as those moving along the bed. Although there are some important principles for the design of sediment traps deployed in the water column (Gardner 1980, Butman 1986, Butman et al. 1986, Yund et al. 1991), there are no clear guidelines for traps installed flush with the sediment surface to capture particles in the bedload and suspended load. Experiments with traps over a wide range of heights, diameters, and aspect ratios (height : diameter) showed clearly that for short-term deployments at Tom's Cove during weather conditions like those in this study, the particle capture rate was proportional to trap diameter but not height or aspect ratio (C. A. Currier and J. A. Commito, *unpublished data*). Traps for this study were glass jars 4.4 cm in diameter and 5.0 cm in height (13.8 cm² cross-sectional area, 70.0 cm³ volume) embedded flush with the sediment surface at low tide. Sediment excavated for the placement of traps was removed from the study site. Each array was established in the mid-intertidal zone and consisted of traps placed 2 m apart in four rows established 2 m apart and parallel to shore. In some arrays, control cores were taken to sample *Gemma* in the background sediment. They were obtained with the same 4.0 cm diameter coring device described above, but to a depth of 5 cm. Controls were positioned between the traps 1 m from each trap within the rows.

The first winter array consisted of 16 traps installed on 10 November 1985 (day 0). Sixteen control samples were taken on 15 November 1985 (day 5) when traps were removed. Two 100-trap arrays were established on 8 and 9 January 1986 (day 0) and removed on 9 and 10 January 1986 (day 1), respectively. Two summer arrays of 50 traps each were established on 18 and 25 June 1986 (day 0). Traps were removed and control samples taken 1 d after installation on 19 and 26 June 1986 (day 1), respectively. All traps and control samples were processed as described above for the simulated-pit experiments. In addition, the amount of sediment in each summer array trap was estimated to the nearest 0.5 cm³ by volumetric displacement.

## Evaluating the hypotheses

If $H_1$ is correct, *Gemma* densities in freshly dug natural and simulated pits should be lower than in control samples from undisturbed background sediment.

If $H_2$ is correct, there should be a positive correlation between the volume of sediment and the number of *Gemma* collected per trap. $H_2$ was also tested in another way. If dispersal is passive, the shape of the frequency distribution of the number of *Gemma* collected per trap should be predicted by the interaction of two empirically-derived frequency distributions. These are the number of *Gemma* per unit area of background sedi-

ment (i.e., per control core) and the volume of sediment collected per trap:

$$[a_i, F(a_i)] \in \{[a, F(a)]\} \quad |$$

$$a = \text{number of } Gemma \text{ per control core}$$

$$F(a) = \text{frequency of } a$$

and

$$[b_j, F(b_j)] \in \{[b, F(b)]\} \quad |$$

$$b = \text{sediment volume collected per trap}$$

$$F(b) = \text{frequency of } b.$$

A program was written that forms all products $[a_i b_j, F(a_i)F(b_j)]$ and sorts these products into a new frequency distribution: the predicted number of *Gemma* per trap. The model ignores any active, density-dependent movement of *Gemma*. It is based on the premise that a constant proportion of the *Gemma* within the sediment is moved into the bedload and suspended load to be deposited with sediment particles into traps. However, the magnitude of that proportion remains˙ unknown. As a result, the model predicts only the shape of the *Gemma* density frequency distribution in traps. The abscissa is not scaled in actual numbers of *Gemma* per trap, but in relative abundance values. The model depends solely on passive dispersal, so if $H_2$ is correct, the actual and predicted frequency distributions of *Gemma* per trap should be the same.

Diffusion models have been used successfully to describe some types of dispersal (Kareiva 1983), but they assume that diffusing organisms move independently, execute simple random walks, and encounter no barriers (Johnson and Milne 1992, Holmes 1993). When these assumptions are not met, large discrepancies arise between diffusion model predictions and actual animal dispersal (Johnson and Milne 1992). At Tom's Cove, topographic irregularities such as crest–trough ripple systems and pit depressions and rims may be partial barriers to movement. More importantly, clams carried along by hydrodynamic forces are not moving independently or randomly. For these reasons, diffusion approaches were not used in this study to model *Gemma* dispersal.

If $H_3$ is correct, the proportion of small *Gemma* in relation to large individuals should be greater in pits and traps than in control cores.

## RESULTS

### Natural crab pits

A total of 22 species was collected in pit and control samples during the course of this investigation. *Gemma* was by far the most abundant, comprising about two-thirds of all the animals in controls and accounting for up to 100% of the individuals in any single sample. Sixteen polychaete species, four amphipod species, and one gastropod species made up the remainder, with low and variable numbers per sample. The only species

other than *Gemma* to appear in numbers greater than one individual per sample were the snail *Ilyanassa obsoleta* and the polychaetes *Spiochaetopterus oculatus, Capitella capitata, Streblospio benedicti, Aricidea jeffreysii,* Syllidae sp., and Phyllodocidae sp. All of the species found are small and live close to the sediment surface, except for *S. oculatus* which inhabits a deep, tough tube.

On day 0, the total density of all species combined was lower in pits than in controls (Wilcoxon 2-sample test, $P < 0.001$; Fig. 1). Comparison of total densities revealed no significant differences ($P > 0.20$) between pits and controls after 14 and 104 d (Fig. 1). There were no significant differences ($P > 0.20$) between pits and controls on any date for the combined densities of all species exclusive of *Gemma* (Fig. 1). However, *Gemma* density was significantly lower in pits than in controls on the first sampling date ($P < 0.001$) but not thereafter ($P > 0.20$; Fig. 1). These results indicate that *Gemma* may have been more susceptible than other species to pit excavation. An alternative explanation is that the densities of the other taxa were too low to detect any significant differences between new pits and controls.

Neither the number of species ($S$, $P > 0.20$) nor the Shannon-Wiener diversity index ($H'$, $P > 0.20$) was significantly different between pits and controls on any date (Fig. 2). However, species equitability, $J'$, was significantly greater in pits than in controls on the first sample date ($P < 0.005$; Fig. 2) because of the reduction in *Gemma* abundance, the numerically dominant organism. Equitability was not different between pits and controls after the first sampling date ($P > 0.02$; Fig. 2).

Because pits were marked and resampled, trajectories could be constructed to characterize the responses of individual pits for the first 14 d after they were excavated. Trajectories were not continued beyond this time because there was no longer a difference in density and there were only two marked pits after winter ice formation. *Gemma* density increased in nine pits and decreased in one pit that had an unusually high density on the first day. The proportion of pits that increased in density was significantly greater than the proportion that decreased (sign test, $P = 0.022$). These results revealed a consistent recolonization response by *Gemma* to pit formation. On the other hand, for speeies other than *Gemma*, the density increased in six pits, remained the same in two pits, and decreased in two pits. There was no significant difference between the proportion of pits increasing and the proportion decreasing ($P = 0.29$). The pattern of recolonization for community members other than *Gemma* was highly variable from pit to pit.

.Size-class histograms for *Gemma* show unimodal distributions (Fig. 3). The Kolmogorov-Smirnoff goodness of fit test revealed no significant difference ($P > 0.50$) between size class distributions from pits and controls on day 0 (Fig. 3). These results indicate that
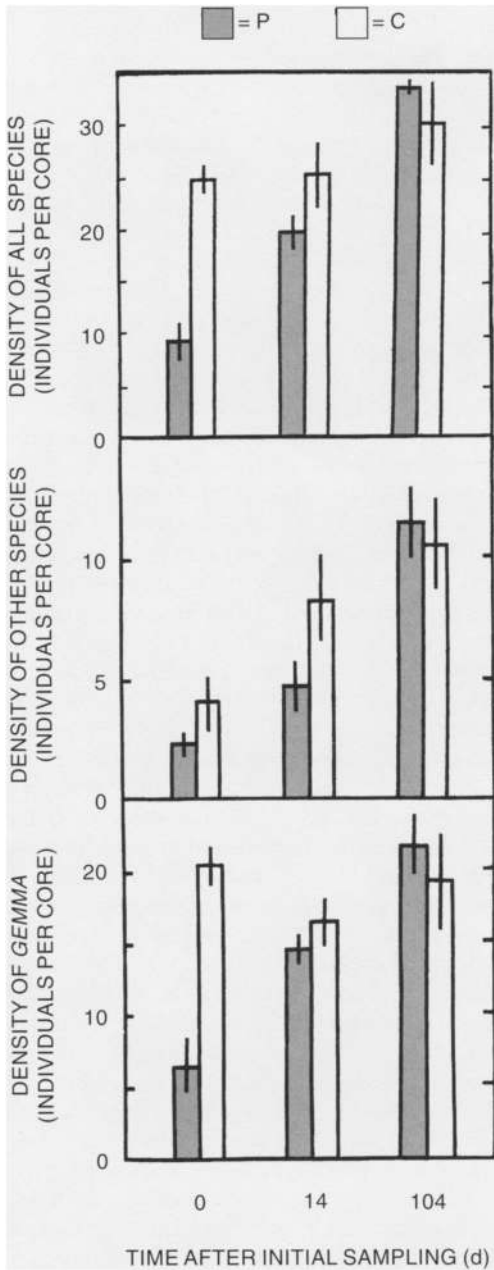
FIG. 1. Densities of organisms (mean ± 1 SE) in natural crab pits (P) and control locations (C) on three sampling dates. A core consisted of two combined subsamples with total area of 10.6 cm². $N = 10$.
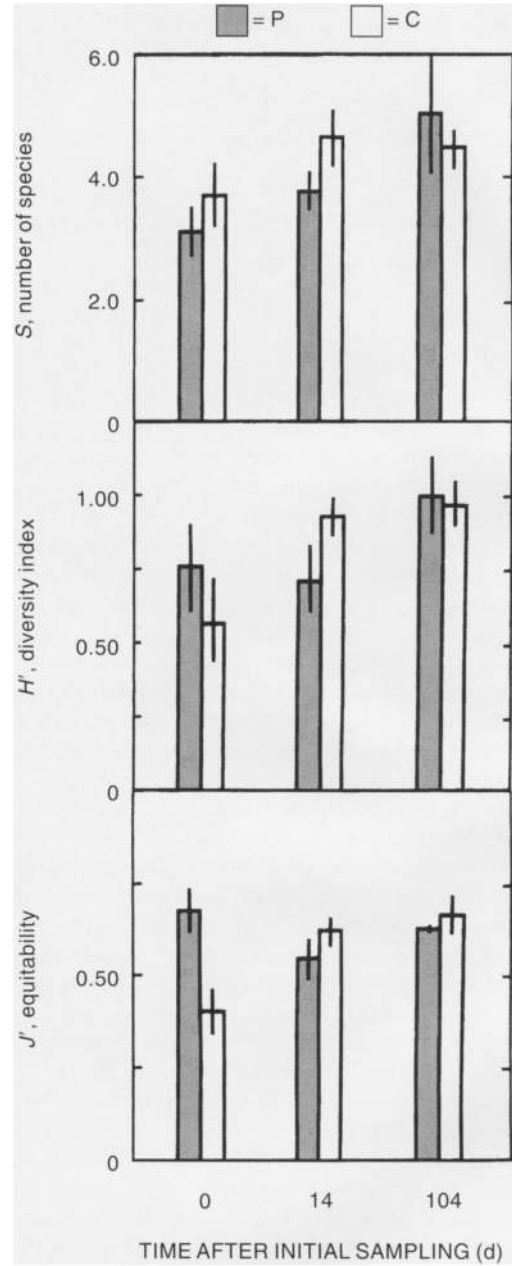


FIG. 2. Number of species ($S$), Shannon-Wiener species diversity index ($H'$), and equitability ($J'$) in core samples from natural crab pits (P) and control locations (C) on three sampling dates. A core consisted of two combined subsamples with total area of 10.6 cm². Data represent mean ± 1 SE, $N = 10$.

pit excavation did not result in size-specific mortality or removal of *Gemma*. There was also no significant size class distribution difference ($P > 0.20$) between pits and controls 14 d later (Fig. 3), indicating that *Gemma* dispersal into pits was not size-selective. Size class distributions are not presented for January because only two marked pits remained after winter ice formation.

### Simulated crab pits

*Winter.*—In the winter array of simulated crab pits (Fig. 4), *Gemma* density was significantly lower in pits than in controls on day 0 (Wilcoxon 2-sample test, $P < 0.01$), indicating that simulated pits were like natural pits in terms of initial *Gemma* removal. There was no significant difference between pits and controls on day
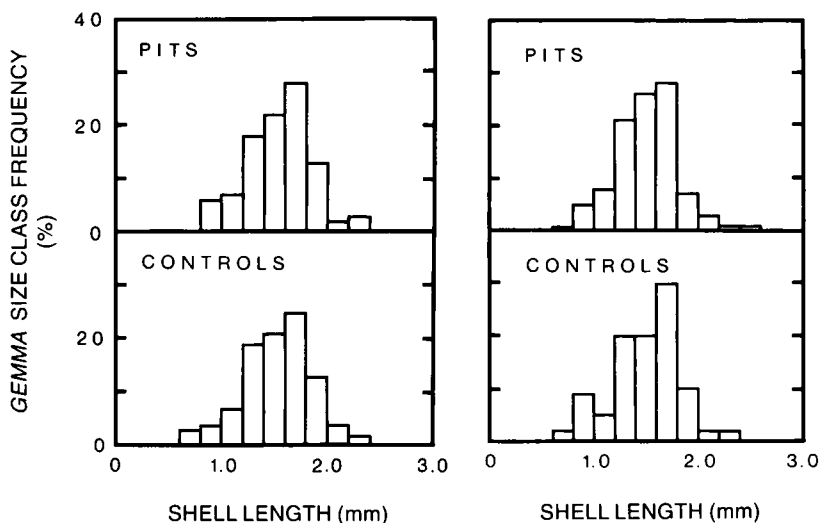
FIG. 3.   Size class frequency distributions for *Gemma* in natural crab pits and control locations on two sampling dates. Left panels: Day 0 and right panels: Day 14. For Day 0, $N$ = 67 for pits, 206 for controls; for Day 14, $N$ = 148 for pits, 168 for controls.

1 ($P$ > 0.02), demonstrating that dispersal into pits quickly brought *Gemma* density back to control levels. This lack of a significant difference between pits and controls was observed on each of the last three sampling dates as well ($P$ > 0.20). Control densities decreased during the course of this experiment, as did pit densities after initial recolonization. The reason for this decline is unclear, although winter declines in *Gemma* abundance have been observed elsewhere (Sellmer 1967).

In the simulated-pit experiment, both pits and control locations were repeatedly sampled to yield *Gemma* density trajectories. From day 0 to day 1, by which

time there were no differences in density between pits and controls, more pits showed increases than decreases in density (11 vs. 4 pits, and no change in 5 pits), but this difference was not significant (sign test, $P$ = 0.119). Control locations showed fewer increases than decreases (6 vs. 11 pits, and no change in 3 pits), but this difference was not significant either ($P$ = 0.334). *Gemma* density initially increased in new pits at the same time it was decreasing in control locations. The consistent initial response to excavation was similar to that observed in natural pits.

In general, the *Gemma* size class distributions from the winter simulated-pit experiment were like those
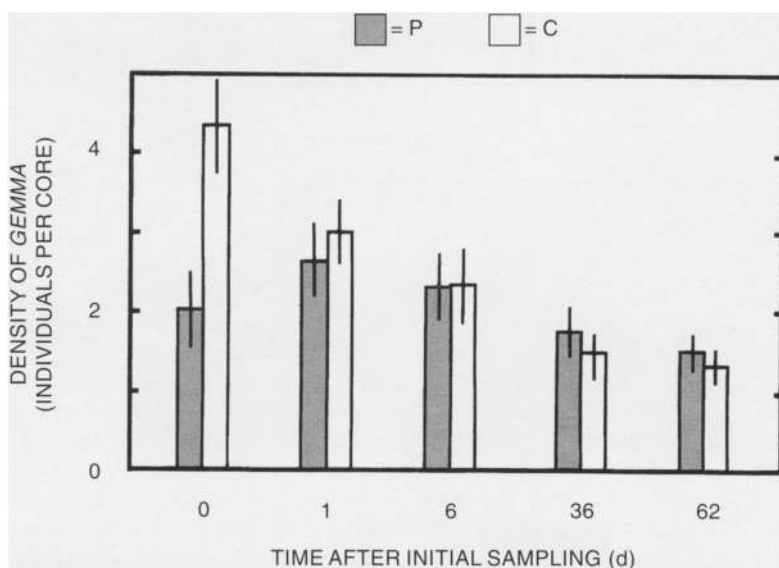


FIG. 4.   Densities (mean ± 1 SE) of *Gemma* in winter array of simulated crab pits (P) and control locations (C) on five sampling dates. Core samples were 12.6 cm² in area. $N$ = 20.
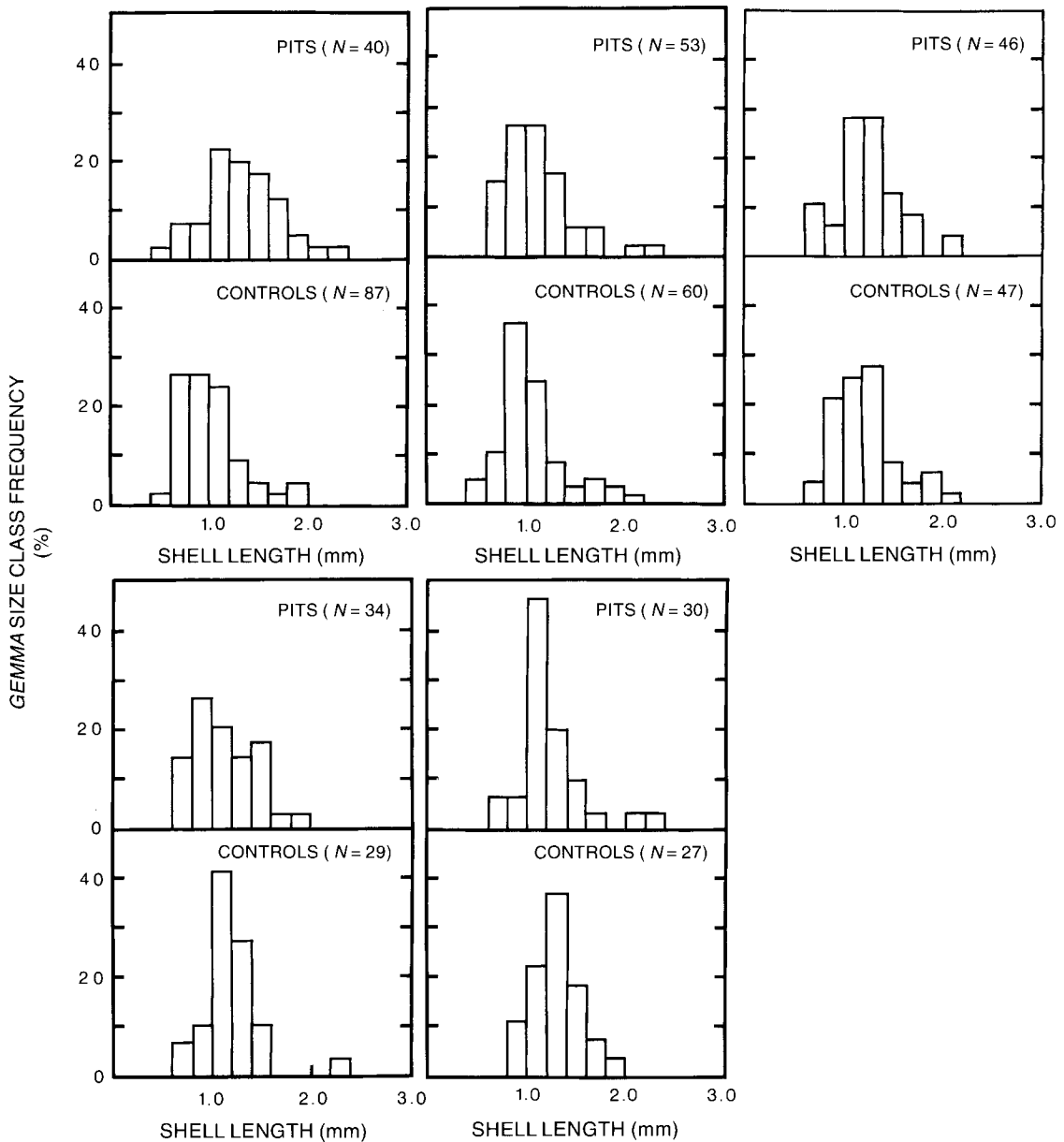
FIG. 5.  Size class frequency distributions for *Gemma* in winter array simulated crab pits and control locations on five
sampling dates. Panels, left to right: Day 0, Day 1, Day 6, Day 36, and Day 62, after initial sampling.

from the natural pits (Fig. 5). However, unlike the nat-
ural pits, on day 0 the simulated pits had a slightly
lower proportion of small individuals than did controls
(Kolmogorov-Smirnoff test, $P < 0.002$), suggesting
size-specific mortality or removal from freshly dug
pits. There were no size class differences between pits
and controls on day 1 ($P > 0.20$) and day 6 ($P = 1.00$).
Differences were apparent again on day 36 ($P < 0.002$)
and day 62 ($P < 0.002$), but pits had larger proportions
of small individuals than did controls. These results
indicate that simulated pits started out with relatively
fewer small *Gemma* than did controls, but that at pit

sites small *Gemma* accumulated or large *Gemma* died
or emigrated selectively during the 2-mo experiment.

*Summer.*—Summer densities of *Gemma* were much
higher than in the winter (Fig. 6; compare with Figs.
1 and 4). In the summer array, *Gemma* density was
significantly lower in pits than in controls on day 0
(Wilcoxon 2-sample test, $P = 0.045$), the same result
observed in the natural and winter simulated pits. Thus,
the results from the investigation of natural pits and
both simulated-pit experiments support $H_1$, that *Gemma*
density in newly dug pits is lower than the background
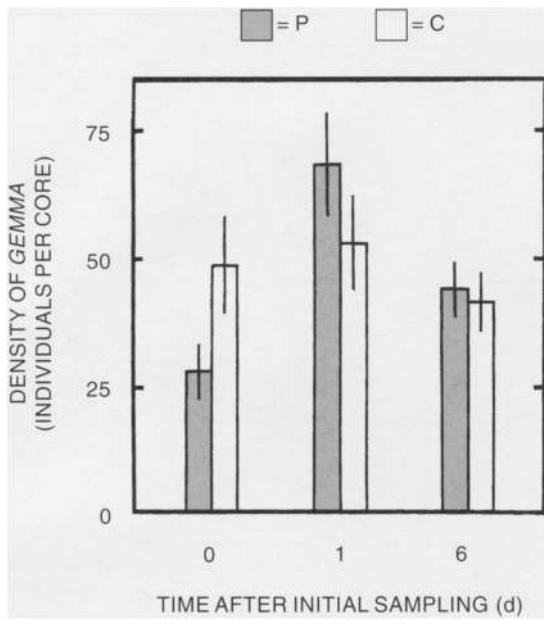density in undisturbed sediment. There were no sig-

FIG. 6. Densities of *Gemma* (mean ± 1 SE) in summer array of simulated crab pits (P) and control locations (C) on three sampling dates. Core samples were 12.6 cm² in area. *N* = 15.

nificant differences between pits and controls on day 1 (*P* = 0.130) and day 6 (*P* = 0.333), indicating that recovery of pits to control densities occurred during the first day.

Individual density trajectories indicate clearly that from day 0 to day 1, when there was no longer a density difference between pits and controls, more pits showed increases than decreases (13 vs. 2 pits; sign test, *P* = 0.007). Controls showed no difference between the number of locations increasing and decreasing (8 vs. 7 pits; *P* = 1.00). As was the case for natural and winter simulated pits, the summer pits responded quickly to excavation and were indistinguishable from controls by the first sampling date after day 0.

Dispersal rates of *Gemma* into pits were calculated in two ways. The absolute dispersal rate is the accumulation of *Gemma* in pits over time, or the change in density in pits between day 0 and the next sampling date. The relative dispersal rate takes into account the background density of *Gemma* in undisturbed sediment, the value of which varies spatially and over time. The relative dispersal rate equals the absolute dispersal rate divided by the background density in control cores. The absolute and relative dispersal rates into simulated pits were 62 and 3.5 times greater, respectively, in the summer array than in the winter array (Table 1). It would be premature to claim that these rate values represent true seasonal differences because they are based on a limited number of sample dates.

Unlike the unimodal *Gemma* size class distributions from the fall and winter, those from the summer experiment revealed a bimodal pattern in both pits and controls on all three sampling dates (Fig. 7). The bimodal size class distributions indicate that successful *Gemma* recruitment occurred in the summer during the course of this investigation. Size class distributions in pits and controls were not significantly different on any sampling date (Kolmogorov-Smirnoff test, day 0, *P* = 1.00; day 1, *P* = 1.00; day 6, *P* = 0.15). Compared to day 0, however, there was a slight trend for day 1 and day 6 pits to have a lower proportion of the smallest sizes of *Gemma* than controls. The data suggest that small clams did not disperse more readily than large ones back into pits. These summer size class results are the opposite of those from the winter. Since $H_3$ predicted that a greater proportion of small, young *Gemma* would collect in pits than would be found in undisturbed sediment, the hypothesis is supported by the winter results but not by those from the summer.

The summer bimodal size class distributions were divided into discrete age classes corresponding to yearly cohorts (Sellmer 1967, Weinberg 1985). Separating summer *Gemma* samples into 0-yr class (juvenile) and 1-yr class (adult) individuals was achieved by using

TABLE 1. *Gemma gemma* dispersal into simulated horseshoe crab pits during the winter (*N* = 20) and summer (*N* = 15). Density values represent means ± 1 SE; the simulated pits were established on day 0.

| | Sampling time | | | |
| --- | --- | --- | --- | --- |
| | Winter | | Summer | |
| Sample parameter | Day 0 | Day 1 | Day 0 | Day 1 |
| Control density (no. individuals per core) | 4.35 ± 0.63 | 3.00 ± 0.40 | 48.93 ± 10.43 | 53.13 ± 9.15 |
| Pit density (no. individuals per core) | 2.00 ± 0.50 | 2.65 ± 0.45 | 28.07 ± 5.29 | 68.47 ± 9.99 |
| Percentage change in pit density (%) from day 0 to day 1 | 32.50 | | 143.93 | |
| Absolute dispersal rate* | 0.65 | | 40.40 | |
| Relative dispersal rate† | 0.22 | | 0.76 | |

* Absolute dispersal rate (no. individuals·pit core$^{-1}$·d$^{-1}$) = $\dfrac{\text{(pit density on day 1)} - \text{(pit density on day 0)}}{1\ \text{d}}$.

† Relative dispersal rate (no. individuals·pit core$^{-1}$·no. control individuals$^{-1}$·d$^{-1}$) = (absolute dispersal rate) ÷ (control density on day 1).
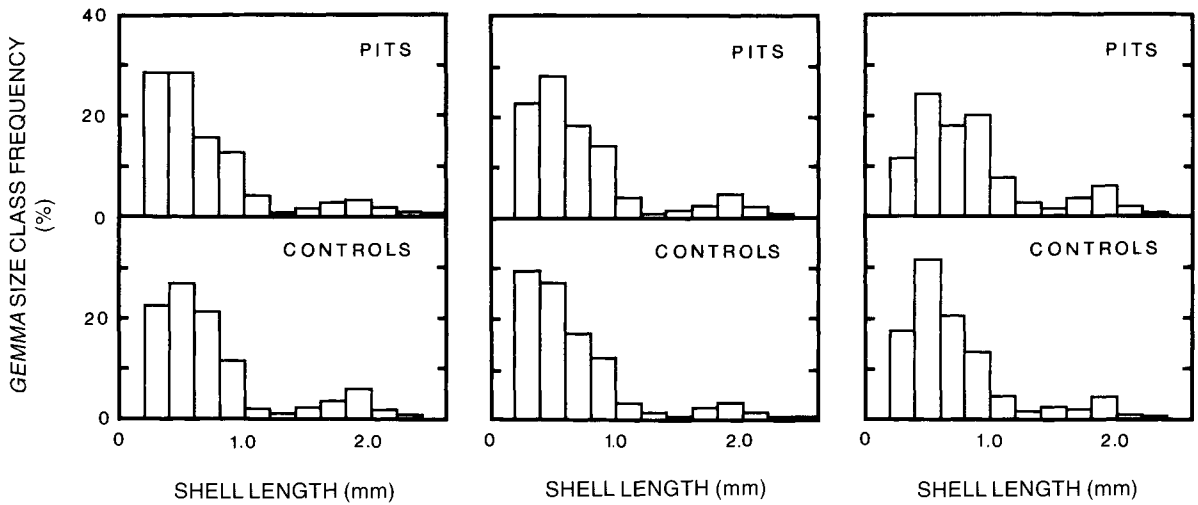
FIG. 7. Size class frequency distributions for *Gemma* in summer array simulated crab pits (P) and control locations (C) on three sampling dates. Panels, left to right: Day 0, Day 1, and Day 6 after initial sampling. For Day 0, $N = 414$ for P, 734 for C; For Day 1, $N = 795$ for P, 1027 for C; for Day 6, $N = 620$ for P, 661 for C.

1.30 mm as the dividing point between the two modes (Fig. 7). In pits, 90.2%, 88.0%, and 84.4% of the clams were in the 0-yr class on days 0, 1, and 6, respectively, with 9.8%, 12.0%, and 15.6% in the 1-yr class. In controls, the corresponding results were 84.9%, 90.6%, and 88.1% in the 0-yr class and 15.1%, 9.4%, and 11.9% in the 1-yr class. There was a significantly greater proportion of 0-yr class individuals in pits than in controls on day 0 (chi-square test, $P < 0.005$), but a significantly smaller proportion of 0-yr class individuals on day 1 and day 6 ($P < 0.005$ for both days). These results suggest that pit-digging altered the age-class distribution by selectively removing the 1-yr class clams, but that the 1-yr class individuals dispersed into pits more readily than did 0-yr class individuals. Thus, the

*Gemma* summer age-class results, like those for the summer size class distributions, fail to support $H_3$.

### Bottom traps

*Winter.*—The small winter bottom trap array consisted of 16 traps in place for 5 d. There were 9.25 ± 1.53 (means ± 1 SE) *Gemma* collected per trap. The control density was 9.44 ± 1.55 clams per core on the day the traps were removed. Size class frequency histograms (Fig. 8) revealed that a larger proportion of small *Gemma* dispersed into traps than was found in controls (Kolmogorov-Smirnoff test, $P < 0.005$).
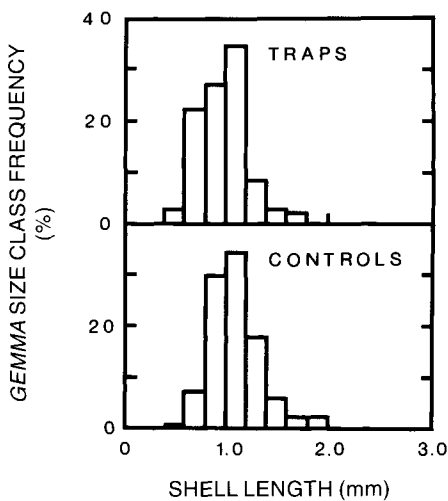


FIG. 8. Size class frequency distributions for *Gemma* in small array of winter bottom traps ($N = 148$) and control locations ($N = 151$).
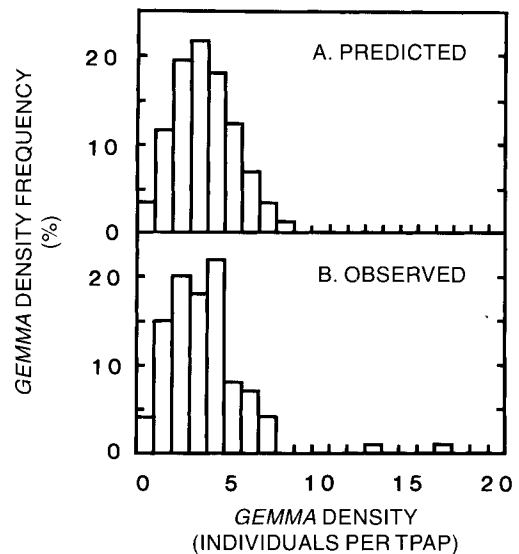


FIG. 9. Density frequency distributions for *Gemma* in first large array of winter bottom traps. (A) Predicted density frequencies based on the Poisson distribution. (B) Observed density frequencies. $N = 337$.

FIG. 11. Density of *Gemma* vs. volume of sediment collected per trap in the first large array of summer bottom traps. Traps were 4.4 cm in diameter, 5.0 cm high.
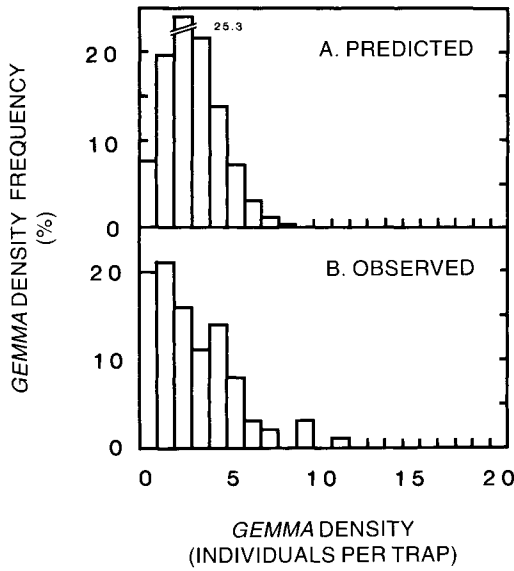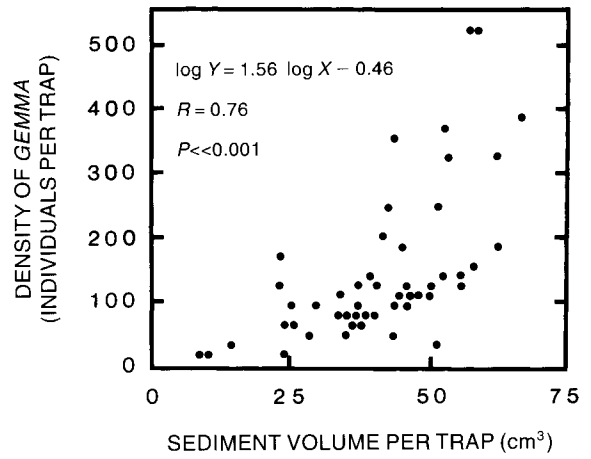
FIG. 10. Density frequency distributions for *Gemma* in second large array of winter bottom traps. (A) Predicted density frequencies based on the Poisson distribution. (B) Observed density frequencies. $N = 256$.

These size class results were consistent with those observed in the winter simulated-pit experiment conducted over the same time period.

The two large winter arrays consisted of 100 traps each (no background control cores) left in place for 1 d. These arrays had densities of $3.37 \pm 0.02$ and $2.56 \pm 0.23$ (means $\pm 1$ SE) *Gemma* per trap, respectively. Because of the large numbers of traps deployed and the low *Gemma* densities collected, the density frequency distributions in each array could be compared with the Poisson distributions predicted if dispersal were random. One array was not significantly different from random (Kolmogorov-Smirnoff test, $P > 0.50$; Fig. 9). The other array was not random and had a larger proportion than expected of traps which collected either no *Gemma* or many *Gemma* ($P < 0.05$; Fig. 10).

*Summer.*—*Gemma* densities in the two summer trap arrays, each with 50 traps left in place for 1 d and 50 background control cores, were greater than those in the winter trap arrays (Table 2). The mean absolute dispersal rate was 12 times greater in the two summer arrays than in the small winter array left in place 5 d and 38 times greater than in the two large winter arrays left in place 1 d. The relative dispersal rate was almost 1.5 times greater in summer (mean of two arrays left in place 1 d) than in the small winter array. Like the simulated-pit experiments, these trap results are consistent with the view that there are seasonal dispersal rate differences, but they are derived from too small a number of samples to make that assertion unequivocally.

The first summer array had lower background density but much greater accumulation of *Gemma* in traps than did the second summer array. This result is the opposite of what would be expected if *Gemma* dispersed in a density-dependent manner. The sediment volume collected per trap was $41.2 \pm 1.9$ cm³ in the first array and $45.8 \pm 1.8$ cm³ (means $\pm 1$ SE) in the second. The relationship between the sediment volume per trap and

TABLE 2. *Gemma gemma* dispersal into bottom trap arrays during the winter and summer. Density values represent means $\pm 1$ SE.

| | Winter | | | Summer | |
|---|---|---|---|---|---|
| Sample parameter | Array 1 (5 days)‡ ($N = 16$) | Array 2 (1 day) ($N = 100$) | Array 3 (1 day) ($N = 100$) | Array 1 (1 day) ($N = 50$) | Array 2 (1 day) ($N = 50$) |
| Control density (no. individuals per core) | $9.44 \pm 1.15$ | ··· | ··· | $76.82 \pm 4.26$ | $89.24 \pm 5.20$ |
| Trap density (no. individuals per trap)* | $9.25 \pm 1.53$ | $3.37 \pm 0.02$ | $2.56 \pm 0.23$ | $143.20 \pm 12.02$ | $82.48 \pm 4.20$ |
| Relative dispersal rate† | 0.98 | ··· | ··· | 1.86 | 0.92 |

\* Trap density = absolute dispersal rate (no. individuals·trap⁻¹·sample interval⁻¹) because all traps started with no *Gemma*.
† Relative dispersal rate (no. individuals·trap⁻¹·no. control individuals⁻¹·sample interval⁻¹) = (absolute dispersal rate) ÷ (control density on day trap was sampled).
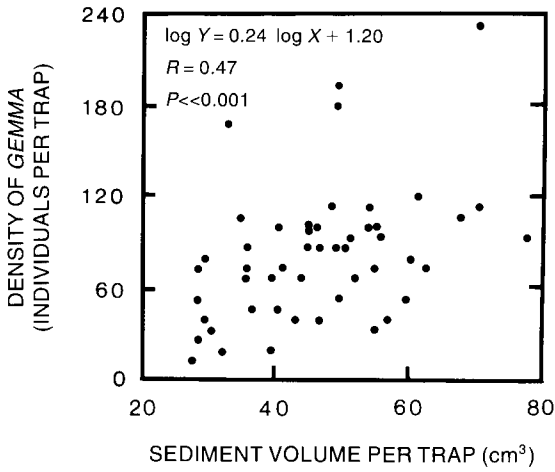‡ Days refer to time after installation of the traps.

FIG. 12. Density of *Gemma* vs. volume of sediment collected per trap in second large array of summer bottom traps. Traps were 4.4 cm in diameter, 5.0 cm high.

the number of *Gemma* per trap was curvilinear. The regressions of log-transformed data (Figs. 11 and 12) showed that sediment volume predicted the number of *Gemma* collected per trap, with *r* values of 0.76 and 0.47 in the two arrays, respectively. The regression

results support $H_2$, that *Gemma* dispersal is passive and occurs as part of the bedload.

The dispersal model presented earlier is based on the interaction of two frequency distributions: the number of *Gemma* per unit area of background sediment (i.e., per control core) and the volume of sediment collected per trap. When the control density frequency distributions (Figs. 13A and 14A) and the trap sediment volume frequency distributions (Figs. 13B and 14B) were used in the model, it predicted that the shapes of the trap density frequency distributions in the two arrays would be right-skewed (Figs. 13C and 14C). The model's predictions were qualitatively correct for both arrays (Figs. 13D and 14D). Although the Kolmogorov-Smirnoff test showed a difference between predicted and actual density frequency distributions in the second array (Fig. 14C vs. Fig. 14D, $P = 0.0007$), the actual distribution in the first array was not significantly different (Fig. 13C vs. Fig. 13D, $P = 0.49$) from that predicted by the model. The dispersal model was able to predict at least the general shape of the *Gemma* density frequency distributions in the two trap arrays based solely on two field parameters. The results from the model provide additional support for $H_2$, that *Gemma* disperses passively as part of the bedload.
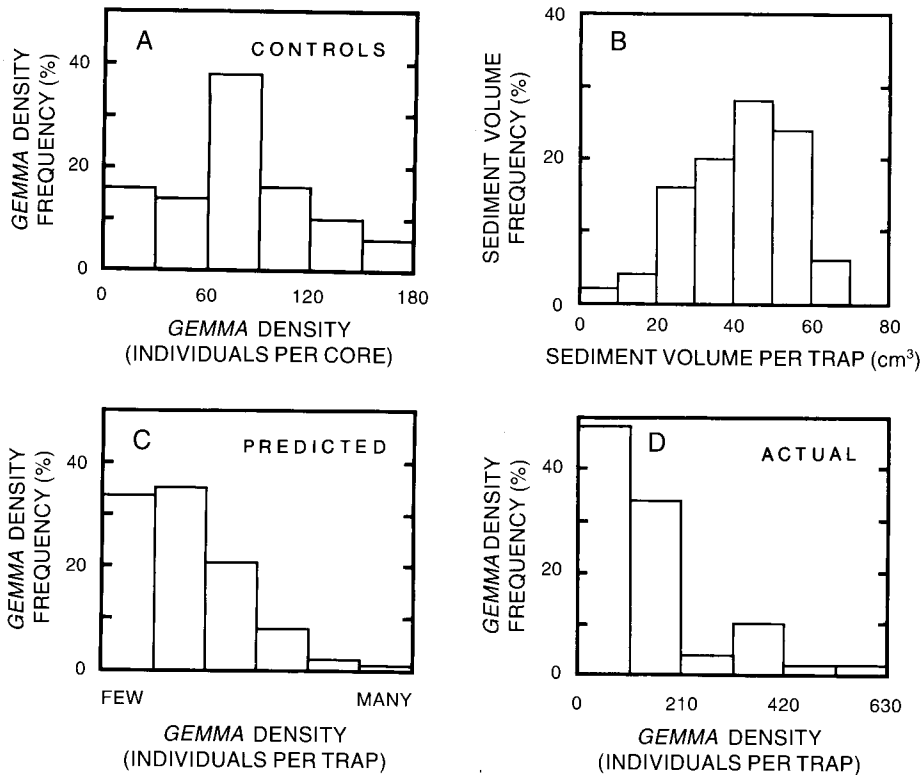


FIG. 13. For the first array of summer bottom traps and control samples: (A) Density frequency distribution for *Gemma* in controls (undisturbed background sediment) ($N = 3841$). (B) Sediment volume frequency distribution in traps. (C) Predicted density frequency distribution for *Gemma* in traps. Abscissa is relative scale. (D) Actual density frequency distribution for *Gemma* in traps ($N = 7159$).
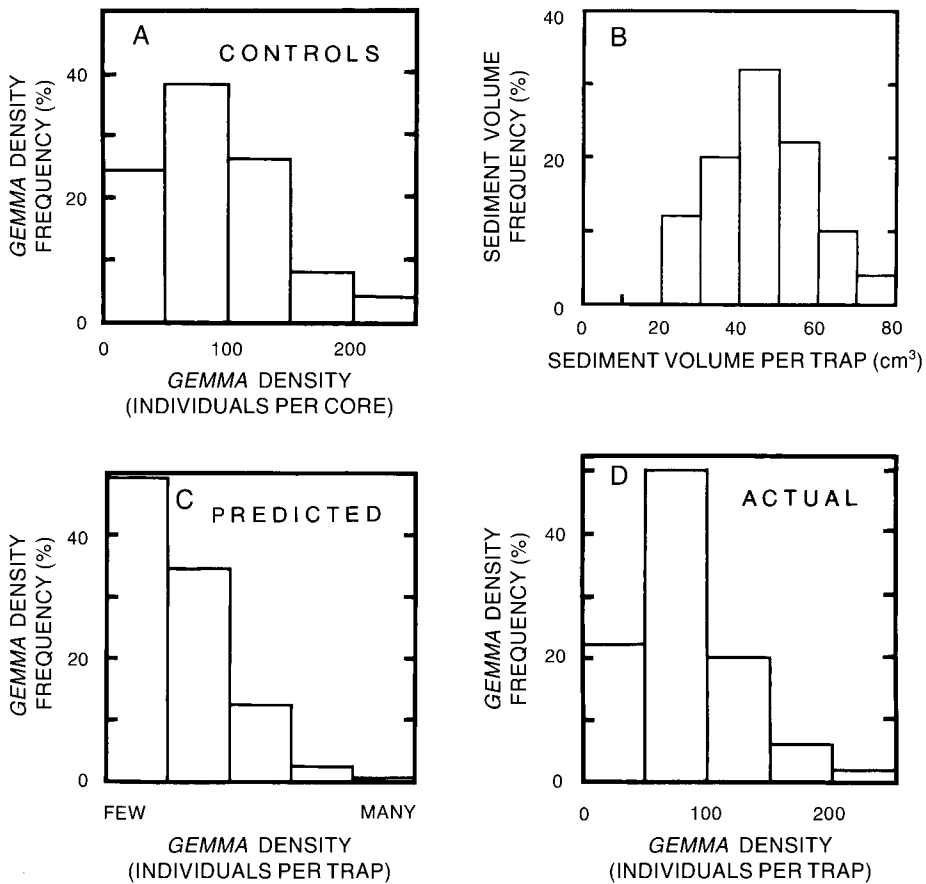
FIG. 14. For the second array of summer bottom traps and control samples: (A) Density frequency distribution for *Gemma* in controls (undisturbed background sediment) (*N* = 4457). (B) Sediment volume frequency distribution in traps. (C) Predicted density frequency distribution for *Gemma* in traps. Abscissa is relative scale. (D) Actual density frequency distribution for *Gemma* in traps (*N* = 4124).

The size class frequency distributions revealed a bimodal pattern in summer traps and controls for both arrays (Figs. 15 and 16), as was observed in the summer simulated-pit experiment. There was no difference between the size class frequency distributions of traps and controls in the first array (Kolmogorov-Smirnoff test, *P* = 0.09), but there was a significant difference in the second (*P* = 0.0002). There was a trend in both arrays for traps to have lower proportions of the smallest *Gemma* than did controls. The trap findings were similar to those from the simulated-pit experiments in that winter results supported and summer results refuted $H_3$ concerning the sizes and ages of dispersing clams.

The bimodal summer trap and control size class distributions were divided into two age classes as described above for the summer simulated-pit experiment. In traps, 90.5% and 80.0% of the individuals were in the 0-yr class in the first and second arrays, respectively, while 9.5% and 20.0% were in the 1-yr class. In controls, 92.9% and 90.2% were in the 0-yr class, with 7.1% and 9.8% in the 1-yr class. There was

a smaller proportion of 0-yr class individuals in traps than in controls in both arrays (Kolmogorov-Smirnoff test, *P* < 0.005; both arrays). Like the age-class results from the summer simulated-pit experiment, these trap results fail to support $H_3$.

## DISCUSSION

The analysis of natural crab pits, simulated pits, and bottom sediment traps at Tom's Cove clearly showed that dispersal plays an important role in regulating the local distribution and abundance of the ovoviviparous bivalve *Gemma gemma*. This study demonstrated that disturbance agents create localized patches with reduced densities of *Gemma*, that all sizes and ages of *Gemma* quickly disperse into these low-density patches, and that the mechanism of dispersal is passive bedload and suspended load transport.

Winter and summer results consistently supported the hypothesis ($H_1$) that natural and simulated pits have lower *Gemma* densities than does the background control sediment. A wide variety of crabs, fish, and marine mammals dig pits in the intertidal, shallow subtidal,
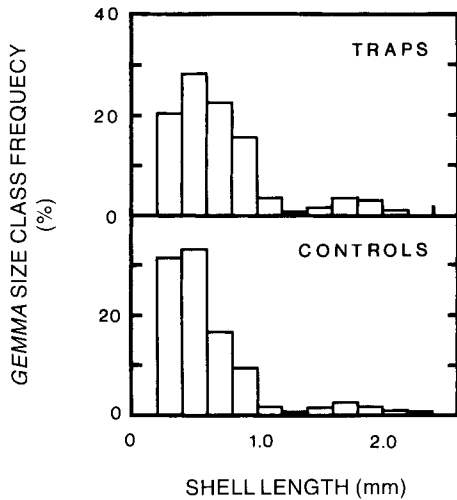
FIG. 15.  Size class frequency distributions for *Gemma* in first array of summer bottom traps (*N* = 7159) and control locations (*N* = 3841).

and deep ocean floor. Such pits are common along the Atlantic coast of the United States where blue crabs (Virnstein 1977, Blundon and Kennedy 1982*a*, *b*) and horseshoe crabs (Virnstein 1977, Blundon and Kennedy 1982*a*, *b*) and horseshoe crabs (Botton 1984*a,b*) play major roles in controlling the structure of soft-bottom communities (Woodin 1978, 1981, Bell and Woodin, 1984).

During the course of this study, horseshoe crabs were the primary pit excavators at Tom's Cove. Botton (1984*c*) has demonstrated that horseshoe crabs can ingest *Gemma* but that this bivalve is generally avoided as a prey item. The lower density of *Gemma* in natural pits was most likely due to their being pushed out of the crabs' excavations rather than to their being eaten. Using a laboratory flume, Palmer (1988*a*) was able to separate predation, disturbance, and hydrodynamic effects of epibenthic fish predators on meiofauna. Some putative prey showed higher rates of removal from disturbance-induced mortality and transport in the water column than from direct fish consumption. At Tom's Cove, bioturbation without direct predator consumption was mimicked in the simulated-pit experiments, and the *Gemma* response was similar to that observed in natural pits. Although the raised rims of sediment displaced from pits were not quantitatively sampled, they did contain evicted clams (J. A. Commito, *personal observation*). Experiments have shown that *Gemma* can survive for several days when buried beneath 20 cm of sediment (Bradley and Cooke 1959). As pits filled in with sediment from slumping pit walls and hydrodynamic transport, clams were carried back in. Such an explanation is consistent with the rapid (one day) recolonization times observed in this study.

What were the relative contributions of *Gemma* movement into pits from slumping pit walls and more

distant bedload and suspended load transport? Dispersal rates into pits can be compared with rates into traps, the glass walls of which prevent slumping. The capture efficiencies of pits and traps are probably different, so the comparison provides only a preliminary answer. Both absolute and relative dispersal rates into traps were approximately half of those into pits, suggesting that *Gemma* dispersed into pits about equally from local slumping and more distant sources. As patch size increases, the perimeter-to-area ratio declines, resulting in a reduction in the relative contribution of slumping and an increase in the importance of more distant sources of clams. Only future experiments with marked *Gemma* can adequately assess the relative contributions of the two sources. However, experiments with glass test tubes inserted into defaunated sediment patches at sandflat (Fegley 1988) and saltmarsh (DePatra and Levin 1989) sites demonstrated conclusively that meiofauna moved into traps from >5 cm away, along with transported sediment.

It is difficult to assess seasonal differences in *Gemma* dispersal from the limited number of sample dates reported here. The results from this study suggest that the absolute dispersal rate was greater in summer than in winter. *Gemma* density at Tom's Cove was higher in the summer, so it is not surprising that far more clams dispersed into pits (62 times more) and traps (12–38 times more) in summer than in winter. Even after taking into account the different seasonal densities of *Gemma*, the rate of dispersal was still higher in summer than winter. The relative dispersal rates were 3.5 times higher into pits and 1.5 times higher into traps in summer than in winter. If winds during the summer portions of this study had been stronger than during the winter investigations, then any resulting increase in bedload and suspended load transport might explain these dis-
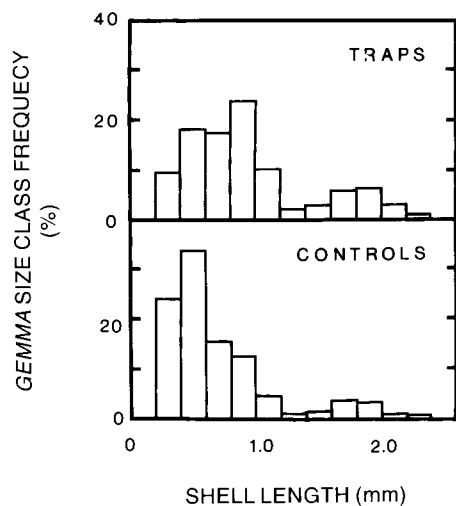


FIG. 16.  Size class frequency distributions for *Gemma* in second array of summer bottom traps (*N* = 4124) and control locations (*N* = 4457).

persal rate differences (Grant 1983, Miller and Sternberg 1988, Miller 1989, Emerson 1991, Emerson and Grant 1991, J. A. Commito, S. F. Thrush, R. D. Pridmore, J. E. Hewitt, and V. J. Cummings, *unpublished manuscript*). However, summer and winter wind velocities were not significantly different during the times when dispersal rates were calculated. In fact, when wind direction is considered, the influence of the wind may actually have been less for the summer dates of this investigation compared to those in winter. United States National Weather Service data indicate that, unlike on the winter dates, wind direction on the summer dates was sometimes from the east across land rather than across the open water of Tom's Cove, thus operating over a shorter fetch.

In her review, Palmer (1988b) argued that bioturbation events causing increased sediment resuspension (Grant et al. 1982) may lead to increased availability of sediment-dwelling organisms for dispersal by water currents. Such disruption of the sediment is especially evident at Tom's Cove over the summer, when crabs dig pits (Woodin 1978). Small, juvenile *Gemma* are most abundant during summer and live closer to the sediment–water interface than do adults (Bradley and Cooke 1959), so sediment disruption may reach more clams in summer than winter and cause them to be released from the sediment. These factors may have contributed to the higher relative dispersal rate observed in summer than winter.

The significant positive correlation between the volume of sediment and the number of *Gemma* collected per trap supports the hypothesis ($H_2$) that dispersal is passive. Clams moved along with sediment particles as part of the bedload and suspended load. Because clams and sediment particles do not have exactly the same transport dynamics, the relationship between the number of clams and bulk sediment volume in traps may exhibit some variability. In this study, two trap arrays had values of $r = 0.47$ and 0.76 for the correlation between sediment volume and number of *Gemma* per trap. At two sites in Nova Scotia, Canada, values of $r = 0.33$ and 0.51 were calculated for *Mya arenaria* (Emerson 1991, Emerson and Grant 1991). On the other hand, J. A. Commito, S. F. Thrush, R. D. Pridmore, J. E. Hewitt, and V. J. Cummings (*unpublished manuscript*) obtained $r^2$ values close to 1.0 for infauna and sediment captured in bottom and water column traps in Manukau Harbour, Auckland, New Zealand.

The relative contributions of bedload and suspended load to dispersal at Tom's Cove remain unknown. However, the Manukau Harbour results demonstrated quite clearly that the bedload contributed more to bivalve dispersal than did suspended load (J. A. Commito, S. F. Thrush, R. D. Pridmore, J. E. Hewitt, and V. J. Cummings, *unpublished manuscript*). In that study, bottom traps always captured far more sediment and bivalves than did traps raised 15 cm above the bottom.

Results from the simple dispersal model provide ad-

ditional evidence that *Gemma* dispersal was passive at Tom's Cove. Without invoking any assumptions about actively-directed movement, the model incorporated two parameters: the frequency distribution of the number of *Gemma* per unit area of background sediment and the frequency distribution of sediment volume collected per trap. Measurement of these two parameters was sufficient to predict the frequency distribution of *Gemma* collected in traps. The shape of that frequency distribution was not the same as that of the sediment volume collected per trap. If it had been, then one could argue that *Gemma* transport was some function of average background density. Instead, it appears that *Gemma* transport was more closely linked to small, localized *Gemma* patches close to traps.

Macrofauna dispersal into sediment excavations has been shown in some studies to be due to active migration. Swimming scavenger amphipods invade ray and whale feeding pits, as do crawling starfish and brittle stars (VanBlaricom 1982, Oliver and Slattery 1985, Oliver et al. 1985). Thrush (1986a, b) attributed high densities of polychaetes and a bivalve inside crab pits to active swimming and crawling. Frid (1989) found rapid rates of subsurface crawling by annelids into defaunated sediment plugs. Physical factors such as sediment movement (Grant 1981), flowing water (Martel and Chia 1991), low seawater temperature (Sörlin 1988), and the interaction of light, oxygen, and salinity levels (Armonies 1988) can cause some macrofauna and meiofauna to emerge from the sediment and actively disperse. Biological factors including food availability (Decho and Fleeger 1988), the presence of predators and sediment disturbers (Ambrose 1984a, DeWitt and Levinton 1985, Tamaki 1988), and high population densities (Wilson 1983, Ambrose 1986, Service and Bell 1987) have also been shown to cause active infauna dispersal, as have chemical cues released from fecal mounds (Varon and Thistle 1988) and sediment contaminated with pollutants (Pridmore et al. 1991).

On the other hand, Sherman and Coull (1980) attributed meiofauna recolonization of disturbed sediment to passive transport along the sediment–water interface. Kern and Taghon (1986) showed that harpacticoid colonization of defaunated sediment was generally proportional to bulk sediment transport. Fegley (1988) found that ciliate and nematode abundances in bottom traps were significantly correlated with sediment volume collected, but other meiofauna were not. Hicks (1988) documented the passive rafting of meiofauna. DePatra and Levin (1989) concluded that meiofauna were passively deposited into natural and simulated fiddler crab burrows in field and flume studies. Perhaps the research most relevant to the analysis of *Gemma* at Tom's Cove is that of Emerson (1991) and Emerson and Grant (1991), who demonstrated that movement of the bivalve *Mya arenaria* was propor-

tional to sediment transport on protected and exposed sandflats.

As Palmer (1988b) and Armonies (1992) have pointed out, both active and passive dispersal mechanisms can be important in the same system. Crowding may cause clams to emerge actively from the sediment and be carried passively by hydrodynamic action, especially in the summer when juvenile *Gemma* densities are highest. Such a possibility is not precluded by the Tom's Cove results, although comparison of the two summer trap arrays showed greater dispersal of *Gemma* into the set of traps with lower background density. Invoking both dispersal mechanisms helps resolve the apparent conflict between the active dispersal (Jackson 1968) and passive dispersal (Sellmer 1967, Green and Hobson 1970) arguments regarding *Gemma*. However, the passive mode of dispersal agrees with Palmer's (1988b) prediction for a highly disturbed soft-bottom system and extends the applicability of her meiofauna model to include macrofauna.

The last hypothesis ($H_3$) was that *Gemma* dispersal is size- and age-selective, with a greater proportion of small, young clams moving into pits and bottom traps than is found in undisturbed background sediment. The results from the winter trap arrays and winter simulated-pit experiment support this hypothesis. Results from the natural pits (no difference between pits and controls) and the summer trap arrays and summer simulated-pit experiment (lower proportion of small, young clams moving into traps and pits than in controls) do not. Such contradictory results lead to an equivocal rejection of $H_3$. *Gemma* size class distributions were unimodal in winter and bimodal in summer, with large numbers of the newly released small clams present during the warm months. It was expected that these 0-yr class individuals would be most easily transported by water currents into pits and traps. It is possible that water currents may have suspended small *Gemma* more readily than large ones, but that small clams remained in suspension and were swept along in the bedload, while large clams fell out of suspension more readily and were deposited into pits and traps (Nowell and Jumars 1984, Butman 1986, Yund et al. 1991). Another possibility is that small *Gemma* may have been resuspended and carried out of pits and traps. DePatra and Levin (1989) found that the abundance and distribution of large and small meiofauna varied among simulated fiddler crab burrows of different shapes due to differing circulation patterns over and within the burrows. At Tom's Cove, the traps and simulated pits were of the same design in winter and summer, yet they still yielded different size class distributions depending on the season. In addition, the shape and size of the simulated pits were different from those of the traps. Yet within each of the two seasons the *Gemma* size class distributions were similar in pits and traps, indicating that the results were dependent upon season and independent of the size and shape of the collecting structure.

Virnstein (1978) and Hall et al. (1990) have argued that cages commonly used by benthic ecologists to exclude epibenthic predators may produce a variety of artifacts, some of which are due to altered water flow. The results of this study on the mobility of *Gemma* support that view and have important implications for the interpretation of caging experiments. For example, Woodin (1981) and Bell and Woodin (1984) clearly showed with an elaborate series of exclosure cages and pens that densities of some infaunal species increased when protected from blue crabs and horseshoe crabs at Tom's Cove. However, densities of *Gemma* inside cages were the same as or even lower than those in controls. The lack of a predation effect inside the cages could simply be due to the avoidance of *Gemma* as a prey item by crabs. Horseshoe crab (Botton 1984c) and shorebirds (Schneider 1978, Botton 1984d) selectively avoid *Gemma*, possibly because of the clam's small size and thick, strong shell. However, *Gemma* density was sometimes lower inside cages than outside, a paradoxical result that cannot be explained by prey selectivity. The results might be explained in the following way. Woodin (1981) and Bell and Woodin (1984) found that the densities of spionid polychaetes, including *Polydora ligni*, increased inside their predator exclusion cages. Weinberg (1984) has demonstrated that *P. ligni* and other spionids lower the survivorship of *Gemma*, in part because they ingest the bivalves. Commito (1982) and Commito and Ambrose (1985) have suggested that such predatory infauna may be important inside cages designed to exclude epibenthic predators, and Ambrose (1984b, c) has demonstrated this phenomenon. If immigration of *Gemma* into cages were reduced because of the mesh walls, then *Gemma* outside the cages could not move inside to compensate for the mortality caused by spionids and other factors. These events would result in lower *Gemma* abundance inside cages than outside.

One way to test this explanation is to compare Woodin's (1981) cage and control densities with those from her pens designed to exclude only horseshoe crabs. These pens consisted of metal rods driven into the sediment 10 cm apart and allowed dispersing *Gemma* access to the inside. In fact, *Gemma* densities were higher inside these pens (even in the presence of elevated spionid densities) than in cages and controls, lending support to our explanation. As Frid (1989) and Hall et al. (1991) have demonstrated, any cage-induced change in the movement of infauna makes it difficult to interpret the results from experiments testing for the importance of predators in controlling soft-bottom community structure.

It is apparent from this study that dispersal by mobile juveniles and adults is an important process in soft-bottom systems. At the community level of organization, Hall et al. (1993) have asked why pit-digging and

other small-scale disturbance events do not always produce long-term, large-scale effects on the infauna. Results from Tom's Cove provide a preliminary answer: high rates of postlarval dispersal may quickly smooth out small-scale patchiness and homogenize infaunal abundances over wide areas. At the population level, such movement is important for *Gemma* because, under crowded conditions, it exhibits reduced rates of body growth and fecundity that lead to subsequent population crashes (Weinberg 1985, 1989). It may be beneficial for *Gemma* to be carried into low density patches such as crab excavations with the result that intraspecific competition is mitigated. As Hastings (1993) has demonstrated theoretically, passive dispersal can serve as an important stabilizing force in model populations with patchy spatial structure. Strathmann and Strathmann (1982) have suggested that small benthic species brood their young because as adults they can be readily dispersed and thus gain little advantage from broadcasting larvae. *Gemma* broods, is small, and has no apparent size or depth refuge from foraging or excavating by predators. Its short generation time (Sellmer 1967), predator-resistant morphology (Schneider 1978, Botton 1984c, d), and adult dispersal abilities may constitute an effective survival strategy in disturbed, patchy environments.

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