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Predation and the mediation of intraspecific competition in an infaunal community in the Bay of Fundy

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Abstract: In the upper Bay of Fundy, the amphipod *Corophium volutator* (Pallas) is the most abundant macrofaunal animal in the extensive intertidal soft-bottom habitats. The population dynamics and demographic changes of *Corophium* were monitored from May 1985 to April 1986. There are two generations of *Corophium* each year with an overwintering generation giving rise to a summer generation in late May. Individuals of the summer generation grow rapidly and reproduce in August. Most individuals die after reproduction, either from senescence or predation. The population dynamics of the other members of the community, mostly polychaetes, were followed as well. Several species of bottom-feeding fish are known to prey heavily on *Corophium*, particularly the larger amphipods. Between mid-July and late August, the flats of the upper Bay of Fundy are used as a staging area for > 1 000 000 semipalmated sandpipers *Calidris pusilla* (Pallas). To assess the effect of predators on the infaunal community, a series of three exclusion experiments was conducted. Two types of enclosures were used, one which excluded only shorebirds and one which excluded both shorebirds and fish. No effects of predators were seen on the infaunal community in the early summer (24 May-7 July) or late summer (19 August-8 October). Significant effects were apparent in the middle of summer from both fish and shorebird predators. However, smallest numbers of amphipods were found in the full exclusion cages. This counter-intuitive result is explained by consideration of (1) the effects of predator manipulation on the size-structure of *Corophium* and (2) adult-juvenile *Corophium* interactions. Control populations were dominated by juvenile amphipods with few adults present. Full exclusion cages had many more adult amphipods and fewer juveniles. Shorebird exclusion cages had intermediate numbers of large amphipods, indicating that both fish and shorebirds significantly affect size-structure. Results suggest that size-selective predators ameliorate competition between adult and juvenile *Corophium*. When adult density is low, juvenile *Corophium* can establish burrows in the vicinity of their mothers but are forced to emigrate when adult density is high. This hypothesis was tested directly by adding large *Corophium* to ambient populations. This augmentation yielded *Corophium* populations whose size-structure was similar to that seen in the full exclusion cages. Significantly fewer small amphipods were found in the treatment with enhanced adult abundance, suggesting that the timing of reproduction in *Corophium* is constrained by the episodic intense predation that occurs in the middle of summer. Adults which reproduce too early risk releasing young into an environment where competition with adults will be severe because adult density has not been significantly lowered by predators. Adults which reproduce too late in the season run the risk of being eaten with their brood intact. Comparison of populations maintained in the laboratory over the winter to the field populations suggests that ice disturbance affects the abundance but not the size-structure of *Corophium*.

Key words: Bay of Fundy; *Calidris pusilla*; *Corophium volutator*; Intraspecific competition; Predation; Soft sediment

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INTRODUCTION

A major goal of ecology is to determine the processes which influence the distribution and abundance of organisms. In marine intertidal communities, rocky shore ecologists have been very successful in demonstrating experimentally the factors that influence the species in a community (Connell, 1961a,b; Paine, 1966, 1974; Dayton, 1971; Menge, 1976; Lubchenco & Menge, 1978; Sousa, 1979a,b; Underwood, 1980, 1981). The organisms in such communities are typically sessile and easily visible, facilitating repeated monitoring. Manipulative experiments in which only the variable of interest (e.g., the density of predators) is controlled while other variables are unaltered (Connell, 1974), have been fruitful. Results of such studies have contributed to the development of general theory and to the understanding of terrestrial and freshwater communities (e.g., Harper, 1977; Morin, 1981).

Despite a rich history of descriptive information, the community organization of soft-sediment communities is less well known although experimental methods have been developed and implemented in recent years. These techniques have demonstrated the importance of competition (Woodin, 1974; Peterson, 1977, 1979, 1982a; Peterson & Andre, 1980; Brenchley, 1981, 1982; Levin, 1981, Wilson, 1981, 1983, 1984; Levinton et al., 1985), predation (Virnstein, 1977; Woodin, 1978, 1981; Reise, 1978; Schneider, 1978; Commito, 1982; Ambrose, 1984; Botton, 1984a,b; Quammen, 1984) and disturbance (Rhoads and Young, 1970; Wiltse, 1980; Van Blaricom, 1982; De Witt & Levinton, 1985; Posey, 1986) in structuring infaunal communities. Because sampling in soft-sediment habitats requires destructive sampling, repeated measurements of the same organisms are not generally possible (Peterson, 1982b; Peterson & Black, 1988). To interpret the effects of various experimental manipulations, species abundance and species richness means are compared between control and experimental treatments. Few soft-sediment ecologists measure demographic consequences of experimental manipulations despite the fact that size is seen to be a critical determinant of competitive outcomes (Brenchley, 1981, 1982; Wilson, 1981, 1983) and of susceptibility to predation (Dadswell et al., 1984; Ambrose, 1986; Peer et al., 1986).

In this study, I describe the population dynamics of the species in an infaunal community in the upper Bay of Fundy. The demography of the most abundant member of the community is analysed in detail. By experimental manipulation, I investigate the importance of predation, competition and physical disturbance in influencing the population dynamics of all the species in the community. I show that failure to consider demographic consequences of these various processes would lead to erroneous interpretation and rejection of the experimental data. Population-level and community-level data are combined to explain the dynamics and organization of the community.

1987). The first migrants arrive in mid-July. Peak abundances occur during the first week of August and most semipalmated sandpipers have departed by the end of August (Hicklin, 1987; Wilson, 1989). These shorebirds prey almost entirely on *Corophium* (Hicklin & Smith, 1979; pers. obs.), concentrating on *Corophium* ≥ 4 mm long (Peer et al., 1986). The birds are able to gain $1.5\text{--}1.8$ g weight \cdot day $^{-1}$ (Hicklin & Smith, 1984; Hicklin, 1987). These fat reserves are used to fuel a nonstop flight of 4000 km to their major wintering grounds in Surinam (Stoddard et al., 1983; Morrison, 1984). Other shorebirds which are common in the upper Bay of Fundy, but in much lower abundance than semipalmated sandpipers, include black-bellied plover *Pluvialis squatarola*, semipalmated plover *Charadrius semipalmatus*, short-billed dowitcher *Limnodromus griseus*, white-rumped sandpiper *Calidris fuscicollis* and least sandpiper *Calidris minutilla*. *Corophium* is the major prey of the latter three species (Hicklin & Smith, 1979).

In addition to the predictable risk of predation in the upper Bay of Fundy, the infauna are also subjected to predictably harsh winter conditions. The flats are usually covered by blocks of ice for 3 months of the year (Gordon & Desplanque, 1983; Wilson, in press). The blocks of ice move off and on the intertidal surface with the changing tides. The blocks are also moved up and down the intertidal zone, scouring the bottom. The top centimeters of sediment are sometimes frozen to the overlying blocks and rafted away (Gordon & Desplanques, 1983; Wilson, in press).

MATERIALS AND METHODS

GENERAL SAMPLING

For all sampling in this study, infaunal samples were taken to a depth of 10 cm with a core 10 cm in diameter (0.008 m 2). All experiments and sampling were done in an area $\approx 40 \times 40$ m at 6.2 m above MLW. This site is in the middle of the intertidal zone, ≈ 0.5 km from the high tide mark. All cores were sieved separately with a 250- μ m mesh screen. This mesh size is sufficiently fine to retain the smallest juvenile *Corophium* and postlarval stages of polychaetes. All material retained on the sieve was fixed in 10% formalin and later sorted and enumerated with a stereomicroscope.

Comparison of abundance means among treatments or sampling dates was done with one-way ANOVA followed by Scheffe post hoc comparisons if the ANOVA was significant. Data were tested for normality (d'Agostino's test) and homogeneity of variance (Bartlett's test) to ensure that the assumptions of ANOVA were met (Sokal & Rohlf, 1981).

Size-frequency data were gathered for *Corophium* on all sampling dates. Boates & Smith (1979) showed that length and biomass are highly correlated ($r = 0.93$ for females, $r = 0.98$ for males) in *Corophium*. Hence, to characterize the distribution of sizes in a sample, one need only measure lengths. Such data were gathered by photographing all of the *Corophium* from a single replicate core, along with a centimeter ruler for scale,

STUDY SITE

This research was conducted in the intertidal zone of the Minas Basin of the Bay of Fundy. The Minas Basin is one of two large embayments at the head of the Bay of Fundy. The upper Bay is notable for its tidal amplitude, the greatest in the world. The amplitude varies from 11 m during neap tides to 16 m during spring tides (Dohler, 1970). Approximately one-third of the bottom of the Minas Basin is intertidal (Amos & Joice, 1977; Cranford et al., 1985). My study site was located on the expansive intertidal flats near Avonport, Nova Scotia (45°9' N, 64°23' W). Hicklin & Smith (1984) provide maps of the area.

The tremendous volume of water moved through the upper Bay of Fundy by the tides has fundamental effects on the soft-sediment biota. The heavy sediment load and the strong vertical mixing, in concert, curtail phytoplankton growth. Phytoplankton production in the upper Bay is an order of magnitude lower than production in areas in the lower Bay and the Gulf of Maine (Gordon, 1986). Evidence suggests that the zooplankton community in the upper Bay is detritus-based rather than phytoplankton-based (Daborn, 1984). The soft-sediment benthos of the upper Bay is accordingly depauperate in numbers of suspension-feeding organisms. A review of the checklist of Bromley (1979) indicates that only 10.2% of the invertebrate species are suspension-feeders. The flats are dominated by deposit-feeding organisms, the most abundant of which is the amphipod crustacean *Corophium volutator* (Pallas). This ampho-Atlantic species (Bousfield, 1973) is restricted to boreal waters. *C. volutator* (henceforth, *Corophium*) builds a U-shaped burrow in the top few centimeters of sediment from which it extends its elongate second antennae to gather detrital material (Hart, 1930). Densities of *Corophium* may exceed $100\,000 \cdot \text{m}^{-2}$. Other common deposit-feeding species include the polychaetes *Aglaothamum neotenus* Noyes, *Pygospio elegans* Claparede, *Streblospio benedicti* Webster et Benedict, *Tharyx acutus* Webster et Benedict and *Heteromastus filiformis* (Claparede).

A number of epibenthic fish predators are seasonally abundant on the flats of the upper Bay of Fundy between spring and fall (Dadswell et al., 1984). The most abundant predatory fish is the tomcod *Microgadus tomcod* which feeds extensively in the intertidal zone. The smooth flounder *Liopsetta putnami* is a conspicuous predator on the infauna. Other predatory fish include the smelt *Osmerus mordax* and Atlantic silversides *Menidia menidia*. All of these species feed primarily on *Corophium* (Gilmurray & Daborn, 1981; Imrie & Daborn, 1981; Dadswell et al., 1984).

Shorebirds are seasonally abundant on the upper Bay of Fundy flats (Hicklin, 1987). The upper Bay is the most important migratory stop-over area for semipalmated sandpipers *Calidris pusilla* during their autumn migration to their South American wintering grounds (Harrington & Morrison, 1979; Morrison, 1984; Hicklin, 1987). A significant proportion (42–74%) of the semipalmated sandpipers from the eastern and central Canadian Arctic breeding grounds spend time in the upper Bay of Fundy (Hicklin, 1987). Their numbers have been estimated at 800 000–1 400 000 birds (Hicklin,

on a single negative. Lengths of each amphipod (rostrum to posterior tip of telson) were measured from 20 × 25-cm photographic prints with a digitizing tablet connected to an Apple 11E personal computer. For each sampling date or experimental treatment, three replicates were randomly chosen for the determination of the size-structure of the population. To avoid pseudoreplication errors (Hurlbert, 1984) and to show within-date variability, I report three histograms of size-frequency data for each sampling date or experimental treatment. Goodness-of-fit tests, based on the χ^2 distribution (Sokal & Rohlf, 1981), were used to compare length-frequency distributions between experimental treatments.

POPULATION DYNAMICS

To characterize the dynamics of the community, a sampling program was begun on 16 May 1985. Sampling was conducted biweekly until early September. Monthly samples were taken in October through December. Winter ice prevented further sampling until April 1986. Temporal changes in abundance for each species were analysed with a one-way ANOVA using sampling date as the main effect followed by Scheffe post hoc comparisons.

PREDATOR EXCLUSION EXPERIMENTS

To assess the impact of epibenthic fish and shorebirds on the infauna at Avonport, I conducted a series of predator exclusion experiments. Exclusion cages were constructed of hardware cloth with 6-mm mesh. Each cage was 40 × 40 cm × 35 cm high. Each cage was pressed into the sediment to a depth of 15 cm. Wooden dowels, 8 mm in diameter, were driven to a depth of 40 cm at the corner of each cage. The above ground portion of each cage was fastened to each dowel with plastic cable ties. Each dowel was cut flush to the upper surface of each cage. Such a cage excludes all shorebirds and any fish or invertebrate > 6 mm in its least dimension.

As a control for unwanted effects of the cages (accumulation of organic matter or waterborne infauna), a cage control treatment was used (Virnstein, 1978; Hulberg & Oliver, 1980). For these experiments, partial cages (cage controls) were simply full cages cut along the diagonal, such that each partial cage consisted of two adjacent sides and half of a top. These partial cages were emplaced in the sediment in similar fashion to the full cages.

A total of five full cages and five cage controls were erected in a line parallel to the shoreline at the mid-intertidal site. The ordering of cages and cage controls was randomly determined. Each experimental unit was separated from the adjacent units by a distance of 1.5 m. The orientation of the two open ends of the partial cages was varied among all four possible arrangements. The cages and cage controls were erected on 24 May and five replicate cores were taken from the experimental area. The cages needed no maintenance except for reanchoring of two experimental units which were

partly freed by gale force winds on 1 June. The cages were sampled on 7 July, 19 August and 8 October.

At each sampling, a single 10-cm diameter core was removed from each cage through a triangular slit in the top of each cage. A single core was taken from each cage control. $\approx 5\%$ of the surface area of each cage was removed during each sampling. Five cores from the ambient, unmanipulated mudflat were taken around and between the experimental units. Comparison of abundances of organisms between ambient controls and cage controls allows one to determine if hydrodynamic effects are severe enough to influence infaunal abundance. The abundance data were analysed with a one-way ANOVA and Scheffe post hoc comparisons to search for differences among experimental treatments. Because the same cages were sampled during the three sampling periods for this experiment, samples are not independent between sampling periods. Thus, a two-way ANOVA using date as a second main effect could not be performed.

A second exclusion treatment was begun in June to separate the effects of shorebird predation from fish predation. Each exclusion cage consisted of four wooden stakes driven into the sediment in a rectangular pattern (0.6×2 m). A roof of chicken-wire with 25-mm mesh was fastened to each stake with a staple gun. The roof was 12 cm above the sediment surface. Five shorebird exclusion cages were erected near the experimental battery of cages described above. The roofs effectively exclude shorebirds which refuse to go beneath the chicken-wire, yet allow fish to forage freely underneath when the tide is high.

As with the full cages, the effects of the shorebird exclusions on the hydrodynamic regime which might confound interpretation of experimental results must be considered. The shorebird enclosures are so simple that it is impossible to alter them to construct a partial cage which would alter flow but not exclude shorebirds. I chose instead to perform a control experiment, temporally separated from the period when shorebirds were present. The procedure involved conducting a shorebird exclusion experiment which was terminated before the arrival of the first semipalmated sandpipers. Any difference in abundance or demography of the infauna in the two treatments would then be attributable to differences in hydrodynamics between roofed areas and adjacent, unmanipulated areas. This control experiment for secondary effects of shorebird exclusion was begun on 16 June and terminated on 7 July. The first shorebirds were noted on 16 July. On both 16 June and 7 July, one 10-cm core was taken from each of the five shorebird exclusion cages. Five cores from unmanipulated areas around the cages were also taken on the two sampling dates. The shorebird exclusion areas were later sampled on 19 August along with the battery of cages and partial cages. The three cage treatments (full cage, shorebird roof, cage controls) along with control (ambient) samples were analysed for differences in abundance by ANOVA and Scheffe post hoc comparisons. Size-frequency data for *Corophium* in each treatment were compared to search for demographic effects of predator exclusion. The shorebird exclusion areas were not sampled in October because most of the shorebirds had departed by 19 August.

WINTER DISTURBANCE

To best assess the effects of winter ice, one should protect experimental areas from ice scour. However, the quantity of ice and the power of the tides in the upper Bay of Fundy render any attempt to maintain areas free of ice scour futile. Instead, I used a laboratory comparison. Samples taken on 8 December 1985 and on 1 April 1986 span the winter season. To test the effects of winter ice on infaunal abundances, I brought five intact cores, each enclosed by a section of 10-cm diameter PVC pipe, into the laboratory on 8 December. The cores were placed in running seawater having a temperature of 2–4 °C. Each core was encircled by a fence of 1-mm mesh insect screening, projecting above the surface of the water, to prevent *Corophium* from emigrating. These organisms spent the winter in water of similar temperature to field populations but did not have to endure any ice-related disturbance. On 1 April, the laboratory cores were sieved on a 250- μ m screen. Abundances from the December and April field samples and the laboratory samples were analysed with ANOVA and Scheffe comparisons. Length-frequency distributions of *Corophium* were compared between treatments.

COROPHIUM COMPETITION EXPERIMENT

Results of predator exclusion experiments conducted in 1985 suggested that adult and juvenile *Corophium* compete when predators are excluded. To test this hypothesis directly, a *Corophium* addition experiment was performed in August 1986. The bottoms of eight 10 \times 10-cm papier mâché berry containers were removed. The bottomless containers were pressed into the sediment until the tops were flush with the sediment surface. The containers were arranged in a row parallel to the shoreline, with each container separated from adjacent ones by 30 cm. Half of these containers had 250 adult *Corophium* (>4 mm in length) added to them. This addition raised the density of adults to the same density observed in predator exclusion areas during the August 1985 experiments. The remaining four containers had no *Corophium* added and served as controls for the effects of the container. A final treatment, the control treatment, consisted of four 0.01-m² cores taken adjacent to the papier mâché containers. The experiment was begun on 7 August and was terminated on 12 August. The abundance data for all species were analysed by ANOVA and Scheffe comparisons. One of the container control replicates was rejected because some of the retained material was lost during the sieving process. All *Corophium* were measured and classified as either small (<4 mm in length) or large (>4 mm in length). Most adults were considerably >4 mm and few small juveniles were >3 mm. The abundances of small and large *Corophium* were analysed separately. A Pearson correlation coefficient was used to test for significant association between large and small *Corophium*.

RESULTS

POPULATION DYNAMICS

Fig. 1 presents data on the population dynamics of the four most common infaunal species at Avonport from May 1985 until April 1986. Two statistically significant changes in abundance occurred for *Corophium*, one increase in early June and a second increase in August. Fig. 2 shows the size-frequency distributions for *Corophium* at each

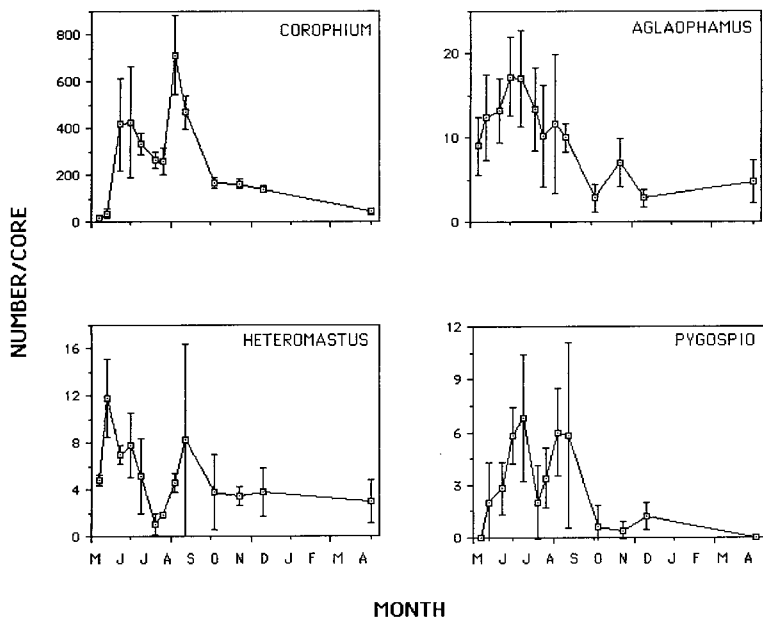


Fig. 1. Population dynamics for *Corophium* and three polychaetes between May 1985 and April 1986. Each core has an area of 0.008 m². All data represent means of five replicates. Two SE values are plotted for each \bar{x} value.

of the sampling periods. For these data and most other length-frequency data, I will avoid tedious description of all of the goodness-of-fit tests which compare the distributions of replicates within dates and between sequential dates. In most cases, the patterns are clear and require no statistical persuasion. Results of the goodness-of-fit analyses are available from the author. Fig. 2 reveals that most of the *Corophium* which survived the winter are large individuals at low densities (Fig. 1). Females release young in late May which results in the significant rise in abundance in early June (Fig. 1). The proportionate decline in large amphipods is not due entirely to numerical swamping by recently released juveniles; few adults live beyond a single reproductive season (Gratto et al., 1983). The June cohort grows rapidly through June and July, ultimately approximating a normal distribution of body sizes. In late July and early August, some of the

June cohort have begun to reproduce as evidenced by the appearance of juveniles (< 1 mm in length). The majority of amphipods born in the spring do not reproduce until August; this reproduction produces distinctly skewed distributions in late August and results in the second significant rise in abundance (Fig. 1). As in early June, mortality

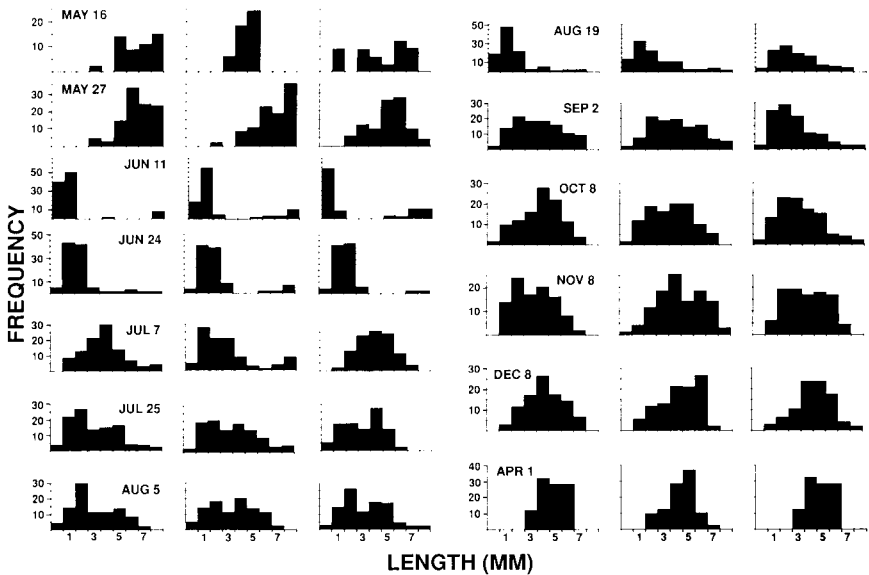


Fig. 2. Temporal changes in length-frequency distributions of *Corophium* between May 1985 and April 1986. Three replicates are presented for each sampling date.

of many of the adults after reproduction contributes to the skew in the distribution. The late summer cohort grows through the fall. Little growth occurs over the winter, as seen by comparison of December and April histograms. The amphipods in April presumably would grow to yield length-frequency distributions like those seen in May, completing the annual cycle. Thus, two generations span the year, one born in late May or early June which grow rapidly to produce a generation in August which overwinters and reproduces in late spring.

The three most common polychaetes in the study area show little significant variation during the year (Fig. 1). Variances are frequently high. The only significant change in *Aglaothamus* in sequential samples occurred in October when the density dropped significantly. *Heteromastus* does not show any significant changes between sequential sampling periods although significant differences are found in comparing samples more distantly separated in time, such as a significant drop between early May and late July. The only significant change between adjacent points for *Pygospio* occurs over the winter.

PREDATOR EXCLUSION EXPERIMENTS

Table I presents the abundance data for the control experiment with the shorebird exclusion cages, testing for effects of the cages on flow which might affect infaunal

abundance. The entire experiment was conducted in the absence of shorebirds so no difference in abundance is expected between control and caged areas. Table IA presents the abundance data at the beginning of the experiment. As expected, no significant difference in the abundance of any species or in the total number of species is seen. Table IB gives the data at the conclusion of the experiment. No species differed

TABLE I

Results of control experiment for bird exclusion cages. 16 June samples were taken when cages were erected; 7 July samples were taken shortly before arrival of shorebirds. Means which are underlined are not statistically different in Scheffe post hoc comparisons ($P > 0.05$). Two SE values are given in parentheses. Densities are expressed as number · 10-cm diameter core $(0.008 \text{ m}^2)^{-1}$.

TABLE A		
16 June Species	Control	Experimental
<i>C. volutator</i>	352.0 (163.67)	401.8 (183.34)
<i>P. elegans</i>	<u>6.0</u> (3.16)	6.6 (3.26)
<i>A. neotenus</i>	14.2 (5.81)	15.8 (4.12)
<i>H. filiformis</i>	4.8 (2.48)	5.6 (3.93)
Oligochaeta	10.6 (11.93)	3.0 (3.63)
Number of species	7.0 (1.09)	6.4 (1.74)

TABLE B		
7 July Species	Control	Experimental
<i>C. volutator</i>	408.6 (58.82)	406.0 (61.48)
<i>P. elegans</i>	6.6 (2.33)	4.2 (2.14)
<i>A. neotenus</i>	12.4 (3.93)	11.0 (3.41)
<i>H. filiformis</i>	4.0 (1.41)	5.0 (4.10)
Oligochaeta	5.2 (6.05)	6.4 (7.50)
Number of species	5.8 (0.75)	6.6 (0.8)

significantly in abundance between the two treatments. Fig. 3 presents length-frequency data for *Corophium* in the two treatments, testing for differences in growth rate. The distributions between the two treatments at the beginning of the experiment on 16 June are not statistically different. Similarly, at the conclusion of the experiment, the variability between treatments is no greater than the variability among replicates within a treatment. Thus, the presence of the shorebird exclusions has no significant effect on the abundance of any infaunal species or on the size-structure of the dominant organism, *Corophium*.

Table IIA presents the results of the predator exclusion experiment spanning the time period of late May to early July. The full cages exclude only fish at this time of year as shorebirds have yet to arrive during their postbreeding migration. The exclusion of predators during this interval has no discernible effect on the abundance of *Corophium* (Table IIA) or any of the associated infauna ($P > 0.05$ in all cases). Fig. 4 presents demographic data for *Corophium*. Although the histograms for the Control treatment are

variable, there is no discernible effect of either full cages or cage controls on the length-frequency distribution.

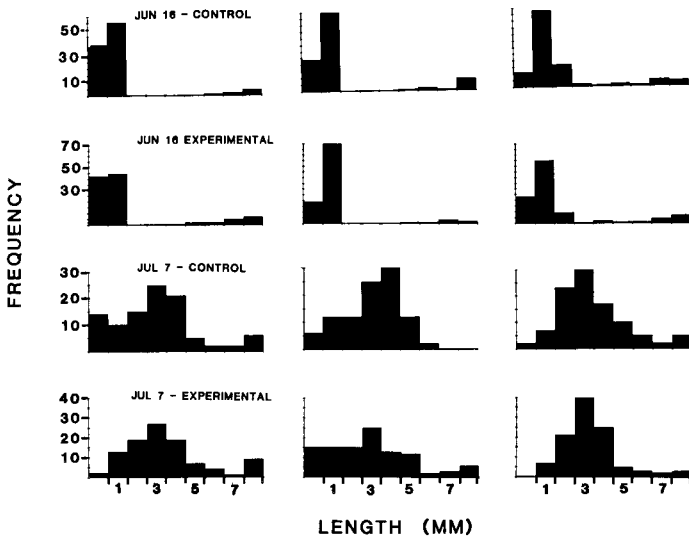


Fig. 3. Length-frequency distributions of *Corophium* in shorebird enclosure control experiment. Three replicates are presented for Control and Experimental treatments at beginning of experiment and at termination.

TABLE II

Results of sampling of exclusion experiments in 1985. Control refers to ambient areas adjacent to experimental cages; Cage Control refers to areas covered by half cages; Cages refer to complete exclusion cages. \bar{x} values which are not different in Scheffe post hoc comparisons ($P > 0.05$) are connected by solid lines. Error terms in parentheses are 2 SE. Densities are expressed as number \cdot 10-cm diameter core $(0.008 \text{ m}^2)^{-1}$.

		TABLE A			
7 July	Species	Control	Cage Control	Cage	
	<i>C. volutator</i>	<u>332.0 (47.46)</u>	<u>344.50 (39.75)</u>	<u>273.5 (16.54)</u>	
		TABLE B			
19 August	Species	Control	Cage Control	Bird Exclusion	Cage
	<i>C. volutator</i>	<u>713.4 (168.16)</u>	<u>554.6 (137.42)</u>	<u>500.6 (78.30)</u>	<u>469.8 (43.10)</u>
		TABLE C			
8 October	Species	Control	Cage Control	Cage	
	<i>C. volutator</i>	166.0 (25.23)	169.2 (28.22)	161.4 (55.37)	

Table IIB presents the results of the 19 August sampling of the exclusion experiments. During this period, both fish and shorebird predators are present at the study site. Only one significant difference is seen among treatments: *Corophium* is more abundant in control areas, subject to both fish and shorebird predation, than it is in full cages which

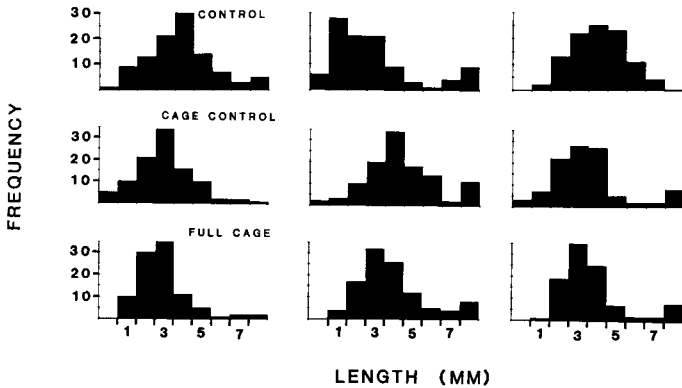


Fig. 4. Length-frequency distributions of *Corophium* for 7 July 1985 sampling of predator exclusion experiment. Three replicates are presented for each of treatments.

excluded both types of predators. The abundance of none of the other species varies as a function of predator presence or absence ($P > 0.05$ in all cases). Consideration of the demographic data for *Corophium* in Fig. 5 permits interpretation of the counter-intuitive result of greater abundance in the presence of predators. Because the data in

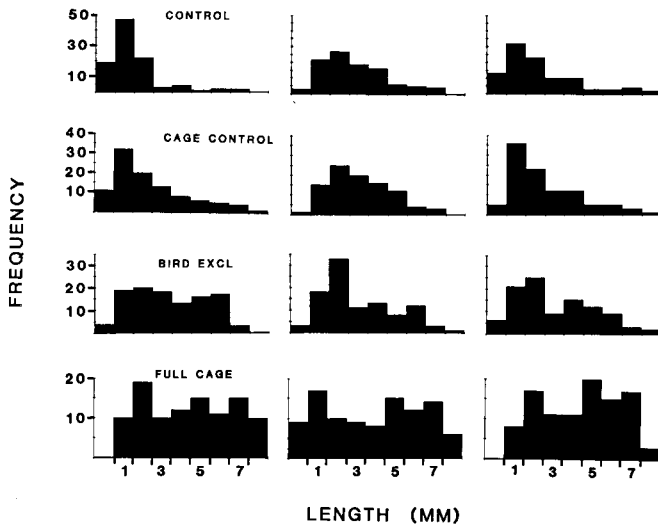


Fig. 5. Length-frequency distributions of *Corophium* for 19 August 1985 sampling of predator exclusion experiment. Three replicates are presented for each of treatments.

Fig. 5 are the most critical data in this paper, I present in Table III the results of all pair-wise goodness-of-fit tests for the 12 replicates. Visual inspection of Fig. 4 and reference to Table III reveal that the histograms for the Control (ambient population)

TABLE III

Results of goodness-of-fit tests for three replicates of four treatments in 19 August sampling. CT, control (ambient) treatment; CC, cage control (partial cage) treatment; SE, shorebird exclusion treatment; CG, total predator exclusion cage treatment. NS, no significant difference; * $0.01 < P < 0.05$; ** $P < 0.01$. Length-frequency histograms are shown in Fig. 4.

	CT2	CT3	CC1	CC2	CC3	SE1	SE2	SE3	CG1	CG2	CG3
CT1	*	NS	NS	NS	NS	NS	*	NS	**	**	**
CT2		NS	NS	NS	*	**	*	**	**	**	**
CT3			NS	NS	*	**	*	**	**	**	**
CC1				NS	*	*	NS	NS	**	**	**
CC2					**	*	NS	**	**	**	**
CC3						*	NS	NS	**	**	**
SE1							NS	NS	NS	NS	**
SE2								NS	*	*	**
SE3									**	**	**
CG1										NS	NS
CG2											NS

and Cage Control (partial cage) treatments are similar. They all show a preponderance of newly released juveniles and few adults. The Bird Exclusion replicates differ from the two control treatments in 11 of 18 comparisons; it seems clear that shorebirds have significant effects on the size-structure of *Corophium*. The effect is a relative increase in the number of large *Corophium* and a concomitant decrease in the number of small *Corophium*. The increase in large *Corophium* is a result of the exclusion of shorebirds which would have eaten the amphipods in the absence of the exclusion. The replicates of the Cage treatment are all statistically identical to each other but differ from the remaining replicates in 25 of 27 comparisons. Full cages have even greater numbers of large *Corophium* and fewer juveniles. Table IV presents biomass data for *Corophium* among the different treatments. Despite having lowest *Corophium* density, the Cage treatment has the highest biomass of *Corophium* · sample⁻¹. The remaining three treatments do not vary significantly from each other. This difference is more striking when

TABLE IV

Biomass of *Corophium* in different treatments in 19 August predator exclusion experiments. Underlined means are not significantly different in Scheffe post hoc comparisons ($P > 0.05$).

	Control	Cage Control	Bird exclusion	Full Cage
Sample biomass (g)	<u>0.0842</u>	<u>0.0836</u>	<u>0.0806</u>	0.1444
Individual biomass (mg)	<u>0.118</u>	<u>0.151</u>	<u>0.160</u>	0.307

the average *Corophium* weight is calculated. The average *Corophium* in the Cage treatment is three times as heavy as those in the Control treatment. With increasing predator protection, there is a trend of reduced abundance and larger average size. This pattern suggests that size-selective predation on large amphipods is mediating intraspecific competition between adult *Corophium* and newly released juveniles.

Table IIC presents the results of the October sampling of the predator exclusion experiment. Bird exclusion areas were not sampled as the majority of shorebirds had departed by the end of August. There are no significant differences among treatments for *Corophium* abundance (Table IIC). Fig. 6 shows that the populations in the different areas have converged from highly disparate distributions in August to statistically equivalent ones. There were no significant differences in abundance among treatments for the other members of the infaunal community ($P > 0.05$ in all cases).

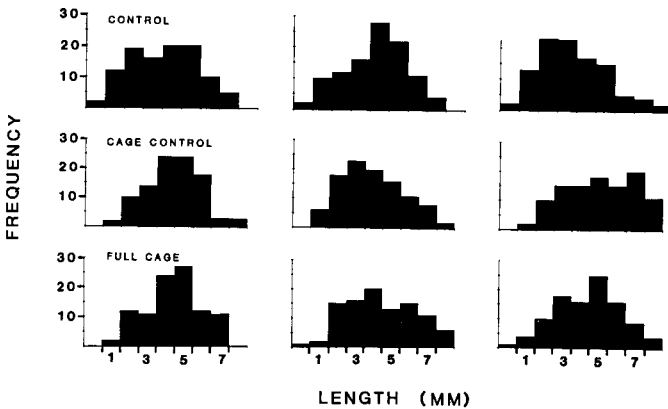


Fig. 6. Length-frequency distributions of *Corophium* for 8 October 1985 sampling of predator exclusion experiment. Three replicates are presented for each of treatments.

WINTER DISTURBANCE EXPERIMENTS

Table V presents the data for the experiment assessing the effect of winter conditions on the infauna at Avonport. The data indicate that significant mortality of *Corophium* occurred in the laboratory over the winter with ≈ 50 of 140 amphipods \cdot sample $^{-1}$ on average dying. However, the number of *Corophium* recovered in April from the field is still significantly lower than the number that survived the winter in the laboratory sea table. The data suggest that the ice conditions present on the flats at Avonport do result in significant mortality that would not occur in the absence of such harsh winter conditions. Fig. 7 presents length-frequency data for all three treatments. All histograms are remarkably similar, showing that little growth of *Corophium* occurs during the winter and that winter mortality is not size-dependent. None of the other members of the community differed significantly among treatments (Table V).

TABLE V

Results of experiment to assess effects of winter conditions on infaunal abundance. December refers to samples which were taken shortly before formation of intertidal ice. Laboratory refers to samples collected in December and maintained in ambient seawater in laboratory. April refers to samples taken from field in April shortly after melting of intertidal ice. Means which are not statistically different in Scheffe post hoc comparisons ($P > 0.05$) are underlined. Errors given in parentheses are 2 SE. Densities are expressed as numbers $\cdot 10\text{-cm diameter core (0.008 m}^2\text{)}^{-1}$.

Species	December	Laboratory	April
<i>C. volutator</i>	137.6 (14.32)	86.4 (14.33)	40.2 (14.29)
<i>A. neotenus</i>	<u>2.8 (0.12)</u>	<u>3.6 (2.23)</u>	<u>5.2 (1.02)</u>
<i>P. elegans</i>	<u>1.2 (0.75)</u>	<u>0.2 (0.40)</u>	<u>0.0 (0.00)</u>
<i>H. filiformis</i>	<u>3.2 (2.14)</u>	<u>3.6 (2.60)</u>	<u>3.8 (2.14)</u>
Oligochaeta	<u>2.8 (1.94)</u>	<u>0.4 (0.49)</u>	<u>1.2 (0.15)</u>
Number of species	6.0 (1.55)	5.4 (2.03)	4.2 (0.98)

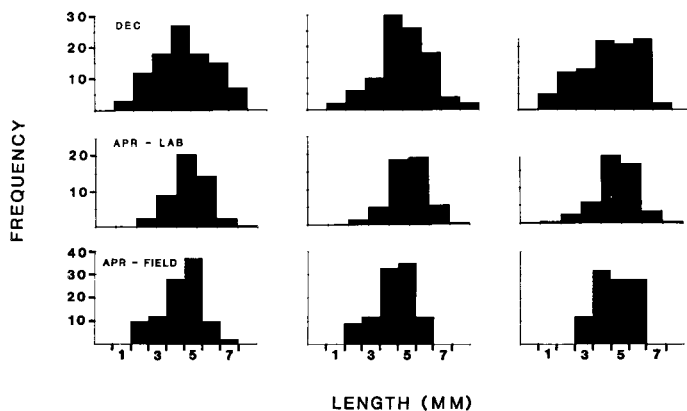


Fig. 7. Length-frequency distributions of *Corophium* for winter ice disturbance experiment. Dec, samples taken from field on 8 December 1985; Apr-Lab, samples brought from field in December and maintained in laboratory until 1 April 1986; Apr-Field, samples taken from field on 1 April 1986. Three replicates are presented for each treatment.

COROPHIUM COMPETITION EXPERIMENT

Table VI presents the results of the August 1986 experiment testing for intraspecific competition between adult and juvenile *Corophium*. There were significantly more large *Corophium* in the Addition treatment, indicating that the enhancement of large *Corophium* abundance persisted for the 6 days of the experiment; 250 amphipods were added to each replicate and, on average, 200 of those were present at the end of the experiment (Table VI). There is a significant difference in the number of small *Corophium* with greater numbers found in the two control treatments. These data strongly indicate that young *Corophium* are forced to emigrate from high densities of adults. There is no significant difference in the total number of *Corophium* at the end of the experiment but

there is a significant difference in mean individual biomass. The relationship between large and small *Corophium* is seen in Fig. 8. There is a negative correlation ($r = -0.65$, $P < 0.05$) between the two variables. For the remaining species in Table VI, no signifi-

TABLE VI

Results of *Corophium* addition experiment. Control refers to replicates taken from ambient unmanipulated mudflat. Container Control refers to replicates which were enclosed by papier mâché containers (0.01 m²) but to which no *Corophium* were added. Addition refers to replicates which were enclosed by papier mâché containers and to which 250 adult *Corophium* were added. Small *Corophium* are <4 mm in length; large *Corophium* >4 mm. \bar{x} values which are not significantly different in Scheffe post hoc comparisons ($P > 0.05$) are underlined. Errors given in parentheses are 2 SE.

Species	Control	Container Control	Addition
<i>C. volutator</i>			
Large	<u>174.8</u> (25.24)	<u>154.7</u> (37.53)	367.5 (41.43)
Small	<u>210.5</u> (38.37)	<u>175.0</u> (24.88)	78.8 (27.33)
Total	<u>385.2</u> (67.24)	<u>329.7</u> (37.54)	446.2 (87.43)
Mean individual biomass (mg)	<u>0.097</u> (0.014)	<u>0.077</u> (0.018)	0.183 (0.028)
<i>E. heteropoda</i>	<u>5.2</u> (1.71)	<u>6.3</u> (3.71)	6.2 (2.99)
<i>A. neotenus</i>	<u>40.8</u> (7.50)	<u>72.7</u> (37.78)	57.0 (15.17)
<i>P. elegans</i>	<u>49.2</u> (22.69)	29.0 (3.46)	48.0 (44.95)
<i>S. benedicti</i>	<u>19.5</u> (8.39)	<u>16.3</u> (12.35)	30.5 (32.65)
<i>T. acutus</i>	<u>92.2</u> (34.93)	<u>208.7</u> (52.29)	185.5 (58.43)
<i>H. filiformis</i>	<u>18.2</u> (5.74)	<u>25.7</u> (15.51)	13.0 (4.76)
Number of species	<u>9.5</u> (1.29)	<u>8.7</u> (1.33)	8.8 (1.26)

cant difference occurs between any of the treatments except for *Tharyx* which is significantly less abundant in the absence of papier mâché containers. There is no change in the total number of species following the addition of large *Corophium* (Table VI).

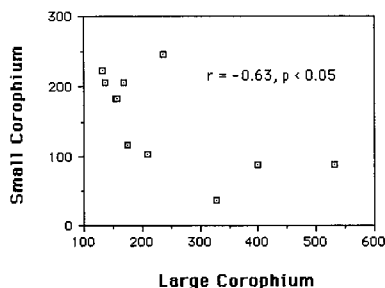


Fig. 8. Results of *Corophium* competition experiment of 7–12 August 1986. Number of small *Corophium* (<4 mm in length) is plotted against number of large *Corophium* (>4 mm in length) for each replicate.

DISCUSSION

POPULATION BIOLOGY OF *COROPHIUM*

Corophium is the most abundant infaunal organism at the Avonport study site (Fig. 1) and in the upper Bay of Fundy at large (Boates & Smith, 1979; Hicklin et al., 1980; Gratto et al., 1983; Hawkins, 1985; Murdoch et al., 1986; Peer et al., 1986). The population dynamics of *Corophium* (Fig. 1) show dramatic changes throughout the year. These patterns of temporal change are similar to patterns documented at other sites in the upper Bay of Fundy (Murdoch et al., 1986). The typical pattern is a sharp rise in abundance in late spring, corresponding to the birth of the summer generation, followed by a decline as the juveniles grow rapidly to adulthood, leading to an annual maximum of abundance as the summer generation reproduces. The young born in late July and early August grow over the fall, overwinter and give rise to the next summer generation during the following May.

A series of experiments tested the effects of seasonal predators on the abundance and demography of *Corophium*. Significant effects of predators were expected. Many fish feed extensively on *Corophium* (Gilmurray & Daborn, 1981; Imrie & Daborn, 1981; Dadswell et al., 1984). The most abundant fish in the intertidal zone during the summer, *Microgadus tomcod*, is a specialist on *Corophium*. Significantly, it is seen to be size-selective, preferring *Corophium* > 4 mm in length (Dadswell et al., 1984). Migratory shorebirds are also seasonally abundant predators in the upper Bay of Fundy. The most abundant of these is the Semipalmated Sandpiper. These shorebirds prey on *Corophium* to the exclusion of all other infaunal prey (Hicklin & Smith 1979; Wilson, in press). Like *Microgadus*, Semipalmated Sandpipers select larger amphipods (> 4 mm in length) (Peer et al., 1986). $\approx 40\,000$ individuals foraged on the intertidal flats at Avonport (1.5 km² at low tide). Observations of feeding of Semipalmated Sandpipers, the most abundant migrant, indicate that each shorebird consumes between 10 000 and 22 000 amphipods each day (Boates & Smith, 1979; Hicklin, 1987; Wilson, 1989).

Exclusion experiments indicated that *Corophium* abundance and demography are affected only in the middle of the summer (Table IIB, Fig. 5) but not early summer (Table IIA, Figs. 3, 4) or fall (Table IIC, Fig. 6). The observed effects of predators during the summer were unexpected, showing a trend of increasing *Corophium* abundance with increasing protection from predation (Table IIB). This result, anomalous at first, can be understood by consideration of prey demography. In accordance with the observation that both fish and shorebird predators preferentially take larger amphipods, large amphipods increase inside exclusion treatments (Fig. 5) while the relative and absolute numbers of juvenile amphipods decline. This effect results in greatest biomass, despite least abundance, in the Cage treatment (Table IV). A parsimonious post hoc explanation for these results is that size-selective predation is ameliorating competition between adult and juvenile *Corophium*. When adults are protected from predators, one predicts that little space or food is available for establishment of juveniles in the vicinity of the mother's tube, forcing emigration of juveniles.

A direct test of this post hoc hypothesis was conducted by augmenting experimental areas with adult *Corophium* (Table VI, Fig. 8). The experimental areas mimicked the abundance and demography of *Corophium* inside the predator exclusion cages (Fig. 5). The results clearly show a decrease in the number of juvenile *Corophium* in the presence of high adult *Corophium* density. This result is conservative since the high adult *Corophium* treatment had over twice as many adult females, many of which certainly released juveniles during the course of the experiment.

The results have important implications for the timing of reproduction in *Corophium*. The life history of *Corophium* varies geographically. Populations from the upper Bay of Fundy, Britain and Sweden have two generations $\cdot \text{yr}^{-1}$ with few animals living to produce a second set of broods (Hart, 1930; Watkin, 1941; Fish & Mills, 1979; Moller & Rosenberg, 1982; Gratto et al., 1983; Fig. 2). Populations in the lower Bay of Fundy, Scotland and the Baltic Sea have a single generation each year (Seegerstrale, 1940; McLusky, 1968; Gratto et al., 1983). Although I do not claim that the life history of *Corophium* in the upper Bay has been molded by predictable, intense, episodic predation, the exclusion experiments do suggest that predation constrains the period of reproductive success. Given that each female produces two broods, ≈ 1 month apart (Gratto et al., 1983), the experimental data (Tables IIB, III, IV; Fig. 5) suggest that there is a window in time in which reproduction will be most successful. Reproducing too early in the summer will release juveniles into an environment which is densely populated by adult *Corophium*. The juveniles will have difficulty establishing tubes in the presence of high densities of adults (Table VI). Conversely, delaying reproduction carries the risk of being eaten by a fish or shorebird with a brood intact. The fact that brood release follows a lunar or semilunar cycle (Fish & Mills, 1979; Gratto et al., 1983) imposes another constraint on timing of brood release. The demonstration of a strong interaction between size-selective predation and intergenerational competition in *Corophium* accounts for the concordance of maximal *Corophium* abundance with maximal predation intensity (Fig. 1). The successful recruitment of *Corophium* hinges on the removal of summer generation adults by predators which frees space for the establishment of juveniles of the overwintering generation. Virtually none of the summer generation adults will live through the winter to produce a second set of broods in the following spring (Gratto et al., 1983; Fig. 2). Hence, once these animals have released two broods in late July and August, their reproductive value plummets. From the perspective of a female *Corophium* which has reproduced within the constrained time interval, removal of adults (including herself) by predators will likely increase the survival of her offspring. The life history of *Corophium* takes advantage of the presence of predators which crop adults of low reproductive value (Slobodkin, 1960), enhancing the survivorship of the juveniles which will grow through the fall and give rise to a summer generation the following spring.

Winter conditions impose severe stresses on *Corophium* and other infauna. Temperatures may fall low enough that the top layers of sediment freeze. Freezing is not lethal to *Corophium* (Linke, 1939; Smidt, 1951; Mills & Fish, 1980); *Corophium* survived 6 wk

in frozen sediment (Crisp, 1964). However, scour of the surface sediments by ice blocks is a potential source of mortality. Particularly during the early and late portions of winter, when ice is partly melting during the day, ice blocks may freeze to the upper cm of sediment. The sediment crust is then rafted to other parts of the flat, depending on the movement of the ice block. Such rafting results in relocation of infauna to other areas which may be less habitable (Wilson, in press). The laboratory experiment (Table V, Fig. 7) demonstrated that significant mortality of *Corophium* occurred in the field which could not be explained by natural mortality which would have occurred in the absence of ice-related disturbance. Smaller *Corophium* were not more susceptible to ice disturbance than larger conspecifics (Fig. 7). It is possible that some of the *Corophium* swam to deeper waters although Essink et al. (1989) indicate that only 0.06% of a European population was found in the water column.

In the annual population cycle, two periods of rapid population decline are seen (Fig. 1): from 11 June to 7 July and from 19 August to 8 October. Although no experimental data were obtained, the declines are probably best explained by appeal to intraspecific competition. During both intervals, abundance falls while size increases. While these patterns are consistent with a competition hypothesis, they are not compelling. More insight into the process is available by comparing the trajectories of population change between 19 August and 8 October in the predator exclusion experiments (Table IIC, Fig. 6). No significant effects of predators were seen during this time. There are no differences in abundance or length-frequency of *Corophium* in any of the three treatments (Table IIC, Fig. 6). Yet, the differences in abundance and demography on 19 August were striking. The populations in the three treatments (the Bird Exclusion treatment was not sampled on 8 October) have all converged by October. This convergence must be a result of the death of the adult *Corophium* and migration of juvenile *Corophium* into the predator exclusion cages. Although some amphipods are known to be predatory (Oliver et al., 1982; Elmgren et al., 1986), the morphology and gut analyses of *Corophium volutator* (Icely & Nott, 1984; Miller, 1984; Stuart et al., 1985; Murdoch et al., 1986) suggest strongly that cannibalism does not occur in this species and hence is not a likely explanation for the observed changes in the size frequency of *Corophium* in different treatments. The convergence of the three treatments clearly arose by nonrandom processes. The suggestion that *Corophium* abundance is limited by resource availability seems a parsimonious explanation.

To summarize, the annual population dynamics involve a pulse of reproduction in early June and a second pulse in the middle of August. Competition between animals of the same generation may explain declines in abundance after the peaks. Winter conditions reduce the abundance of the fall population significantly. Finally, size-selective predation by both fish and shorebirds remove reproductive adults from the population between early July and middle August. The importance of these predators is belied by the peak of *Corophium* abundance during the time of maximal predation intensity. Rather than assuming that predators arrive in the Bay of Fundy when *Corophium* abundance is at its maximum (Hicklin et al., 1980), I argue that the presence

of the predators allows *Corophium* to attain high densities by ameliorating competition between adults and juveniles.

INFAUNAL COMMUNITY STRUCTURE

Although *Corophium* is the most abundant member of the community at Avonport, a number of polychaetes is predictably present (Table I, Fig. 1). All of these animals are deposit-feeders. All but *Heteromastus* feed on surface deposits and would be expected a priori to compete with *Corophium* for food or for space to build tubes. The population dynamics of the three most abundant species (Fig. 1) show little change through time. Their abundances clearly are not inversely related to the changes in *Corophium* abundance (Fig. 1).

The predator exclusion experiments demonstrate that none of the polychaetes is significantly affected by predators ($P > 0.05$ in all cases). If the polychaetes are competing with *Corophium*, one would predict that polychaete abundances would decline inside predator exclusions when significant effects on *Corophium* are seen (Table IIB, Fig. 4). No such differences are seen. Thus, no evidence can be marshalled to indicate that either predation or competition with *Corophium* influences the distribution and abundance of the polychaetes. These results agree with experimental manipulations which failed to show significant competitive interactions among adult infauna at this site (Wilson, 1988). No effects of winter conditions are seen on the polychaete fauna (Table V).

IMPORTANCE OF SIZE

The outcomes of interactions of infaunal organisms are strongly influenced by the sizes of the interacting animals. Small infaunal organisms are more susceptible to bioturbation and other disturbance than are larger conspecifics (Brenchley, 1981, 1982). Smaller organisms are generally poorer competitors than larger conspecifics (Table VI, Fig. 8). Individuals from smaller species are inferior competitors to larger conspecific species (Wilson, 1983). It would seem that, for organisms of the same trophic level, larger animals are better competitors and accommodate disturbance better than smaller organisms.

Considering susceptibility to predation, one would predict that a large organism may be at a disadvantage. Numerous epibenthic predators prefer larger prey (Kent & Day, 1983; Dadswell et al., 1984; Ambrose, 1986; Peer et al., 1986; Fig. 5, Table IV). The conflicting attributes of size, where larger animals are generally better competitors but more likely to be preyed upon, are apparent for *Corophium* in the upper Bay of Fundy. Large amphipods are at risk to shorebird and fish predation during the summer (Fig. 5, Table VI) but are competitively superior to juvenile conspecifics (Table VI). A comparable interaction was noted in a sewage-enriched mudflat in Australia where shorebirds and fish prey upon large nereid polychaetes (*Ceratonereis pseudoerythraeensis*) (Kent & Day, 1983). Large *Ceratonereis* exclude smaller conspecifics, presumably by a competi-

tive mechanism although cannibalism has been reported in nereid polychaetes (Roe, 1975). Although higher numbers of *Ceratonereis* were found inside exclusion cages, greater numbers of juveniles were found in control areas. As with the present study, failure to consider the demography of populations in all of the experimental treatments would have led to erroneous conclusions about the effects of predators.

The results of predator exclusion experiments (Virnstein, 1977; Woodin, 1978, 1981; Peterson, 1982b; Ambrose, 1984; Wilson, in press) have generally resulted in increases in species abundance but without the predicted emergence of a dominant competitor which monopolizes space in treatments protected from predators. Most of these studies have measured the effects of predation by comparing abundances and species diversity between control and experimental treatments. Such measures may be too coarse to detect more subtle interactions of size-selective predation and size-dependent competition which may interact to yield counter-intuitive results. The effects of biological and physical processes on the demography of infaunal populations deserves greater attention than has been given.

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