LENGTH-WEIGHT RELATIONSHIPS, ENERGY CONTENT AND THE EFFECTS OF PREDATION ON COROPHIUM VOLUTATOR (PALLAS) (CRUSTACEA: AMPHIPODA)

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An intertidal population of *Corophium volutator* (Pallas) was studied at Starrs Point, N.S. where the species occurs in densities up to 52,280/m² Length-dry weight equations for males are different from those for females, and females collected in May show a higher weight to length ratio than those collected in June or July. Energy values averaged 15.07 J mg⁻¹ dry weight for animals $\geq$ 4.5 mm and 17.21 J mg⁻¹ dry weight for those < 4.5 mm. Preliminary experiments to measure the effects of migrant shorebird predation on *C. volutator* show dramatic declines in biomass resulting from the reduction in numbers and mean length of *C. volutator*.

Introduction

The tube dwelling amphipod *Corophium volutator* (Pallas) is widespread and abundant in many of the intertidal mud flats in the upper Bay of Fundy. High densities have been recorded locally for Cobequid Bay (65,000/m²; Yeo 1977), Chignecto Bay (21,300/m²; P.W. Hicklin in verb.) and the Minas Basin (52,280/m²; Boates 1978).

Past studies of this species have concentrated on European populations. Watkin (1941) described the life cycle of *C. volutator* in Wales and Birklund (1977) studied biomass, growth, and production in Denmark. Most relevant to this discussion are the works of Goss-Custard 1977a; b; 1969; (Goss-Custard et al. 1977) in which several aspects of the biology of *C. volutator*, such as density, size frequency distribution, and behavior were considered in relation to the foraging of overwintering redshank *Tringa totanus* (L.). Eighty-seven percent (in terms of numbers) of the diet of this shorebird consisted of *C.volutator* (Goss-Custard 1969).

Only recently has the importance of *C. volutator* as a food resource in the Minas Basin been realized. This amphipod forms a large part of the diet of ground-feeding fishes in the region (Imrie 1979; Yeo 1977). In the summer and autumn, hundreds of thousands of migrant shorebirds, predominantly Semipalmated Sandpipers *Calidris pusilla* (L.), prey heavily upon *C. volutator* prior to further migration to their overwintering grounds in Central and South America and the West Indies.

This paper deals with the relationships of dry weight to length and energy content of *C. volutator*, and also reports on a preliminary 'exclosure' experiment that was devised to measure the effects of vertebrate predation upon this amphipod.

Materials and Methods

Study Area

The study was located at Starrs Point, Kings Co., N.S. (45°08'N, 64°22'W), 6 km north of Wolfville (Fig 1). Here the extreme diurnal tides, characteristic of the region, uncover a long triangular mud flat which at low water extends over 5 km to the northeast. Sediments of the area range from fine sand to clay.

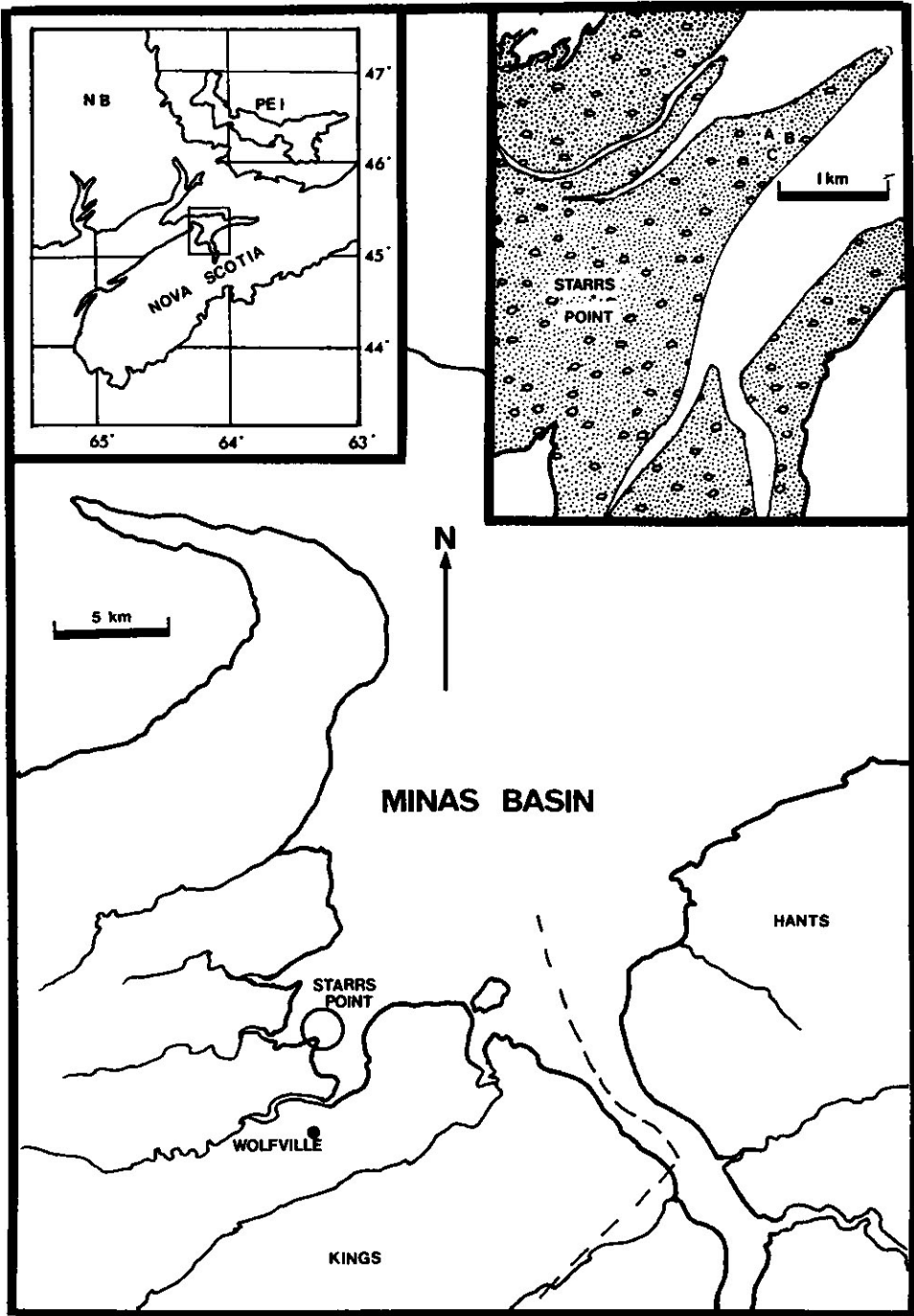Fig 1.   Map of the Minas Basin showing the Starrs Point study area
                          and the location of the sample sites. A—site of *Corophium
                          volutator* collections; B—high density exclosure; C—low densi-
                          ty exclosure.

Corophium volutator **Collections**

C. volutator samples were collected for the length-weight studies on 6 May, 8 June, and 15 July 1978 at the location (A) shown in Figure 1. Specimens were removed from the sediment by sieving (Tyler No. 20), placed in jars of seawater, returned to the laboratory and, immediately frozen (-10°C).

Later, the samples were thawed and individuals were sexed, checked for the presence of eggs and/or embryos, and measured to the nearest 0.1 mm (straightened; rostrum to telson) with calipers. Care was taken to ensure that specimens of all lengths present in the sample were included. Specimens were dried to a constant weight (12 h, 70°C) and weighed to the nearest 0.001 mg on a Cahn electrobalance.

C. volutator from the 8 June collection were used for energy determinations. These were sorted into millimeter size classes and dried (24 h, 70°C). Animals in each size class were ground to a homogenous mixture, pressed into pellets, and combusted in a "Phillipson" oxygen microbomb calorimeter.

Ash content was determined by loss of ignition (520°C, 12 h) for each of 13 individuals.

Exclosure Experiments

Two exclosures (each 5 m²), consisting of a metal frame covered with nylon string, were used to exclude predators from 2 areas of mud flat (locations, Fig 1). One exclosure was placed where *C. volutator* were present in high densities and the second in an area where densities were low. The structures were planted on 26 June near the onset of shorebird migration. At this time 6 cores (15 x 15 x 10 cm) were obtained from inside each exclosure and 6 from an adjacent control area 15 m distant. On 6 September, after migration peaked, this procedure was repeated except that 4 cores were collected from each of the 2 control areas. All samples were sieved in the field, preserved, and returned to the laboratory where numbers and lengths of *C. volutator* were determined.

Periodic observation of the exclosures verified that shorebirds feed in their immediate vicinity but rarely inside. The exclosures did not induce any observable changes in the sediment upon which they rested.

Results and Discussion

Length-Weight Relationships

Biomass is often calculated indirectly from its relationship to a more conveniently measured parameter such as length. The need for many biomass determinations for our work on shorebird foraging necessitated the derivation of length-dry weight relationships for juvenile and adult female *C. volutator* in May, June and July. A few measurements were also determined for the less abundant adult male *C. volutator* over the 3 mo of this study.

An exponential relationship described by the equation

$$W = qL^b$$

where q is a constant and the exponent b is the slope or regression coefficient that relates length (L) to weight (W) (Winberg 1971) fits the data best. The results are expressed graphically in Figures 2, 3, and the regression data are found in Table I. In all 4 cases length is highly correlated with dry weight ($r \geq 0.92$). The fact that the regression coefficients for the juvenile-female equations are near 3 suggests that length and weight are added proportionally during growth (Winberg 1971; Daborn

Table I. Length-dry weight regression data for *Corophium volutator.*

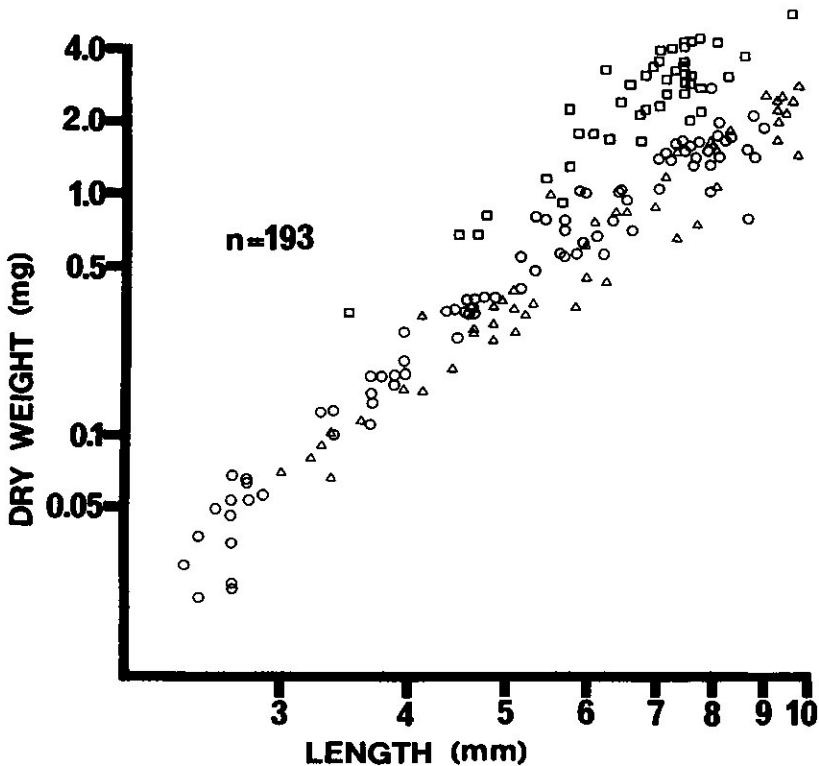|	N	q	b	r	length range (mm)
	Juvenile-Female				
May	44	0.0054	2.939	0.927	3.5-9.6
June	50	0.0021	3.089	0.978	3.0-9.7
July	99	0.0023	3.164	0.978	2.7-9.0
~	Male				
	22	0.0004	4.321	0.958	4.3-9.0

Fig 2.   Length-dry weight relationships for juvenile and female *Corophium volutator* in May (□), June (△) and July (o).
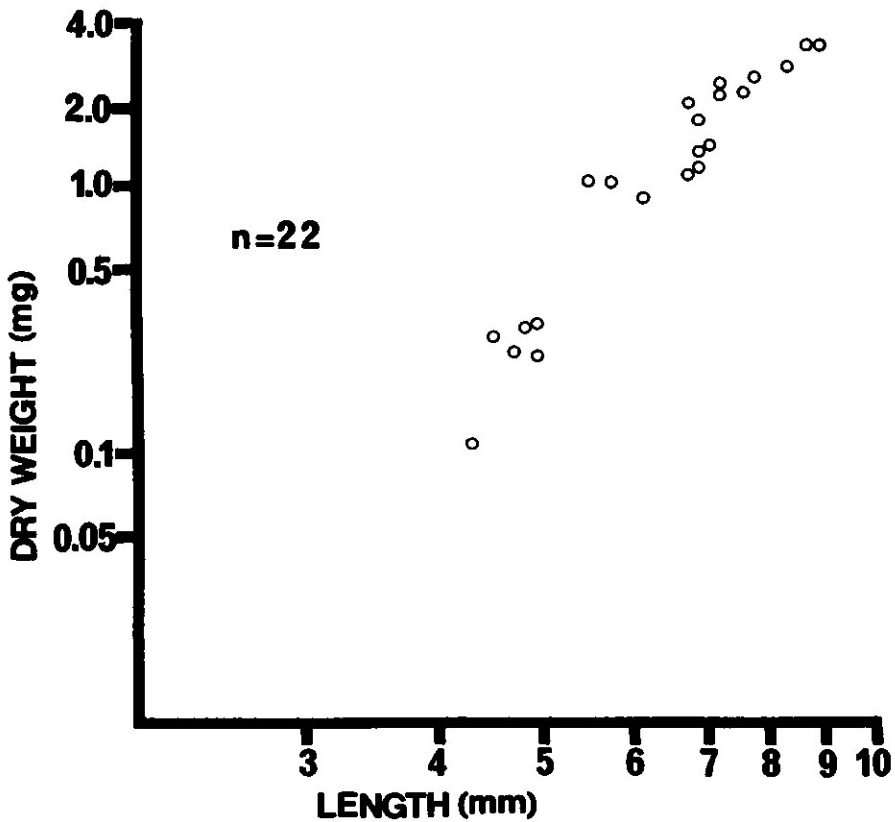
Fig 3.   Length-dry weight relationships for male *Corophium volutator*.
                                (May, June, July combined).

1974). This is not true for adult males where a regression coefficient of 4.32 was
calculated. This anomaly can be explained by the sexual dimorphism in antennae
length characteristic of *C. volutator*. Growth of these appendages in males increases
at sexual maturity ($\sim$4.5 mm) and the ratio of length^3 to weight decreases
throughout the growth period. Because our measurements of length (rostrum to
telson) do not include antennae, increases in antennae length add to the weight but
do not affect length.

An analysis of covariance was used to compare the regressions for juveniles and
females combined in May, June and July. The variances of the 3 conditions were not
different (Bartlett's test; $X^2 = 0.344$, $p > 0.995$). However, the comparisons of the
regression coefficients showed that all 3 values were significantly different (May vs
June, $F = 129.5$; May vs July, $F = 360.6$; June vs July, $F = 253.9$). In addition to dif-
fering in slope values, the data points for May are displaced above the overlapping
values for June and July (Fig. 2). These differences in slope and the displacement of
the May data points may be related to the reproductive condition of females. In
May 72% of the females were ovigerous whereas in June and July only 17 and 22%
respectively of the females carried eggs and embryos. This hypothesis warrants fur-
ther investigation.

Only 2 accounts of length-weight relationships of *C. volutator* were found in the
literature. These were both incidental to the subject of the studies and lack of detail
and variability in the methods of data presentation make direct comparison with

our information difficult. The regression coefficients of 2.82 (♂♂) and 2.58 (♀♀) of a Danish population (Birklund 1977) are quite low compared with our values. Yeo (1977), working on Cobequid Bay, reported a regression coefficient for males and females of 1.79 which appears unusually low.

Energy Content

In June, the Starrs Point. C. *volutator* population was comprised of 2 distinct cohorts representing numerically dominant juveniles and a smaller potentially breeding adult component (Fig 4). Uncorrected energy values for each millimeter size class are plotted in Figure 4. A distinct drop in energy value occurred between the 4 and 5 mm size classes. The mean value for all determinations for animals $\geq$4mm is 15.07 Jmg^{-1} dry weight$+0.08$ (SE). A consistent trend in energy value for animals < 4.5 mm length is destroyed by a single determination that yielded the lowest value in this study. Assuming that this value is a mechanical error, the energy value for animals < 4.5 mm in length is 17.21 $J mg^{-1}$ dry weight $\pm$ 0.26 (SE).

C. *volutator* $\geq$ 4.5 mm in length have a lower energy content than animals < 4.5 mm. The difference does not directly coincide with the division separating the 2 cohorts ($\sim$ 6 mm). However, 4.5 mm is the approximate length at which C. *volutator* reaches sexual maturity in Wales ($\sim$4.0 mm, Watkin 1941). In our study 97% (57 of 59) of the females carrying eggs and/or embryos exceeded 4.5 mm in length.

Variation in the ash content of C. *volutator* does not explain the difference in energy value. The ash content of 13 individuals was variable, ranging from 18.4 to 39.7% (Table II). The mean value, 27.4%, and the variability encountered are not

Table II. Ash content (% by weight) of *Corophium volutator.*

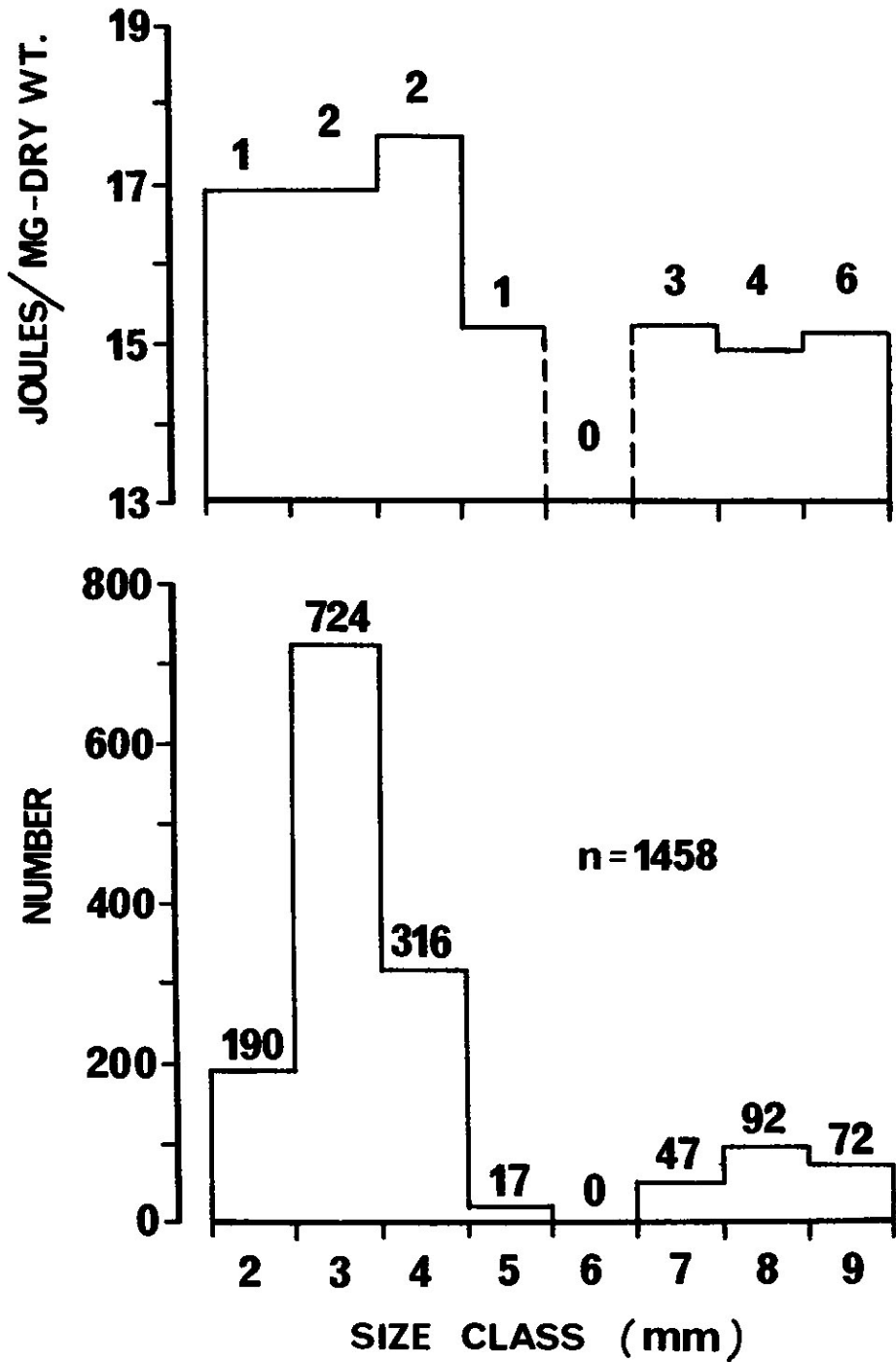| length (mm)	dry weight (mg)	% ash		
7.8	0.720	23.8		
7.4	0.631	18.7		
5.4	0.348	21.6		
8.2	1.499	32.8		
6.4	0.804	26.0		
9.3	1.651	28.1		
6.6	0.806	32.9		
4.7	0.266	18.4		
9.7	2.558	39.7		
3.4	0.099	24.2		
4.5	0.182	18.7		
5.9	0.330	35.8		$\overline{X}$ = 27.49
3.6	0.111	36.6		S.D. = 7.402

Fig 4.   Energy content and size-frequency distribution of *Corophium volutator* in June.

unusual considering those for other crustaceans (Cummins & Wuycheck 1971; Strong & Daborn 1978).

Information on the energy content of C. volutator is limited to a single published record by Wood (in Goss-Custard 1977a). He gives a range of ash-free calorific values for C. volutator in the Ythan estuary of 4.17-4.54 at Kcal g^{-1} dry weight (17.44-19.01 J mg^{-1} dry wt). When our values are corrected for ash content ($\bar{X}$ ash content 27.5%; Table II) respective values for animals < 4.5 mm and ≥ 4.5 mm are 19.21 and 21.25 J mg^{-1} dry wt. These are somewhat higher than Wood's estimates.

Exclosure Experiments

The location selected for the low density exclosure had much lower numbers of C. volutator than adjacent areas. In June, the mean density of C. volutator was 429 and 37/m^2 inside and outside the exclosure respectively (Table III). Inside the exclosure the mean number of animals/sample was the same in June as in September (Mann-Whitney U-test; U = 18.50, p > 0.1). Outside the mean number of animals increased but not significantly (Mann-Whitney U-test; U = 13.9, p > 0.1). The fact that a decrease in numbers was not observed outside the exclosure in September suggests that predation was not greatly affecting the C. volutator population in this area or that at such low densities its effects were small and undetectable. The low densities may also explain the absence of a detectable increase in C. volutator numbers inside the exclosure.

At high densities, changes in C. volutator numbers were more apparent. In June, at the site of the second exclosure (Fig 1), estimates of C. volutator abundance were 3707 and 8273/m^2 inside the exclosure and in the adjacent control areas respectively (Table IV). In September, densities inside the exclosure had increased by a factor of

Table III. Density of Corophium volutator inside and outside the exclosure in a low density area.

sample	26 June		06 September	
	inside	outside	inside	outside
1	17	4	4	17
2	20	1	24	1
3	15	0	16	1
4	3	0	6	5
5	2	0	7	
6	1	0	2	
$\bar{X}$/sample	9.7	0.8	9.8	6.3
S.D.	8.6	1.6	8.5	7.4
$\bar{X}$/m^2	429	37	437	278

Table IV. Density of *Corophium volutator* inside and outside the exclosure in a high density area.

sample	26 June		06 September	
	inside	outside	inside	outside
1	63	263	803	19
2	125	123	1051	20
3	26	240	1038	191
4	94	135	1214	30
5	57	161	841	
6	136	196	1035	
$\bar{X}$/sample	83.5	186.3	977.0	65.0
S.D.	42.5	56.8	61.9	84.2
$\bar{X}$/m²	3707	8273	44267	2886

11.9 whereas the density in the control area decreased by a factor of 2.9. The increase (83.5 to 997.0/sample) represents the growth rate of the population and natural mortality as predation is not a limiting factor here. The decrease in the control area is attributed to predation, largely by shorebirds. Groundfish predation in the immediate area of the experiment was probably low as we did not find any of the feeding pits or traces that are characteristic of the fishes feeding on Minas Basin mud flats (Risk & Craig 1976). If *C. volutator* in the control area had reproduced in the absence of predators, expected densities in September would be 1,527, 627/m², assuming no density dependent limitations on population growth or limitations similar to those inside the exclosure.

Figure 5 shows the size frequency distribution of *C. volutator* inside and outside both exclosures in September. In both the high and low density situations, specimens from inside were on average longer ($\bar{X}$ = 3.50 and 3.15 respectively) than those from the control areas ($\bar{X}$ = 3.16 and 2.59 respectively). Statistical analysis showed that the difference between the distributions inside and outside is not chance (high density: t = 5.40, p < 0.001 and low density: t = 1.70, 0.1 > p < 0.05). In the high density area the differences in length alone represent 27% more biomass inside the exclosure than outside. If the differences are attributed to predation, shorebirds may be selecting for larger individuals. Goss-Custard (1969) found that overwintering redshank similarly selected larger *C. volutator* and P.W. Hicklin (in verb.) observed that migrant Semipalmated Sandpipers in the Bay of Fundy take large *C. volutator*. Analysis of stomachs of shorebirds collected from near the exclosure sites will clarify this observation.

A similar study (Schneider 1978) showed that shorebirds in Massachusetts feed in a manner that equalizes the relative abundance of prey species but he did not investigate size related effects. In our area Semipalmated Sandpipers feed almost en-
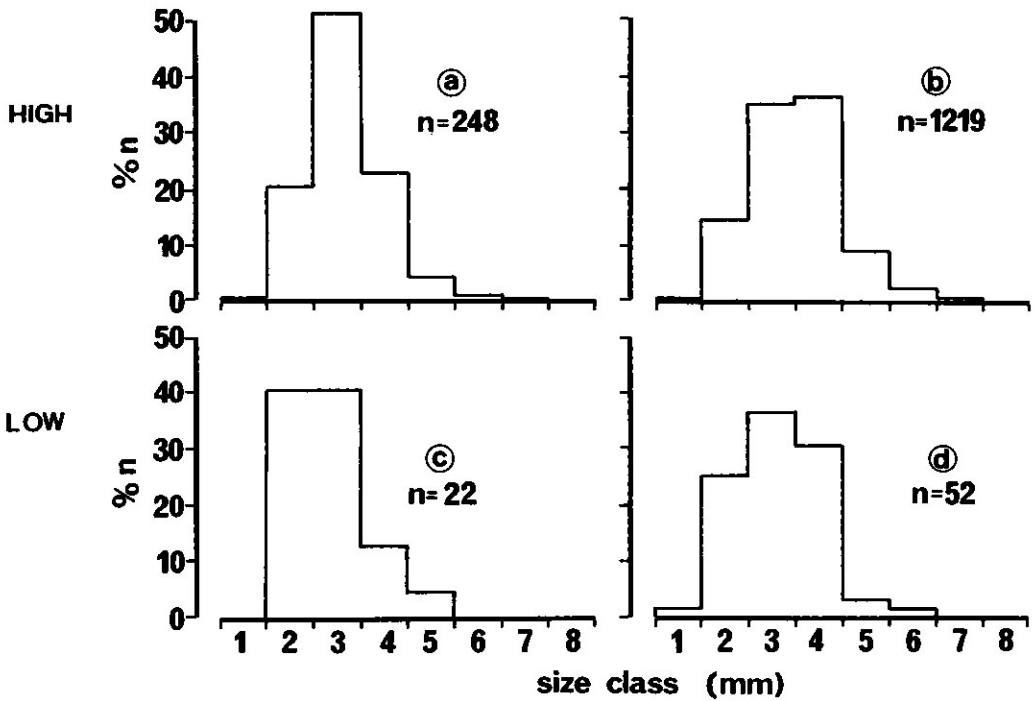
Fig 5.   High (upper) and low density (lower) size-frequency
                         distribution of *Corophium volutator* collected inside the ex-
                         closure (b and d) and outside (a and c).

tirely on *C. volutator,* and it seems that other prey species serve to supplement the
diet when *C. volutator* are unavailable.

Schneider (1978) also found that numbers of invertebrates inside the exclosures
did not change whereas numbers outside declined. This suggests that, unlike *C.
volutator* in our study, reproduction did not occur over the duration of his work.

Our work, thus far, suggests that migrant shorebirds greatly decrease biomass of
C. volutator by reducing numbers and possibly by selecting for larger individuals.

Acknowledgements

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