

THE BIOLOGY OF THE AMPHIPOD *Corophium volutator* (PALLAS)
IN THE WESTERN MINAS BASIN, NOVA SCOTIA

by

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Thesis

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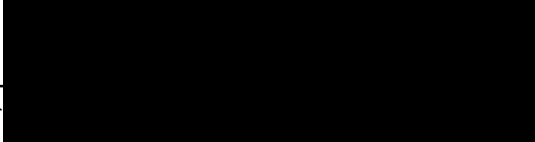
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ABSTRACT

The amphipod *Corophium volutator* (Pallas) was studied at six intertidal transects, five in the Minas Basin and the sixth on the Minas Channel. Samples were taken every four weeks from May 1977 to October 1978 along transects at Kingsport, Starrs Point, Evangeline and Avonport. Transects at Scots Bay and White Water were only sampled from May to August in 1977 and 1978. The densities along transects were compared to each other and to similar time periods at the same transect when such data were available. The greatest densities occurred at Avonport, peaking at 20,000 to 22,000/m² in 1977 and 1978. Males comprised from 8.5% to 18% of the population throughout the year. Egg-bearing females were present from April to October in 1978 with the greatest percentage, 56%, occurring in May. Three cohorts a year were evident on size-frequency histograms. Two were present for only a two to three month period in summer and produced the third cohort in August. The latter cohort overwintered and produced two successive cohorts, in June and July of the following year. Growth rates ranged from 0.06 mm/week in winter to 0.21 mm/week in spring and 0.38 to 1.34 mm/week in summer and early autumn. Yearly production of 21.64 g/m² was calculated using IBP method 2 (Crisp, 1971). The production to biomass ratio was 2.64.

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INTRODUCTION

Corophium volutator (Pallas) is a burrowing amphipod which is amphi-Atlantic in distribution (Bousfield, 1973). The species is widely distributed in Europe, occurring under a variety of conditions from estuarine mudflats to salt marsh pools, in salinities from almost freshwater to marine (Crawford, 1937). In North America its distribution is limited to the Gulf of Maine-Bay of Fundy system (Shoemaker, 1947). Bousfield and Leim (1960) found *C. volutator* to be a dominant intertidal species of mud and sandy-mud bottoms throughout the Minas Basin.

In recent years a number of researchers have worked on the ecology of *C. volutator* in the Minas Basin. In Cobequid Bay, Craig (1977) and Yeo (1978) investigated a number of factors, particularly substrate, as they affected invertebrate species, including *C. volutator*. In the western Minas Basin, Boates (1978) and Hicklin (n.d.) have assessed this amphipod in terms of a prey species for the tens of thousands of shorebirds which pass through the area in July and August. The distribution of *C. volutator* along 40 km of coastline in the western Minas Basin was detailed by Gratto (1978). Gratto (1977) described the summer and autumn portion of its life cycle at Avonport Beach.

Prior to this investigation a detailed 12 month study of the life history of *C. volutator* had not been done in North America. Yeo (1978) took samples during July and August 1975 and May to August plus December 1976. These were very limited during the winter and spring and left large gaps in his data. In Europe the most detailed study was that of Watkin (1941) in Wales. He found that there were two generations produced each year, one in May and the other in August.

The aim of this study was to obtain a more detailed picture of the population dynamics of such an ecologically important species. The life cycle as determined with size frequency histograms was compared to previous European (Hart, 1930; Watkin, 1941) and recent eastern Canadian (Yeo, 1978) research. Seasonal changes in sex ratios were examined. Growth rates at various times of the year and secondary production were calculated. Densities along the five transects where *C. volutator* were commonly found were compared to each other and to previous years where such data were available.

LITERATURE REVIEW

Much of the early research on *C. volutator* has been summarized by Crawford (1937) in his review of the genus *Corophium*. Segerstrale (1959) further summarized the research up to that time especially that of German and Russian researchers. Most of the work up to then was of a general ecological nature.

Since the early 1960's research of a more specific nature has been undertaken. Two of the first topics to be investigated in detail were substrate and salinity, long considered to be the most important factors in determining the distribution of *C. volutator* (Hart, 1930).

In a series of papers, Meadows described the substrate preferences of the species. He found that the presence of algal and bacterial films on the sediment particles enhanced the preference for a type of sediment (Meadows, 1964a). He also found that *C. volutator* were highly specific in the composition of the preferred substrate, consistently choosing sediments with a high percentage of fine grained substrate (Meadows, 1964b,c). In another set of experiments he observed that the species lived slightly longer in finer grained substrates but that growth rates were not different in a variety of substrates (Meadows, 1967). Using Minas Basin sediments, Yeo (1978) duplicated

Meadows' experiments. He determined that the most preferred substrate for the species consisted primarily of very fine sands and coarse silts with a fine silt and clay content of 20% to 40%. The percent of water content of the substrate was also found to be an important factor in determining a preferred substrate for *C. volutator*. The optimum water content was 20 to 25%.

Research on the effect of salinity on the distribution of *C. volutator* was conducted by McLusky (1967). He determined that while the species was able to survive in salinities of 2 to 50‰, maximum growth rates were attained in salinities of 5 to 30‰. Further experimentation (McLusky, 1968) revealed that breeding took place in salinities over 7.5‰ and that in salinities over 5‰ substrate became a more important environmental factor for the species. McLusky (1970) reported that *C. volutator* preferred salinities in the range of 10 to 30‰ despite acclimation to either higher or lower salinities.

Research has also been done on the effect of low oxygen concentrations on *C. volutator*. The species was found to be relatively resistant to low oxygen concentrations (Gamble, 1970a) and preferred such conditions in choice experiments (Gamble, 1971). Pleopod activity changed from intermittent at normal oxygen concentrations to continuous at low oxygen concentrations (Gamble, 1970b).

The feeding and burrowing behavior of *C. volutator*, was first described by Hart (1930). Meadows and Reid (1966) described the feeding, burrowing, swimming and crawling behaviors of the species in some detail. Gregarious behavior, especially in females of *C. volutator* was reported by Campbell and Meadows (1974). Morgan (1965) found that *C. volutator* exhibited a 12.4 h activity rhythm in the laboratory due to the effect of hydrostatic pressure.

Mention of the species in papers concerning predation is very common. Two of these have dealt with invertebrate predators of the species: *Crangon vulgaris*, a commercial prawn of economic importance in Europe (Plagmann, 1939) and the nemertine *Tetrastemma melanocephalum* (Bartsch, 1973). The latter paper reported that in an area with nemertine densities of 126/m², nemertines would consume 10,000 *C. volutator*/m²/month. This would make nemertines an important consumer of *C. volutator*. A wide variety of fish is known to consume the species. These include flounder (Hart, 1930), perch (Seegerstråle, 1940), smelt (Kuhl, 1970), skates, hake, tomcod, eel, rockling (Yeo, 1978). Imrie (1979) cited five species of juvenile fish in the Minas Basin which consume the species. Birds, particularly shorebirds on migration, are important consumers of *C. volutator*. The work of Goss-Custard in Europe is perhaps the most extensive. Two of his earliest

papers dealt with the winter feeding ecology of the redshank (Goss-Custard, 1969), in which he identified *C. volutator* as the main prey species of these birds, and later the response of birds to variations in density of the prey species (Goss-Gustard, 1970). In the Bay of Fundy, Hicklin (n.d.) and Boates (1978) assessed the impact of shorebirds, particularly semi-palmated sandpipers on their main prey, *C. volutator*. In addition to shorebirds, the chicks of the common eider duck feed on the species (Gorman and Milne, 1972).

STUDY AREA

The Minas Basin is an elongate triangular body of water running roughly east-west with the base on the western side (Figure 1). It is approximately 80 km long and 30 km at the base. From the northwest corner the Minas Channel links the Minas Basin with the Bay of Fundy. The southern bight is the name commonly given to the region at the southwest corner. Cobequid Bay forms the eastern apex of the triangle. The total surface area of the Minas Basin is about 1100 km². The shallow configuration of the Minas Basin combined with an average tidal range of 12 m, creates large intertidal flats which comprise over one-third of the total area of the Basin at extreme low water (Bousfield and Leim, 1960). These intertidal flats, exposed twice daily, vary in width from 0.2 km to 4.5 km.

Descriptions of substrate types may be found in Holme and McIntyre (1971).

Five of the six transects sampled for this study were located in the western part of the Minas Basin (Figure 2). These were at White Water, Kingsport, Starrs Point, Evangeline Beach and Avonport. The remaining transect was located at Scots Bay on the Minas Channel (Figure 1).

The transect at Scots Bay started approximately 300 m north of the old wharf. Station 1 was located on a patch

of coarse sand just below the cobbles which occupied the upper part of the intertidal zone. From there the transect ran on a bearing of 250°T for a distance of 900 m. All stations were 150 m apart. Stations 2 to 7 differed little in substrate with a very fine sand predominating at all stations.

At White Water the transect was established on a bearing of 105°T along the south side of the brook running out of Blomidon Provincial Park. The first station was 150 m from the base of the cliff. The distance between Stations 1 and 2 was 50 m with the remaining pairs of stations 100 m apart. The transect was 7 stations long with a total length of 550 m. The substrate at Stations 1 and 2 was a fine sand and silt mixture while that at the remaining 5 stations was mainly coarse pieces of shale with some sand and silt.

The transect at Kingsport started at the bend in the wharf and ran on a bearing of 135°T for 500 m. Station 1 was sandy while Station 2 had a silt substrate. Stations 3 and 4 were primarily sand with a layer of silt on top. During the study period this silt layer varied in thickness from 1 to 5 cm, being greatest in spring and least in late summer. Station 5 was located in a rocky area with sand in between the rocks. Station 6 has a coarse sand and gravel substrate with a variable silt layer on top. The stations were all 100 m apart.

The transect at Starrs Point began at the edge of the bedrock at the very tip of Starrs Point. The bearing of the transect was 17°T . All 9 stations were 150 m apart making a total distance of 1.2 km. The substrate at Station 1 was a very soft silt and clay mixture to a depth of 25 cm over a bedrock of sandstone and became gradually firmer along the transect, until by Stations 7, 8 and 9 the soft silt layer was less than 5 cm deep over firm clay.

At Evangeline Beach the transect was located near the eastern end of the beach. The transect started 50 m from the forested bank and extended 1.65 km on a bearing of 355°T . Station 1 was not sampled after the first two sampling periods as no invertebrates were found there at that time. The substrate became firmer along the transect, gradually changing from a mixture of silt and clay at Station 2 to layered silt and firm clay at Stations 8 to 11. Sand was the dominant substrate at Station 12. Stations 6, 9 and 10 were located in deep silt deposits along the sides of intertidal channels.

At Avonport the transect was located about 20 m west of the transect used by Gratto (1977). Stations 2 and 3 had a very soft substrate of mixed silt and clay. The substrate at Station 4 was layered silt and clay with an upper silt layer 5 to 10 cm deep. Station 5 had the same layered substrate as Station 4 but the silt layer was less

than 2 cm thick. At Station 6 the silt layer was over 10 cm deep. Stations 4 and 6 were located along the sides of channels. The bearing of the transect was 35°T.

MATERIALS AND METHODS

Samples were taken at 4 week intervals for the 18 month period from May 1977 to October 1978. There were 19 regular sampling periods. The extra sampling period occurred at the end of March 1978 and is designated on the graphs and tables of this thesis as March II.

All six transects were sampled from May to August, inclusive, during both 1977 and 1978. From September 1977 to April 1978 and in September and October 1978, sampling was reduced due to lack of time. During these months the transects at Scots Bay and White Water were not sampled while only Stations 1, 3, 5, 7 and 9 and 2, 4, 6, 8, 10 and 12 were sampled at Starrs Point and Evangeline, respectively. The transect at Avonport was sampled every 2 weeks from mid-May to mid-August during both summers, creating three additional sets of samples each summer.

All transects were established approximately perpendicular to the shore. The compass bearing of each was recorded. The direction of the transect was usually first created by driving 1.5 m sections of iron pipe 1 m into the substrate. Stations were marked by wooden stakes driven 0.7 m into the substrate. The iron pipes remained in place throughout the winter but many of the stakes were broken off by ice and had to be replaced in the spring.

Three samples about 0.5 m apart were taken at each station during each sampling period, avoiding such disturbances as footprints, rocks and tidepools. In May 1977 all three samples were taken with a 15 x 15 x 20 cm core sampler. One of these samples was sieved through a Canadian Standard #20 sieve (850 μ) while the other two were sieved with a #40 sieve (425 μ). The latter two samples yielded too much material to be handled efficiently so for the remainder of the study period the core size of these two #40 sieve samples was reduced to 10 x 10 cm. The depth to which the samples were taken varied and was usually taken to several centimeters below the silt and clay interface. This minimized the clay to be sieved while including all of the silt which the *Corophium* were inhabiting.

Samples were normally sieved at the sampling site but the cold weather from January to March II made this impossible. During this period the samples were placed in plastic bags and taken to the laboratory where they were sieved in large basins of tapwater. Immediately after sieving, the material retained in the sieve was placed into jars containing 4% formalin. Prior to sorting, the contents of the jars were washed to remove the remaining fine sediment and dumped into white trays. The invertebrates were then picked out with forceps and placed into vials containing 70% ethanol for storage. This sorting was usually accomplished within 2 weeks of collection.

All of the *Corophium volutator* collected were size classed using a logarithmic scale devised by Dr. Henning Lemche at the University Zoology Museum in Copenhagen. The scale is divided into size classes which become progressively larger with greater lengths (Figure 3). Length was measured from the tip of the rostrum to the end of the telson. For all sampling periods at all of the transects except Scots Bay, size frequency histograms were constructed of the percentage of the population in each size class (Figures 9 to 13).

In all 15 x 15 cm samples taken at Avonport from November 1977 to October 1978 all specimens over size class 0.6 (5.01 mm) were sexed on the basis of antennal characteristics. Males of the species have considerably larger second antennae than females (Bousfield, 1973). The number of females with eggs or young in the brood pouch was also recorded.

Individual cohorts visible on the size frequency histograms were separated. The mean length of each cohort was plotted for every sampling period in which the cohort was present (Figure 15). The growth rate was determined as the amount the mean length of the cohort had increased during the time interval between sampling periods.

Production at Avonport was calculated for all recognizable cohorts using IBP method 2, for populations with recruitment and in which age classes are separable (Crisp,

1971). The following is the formula for production during a given time interval:

$$P_i = \bar{N} \cdot \Delta\bar{w}$$

where \bar{N} is the mean number surviving in the cohort and $\Delta\bar{w}$ is the change in the mean weight of an individual in the cohort during the time interval. Total production (P) of the cohort equals the sum of P_i 's for all of the time intervals in question:

$$P = \sum_{i=1}^n P_i$$

To obtain a value for production over periods of 5 and 12 months, the production by all cohorts present within that time interval are added together (Table 2). The production to biomass ratio was calculated for both summers and the 12 month period from November 1977 to October 1978. The biomass used was the average of the mean biomass of the cohorts present during the time interval.

To convert the length measurements to weight the regressions of weight to length as determined by Boates (1978) were used. His specimens were obtained from the outer half of the Starrs Point mudbar. His regressions for females from July samples and for males were both used. For mean lengths under 4 mm only the female

regression was used. For mean lengths greater than 4 mm both regressions were used. The values obtained were added together in the percentage of each sex present in the samples taken during the sampling period in question.

The Allen curves (Neess and Dugdale, 1959; Peer, 1970) of the spring and late summer cohorts of 1978 and 1977, respectively, were constructed to compare production by the two cohorts (Figure 18). Members of the spring cohort live approximately 10 weeks in the summer while those of the late summer cohort live about 46 weeks, from late summer to the first of the summer the following year. The Allen curve was plotted using the method of Peer (1970) to obtain a smoothed curve. Regression lines, using the formula of Mendenhall (1975), were determined for the logarithm of numbers against time and the logarithm of weight against the logarithm of time, for both cohorts (Figure 16). Values from the two pairs of regressions were used to construct an Allen curve for each of the two cohorts. Figure 17 demonstrates the methods by which production, biomass and elimination may be calculated from an Allen curve (redrawn from Peer, 1970). Productivity and elimination in the time interval t_1 to t_2 equals the area of $t_1w_1w_2t_2$ and $n_1n_2t_2t_1$, respectively. The biomass at the time t_1 equals the area of $t_1n_1ow_1$. The production to biomass ratio was also calculated for the life history of both cohorts.

RESULTS AND DISCUSSION

Distribution

The distribution of *C. volutator* has been shown to depend upon substrate type. Meadows (1964b) described the optimum sediment mixture for the species as fine grained substrates mainly of silt. In the Minas Basin the species was found by Gratto (1977), Yeo (1978) and this study to occur at greatest densities on the lower half of the intertidal flats, where this type of substrate is most commonly located. In the present study the greatest densities were found at Stations 4, 5 and 6 at Avonport.

In Gratto (1978) the term "firm" mudflat was applied to intertidal flats where the dominant substrate type was layered coarse silt over firm clay, the optimum substrate for *C. volutator*. That study identified three main areas where high densities of the species occurred. These were near the outer edge of the Pereau estuary, on the end of Starrs Point mudbar and the adjacent bar to the east and on Oak Island-Avonport Beach.

Unsuitability of substrate at Scots Bay and all but Stations 1 and 2 at White Water, resulted in the low numbers of *C. volutator* found along those transects. At Kingsport the variations in depth of the silt layer created variations in the numbers of the species found at any one

of the stations during the sampling periods. This was the main reason why no *C. volutator* were found during four of the 19 sampling periods. The soft mud and clay mixture predominant along much of the transects at Starrs Point and Evangeline, more suitable for *C. volutator* than sand but not an optimum substrate, resulted in densities which remained below 10,000/m² along the two transects. At Avonport high densities in summer at three of the five stations sampled contributed to densities which reached an average of 20,000 to 22,000/m² along the transect (Appendix I).

A number of studies have also linked high densities of *C. volutator* to deposits along the banks of streams flowing across mudflats in the United Kingdom (Beanland, 1940; Howells, 1964) and Minas Basin (Gratto, 1977; Yeo, 1978). This may be linked to increased organic content of these deposits or to better drainage of the substrate along the stream banks resulting in a drier substrate (Yeo, 1978) or a combination of these and other, as yet, undetermined factors. The results of this study indicated that the highest densities were present along stream banks from mid-summer to early autumn, a time when most previous research had been carried out. Then, surprisingly, the densities along the stream dropped precipitously in October to near zero in December and remained there throughout the winter. Figure 7 shows the relationship between the density of

C. volutator at Station 6, with a 10 to 15 cm silt deposit alongside a 3 m wide stream, and Station 5, with a silt layer of less than 2 cm overlaying a base of firm clay into which *Corophium* were reluctant to burrow. Both stations were at Avonport. The density at Station 6 only rose above that of Station 5 during the period of August to October in both 1977 and 1978 and early June 1977. After October 1977 the density of *C. volutator* at Station 6 fell below that of Station 5. It remained well below 1,000/m² from December to early June when the density rose rapidly to 13,000/m² by mid-June. This increase was due almost entirely to newly released juveniles. With large fluctuations, Station 5 maintained a density of between 7,000 and 15,000/m², well above that of Station 6, from October to early June. At that time it rose to 57,000/m² by mid-June. I believe that this relationship reflects the stability of the substrate at the two stations. Extensive erosion at Station 6 during the fall and winter almost completely destroyed the population each winter for the past three years but fresh deposits each spring enabled the area to support the high densities which occurred in late summer. At Station 5 only a gradual erosion was observed to take place during summer, fall and winter. The effect of a greater than usual spring deposition of sediment may be seen in the extremely high

density of *C. volutator* in early June 1978. Erosion during the two week period prior to the next sampling period brought the depth of the silt deposit almost down to its normal thickness of 2 cm.

Overall Densities

The high density at Station 5 was the main contributor to the peak in overall density along the transect in early June 1978 (Figure 4). In July 1977 this peak was considerably lower as the density at Station 5 was almost one-third smaller than the same sampling period in 1978. The density at Station 6 was virtually identical both years. In both 1977 and 1978 the greatest densities occurred in early September with high densities at Stations 4, 5 and 6 contributing to this peak. Peak densities in September are contrary to previously published results from Wales (Watkin, 1941) and the eastern Minas Basin (Yeo, 1978). They recorded greatest densities in early July, declining steadily after that time. A similar pattern was observed on a transect adjacent to the present one at Avonport (Gratto, 1977).

Therefore at Avonport over a three year period, three different patterns of density peaks have been observed (Figure 4). In 1976 there was a single peak in July, declining to October when sampling was ended that year (Gratto, 1977). In 1977 only a small peak appeared in early July while the greatest densities occurred in September. In 1978 the peaks in early July and September were almost

the same size, although the September peak was slightly larger, and a third, smaller peak was recorded in early August. Both large peaks in 1978 were larger than the September peak of 1977. All of the major peaks in density at Avonport were near the range of 20,000 to 22,000/m² as an average along the entire transect. Individual samples were considerably higher at times with the occasional sample reaching densities of between 68,000 and 75,000/m² at various times during the summer.

At Starrs Point the overall densities fluctuated greatly within a range of 0 to 1,800/m² from May 1977 to May 1978 (Figure 5). The density then peaked in June and declined steadily through to October when no *C. volutator* were found along the transect. This would correspond to the early July peak of previously published research (Watkin, 1941; Yeo, 1978). The peak density in June reflects the dominance of the first brood of the year. This topic will be discussed in the following section.

At Evangeline atypical fluctuations were in evidence from May 1977 to May 1978 (Figure 6). The population then exhibited the more characteristic rise in density in the early summer with the density peaking in August. By September the population appeared to have returned to seemingly random fluctuation.

These fluctuations were created by the nature of the distribution of *C. volutator* along the transects at Starrs Point and Evangeline. On both transects *C. volutator* were found to occupy all of the stations at some point during the sampling period but during individual months the species may be absent from any number of the stations despite the presence of apparently suitable substrate. This led to large variations in the total number of *C. volutator* collected at these transects from one month to the next.

The Adult Population

In the 15 x 15 cm samples taken at Avonport from November 1977 to October 1978 all individuals over size class 0.6 (over 5 mm) were sexed on the basis of the differences in second antennae of males and females. This would place any of the intersexes described by Watkin (1941) in with males. The average size of the males was observed to be smaller than that of the females as reported by Watkin (1941) and Yeo (1978) but no measurement was made of this.

The greatest percentage of males encountered was 18% of the population (Table 1). Hart (1930) and Watkin (1941) also reported a greater percentage of females than males but at one point in the latter study, males accounted for 30.4% of the population. Watkin (1941) related an increased

proportion of males in early spring and midsummer to the dominant breeding periods which occurred at those times of year. My data showed a much less apparent peak in midsummer and none at all in early spring.

The proportion of females with eggs was also determined (Table 1). No females with eggs were encountered from October 1977 to March II 1978. From a very small percentage of females with eggs in April there was a rapid rise to 56% of the females in May. This percentage then dropped gradually to a low in early July. This was followed by a second peak, much smaller than the one in May and June, in late July. The percentage of females with eggs again gradually dropped off in the subsequent months until none were present in October. As is shown in Figure 8 this pattern bears great resemblance to the bimodal pattern reported in Wales by Watkin (1941). As he measured the percent of females with eggs of those females with fully developed brood pouches only, as opposed to the total of all females as was done in the present study, his values were higher. The major difference between the two sets of data were that Watkin's first peak occurred in February, two to three months earlier than the May peak in the Minas Basin.

Watkin recorded egg-bearing females from February to October. This period is several months longer than the

April to October period observed in this study. This was most probably caused by the difference in water temperature between Wales and the Minas Basin especially early in the year. McLusky (1968) found the onset of breeding coincided with an increase in temperature above 7°C. That was approximately the water temperature in Wales in January and February (Watkin, 1941). In the Minas Basin temperatures do not reach that level until late April and early May (Bleakney, unpublished data). Research cited by Segerstråle (1959) included periods of May to November, April to September and May to September for the Zuiderzee, Denmark and the Baltic, respectively. These reproductive periods, from areas with cooler water temperatures than the west coast of the United Kingdom, compare favourably with the reproductive period determined in this study.

The length of the incubation period of eggs is usually three to four weeks (Hart, 1930; Watkin, 1941; Segerstråle, 1959). In the present study periods of about four weeks for both of the major broods (mid-May to mid-June and mid-July to mid-August) from peak percentage of brooding females to a major brood release. Watkin (1941) suggested higher water temperatures during late summer could cause the development time of the second major brood to be reduced by as much as one week. This was not evident in the present study, although more intensive weekly sampling may prove Watkin's hypothesis is applicable to the Minas Basin.

The previously mentioned incongruity between the peak density at Avonport in September and previously published research which showed an early July peak (Watkin, 1941; Yeo, 1978) may be at least partially explained by recent research in England (Sheader, 1978). He reported that in *C. insidiosum* minimum brood mortality occurred from May to August due to a combination of various factors which he enumerated. These included decreased development time of eggs during warmer weather and increased ventilation activity on the part of the female at the same time. This resulted in maximum brood release in May and June similar to that reported for *C. volutator* (Watkin, 1941; Yeo, 1978). Conditions at Avonport, possibly due to the influence of the Avon River, may be such that the combination of factors necessary for maximum juvenile release may occur later there than at the other transects in this study and those of Yeo (1978) in the Cobequid Bay, resulting in later peak densities.

Size Distribution

Size-frequency histograms were used to determine the presence of the different cohorts and observe their growth. These were plotted for the samples taken along the transects at White Water, Kingsport, Starrs Point, Evangeline and Avonport (Figures 9 to 13).

The May 1977 and 1978 samples from all transects showed the presence of a single cohort of predominantly large individuals. The mean length of the population in May 1977 and 1978 was 6.67 and 7.12 mm, respectively, at Avonport (Figure 14). A second cohort first appeared in the samples taken at Avonport on 9 June 1977 and 8 June 1978. By mid-June this group had become the dominant cohort in the population, decreasing the mean size of the population at Avonport in 1978 to 3.87 mm. In early July another cohort appeared in the Avonport samples. The numbers of this cohort were considerably lower than for the previous one. Watkin (1941) attributed a similar July cohort to reproduction by the smaller individuals present in the May samples. Therefore the cohorts produced in June and July make up the group that Watkin called generation I. The overwintering cohort present in May was not apparent by the mid-July samples. In Cobequid Bay, Yeo (1978) found that the overwintering adults also disappeared about mid-July but that they died off faster on transects toward the head of Cobequid Bay. There also appeared to be a similar gradient as one moved into the southern bight of the Minas Basin. Only a few of the overwintering group were present at Avonport in early July. At Evangeline only a few were found in mid-June while at Starrs Point none were present in the mid-June samples in 1977. This may be due to increased rate of development in higher water

temperatures as temperatures have been shown to increase by several degrees moving in from the mouth of the Minas Basin both into the southern bight and Cobequid Bay (Bousfield and Leim, 1960). As the two early cohorts matured the mean size of the population increased in July and early August on all transects.

In mid-August a new cohort appeared. This group was the equivalent of Watkin's generation II. They continued to grow throughout the fall, becoming the only cohort present by October 1977 at Avonport as the spring and early summer cohorts had died off. Several were still present along that transect in the October 1978 samples. Again a more rapid disappearance was noted on the transects further into the southern bight as this group was not found in the September samples at the Starrs Point and Evangeline transects. The presence of all three major cohorts in September at Avonport created the greatest densities of the year during that month.

The late summer cohort of 1977 became the overwintering group and did not reproduce until the following spring. During this period the mean size of the population at Avonport increased from 4.38 mm in September to 7.31 mm in early June. There was a decrease in size from December to January which was probably due to the dying off of the largest individuals who had been produced in early August.

The pattern observed in the summer of 1978 was virtually identical to that observed in 1977.

The average size of *C. volutator* in this study and those of Watkin (1941) in Wales and Yeo (1978) in Cobequid Bay were about the same. For comparison the average size in May was 7.12, 7.3 and 6 to 7 mm and in December was 5.12, 4.6 and 3 to 5 mm, for the three studies, respectively.

Growth Rates

When the individual cohorts were separated and the mean lengths of each plotted on a graph of length versus time (Figure 15), growth rates may be estimated. The life history of all five complete cohorts had a form which approximated a sigmoid curve. There was a brief lag phase which was two weeks long in the spring cohorts of both years and four weeks in the two early summer and the late summer cohorts. Growth rates were highly variable during this period, ranging from a high of 0.63 mm/week in the spring cohort of 1978 to a low of 0.11 mm/week in the early summer cohort of 1978. The lag was due to the production of new broods over the two to four week lag period. The newly released individuals would lower the mean length of the cohort through the lag period, so that growth by the individuals in the first broods would not appear as much as it actually was.

After the release of the entire cohort the growth rates increased. This period usually lasted for four weeks

but in the early summer cohort of 1977, it lasted only two weeks. In that period the mean length of the cohort increased by 2.68 mm, a rise of 1.34 mm/week. The increase in the same cohort in 1978 was 0.63 mm/week for the same growth period. The mean length of the spring cohort rose at a rate of 0.83 and 0.68 mm/week in 1977 and 1978, respectively. The rate of increase in length of the late summer cohort was considerably lower, 0.38 mm/week.

Following this period the growth rate decreased. This transition appeared to take place in the spring and early summer cohorts when the mean length had increased to a range of 5.5 to 6.5 mm. In the late summer cohort this decrease in growth rate was more probably due to the onset of colder weather as it occurred when the mean length of the cohort was only 5 mm. The growth rate of this cohort was negative from November to January as the largest individuals died off, decreasing the mean length of the cohort. Growth proceeded at a rate of 0.06 mm/week from January to April. After April the rate more than tripled, increasing to 0.21 mm/week until early June. This was probably due to a rapid increase in temperature which was observed in the Minas Basin at that time of year (Bleakney, unpublished data). The mean length of the cohort then decreased slightly to mid-July after which the cohort was not visible on the size-frequency histograms. The mean length at maturity of the spring and early summer cohorts

appeared to be lower than that of the late summer cohort, especially in 1977. This may be due to the length of time that the former cohorts were present. The shorter lives of the spring and early summer cohorts may reflect the increased growth rate of these cohorts in the earlier stages of their life histories. This could lead to maturity, and death, at lower mean lengths. The long period of very slow growth during the winter may enable the late summer cohort to live longer and attain greater lengths than the other cohorts.

Production

Secondary production in *C. volutator* at Avonport was calculated using the IBP method 2, for stocks with recruitment and age classes which are separable (Crisp, 1971). By this method production by a cohort within a time interval is equal to the product of the mean number of individuals and the change in the mean weight of an individual in the cohort during that interval. These production values are then summed up from the start of recruitment of the cohort to the end of the period in question. The production attributed to each cohort present during the period are added together. Production is usually expressed as grams of dry weight per m² in this study.

Production was calculated for all recognizable cohorts (Table 4). For the 12 month period from November 1977 to

October 1978, inclusive, production was 22.33 g/m^2 . This value is considerably higher than that calculated with the same method by Yeo (1978) of $8.54 \text{ g/m}^2/\text{year}$ for *C. volutator* at a single intertidal station in Cobequid Bay. Examination of both sets of data indicated that higher densities of *C. volutator* at Avonport were the main contributor to this difference.

For comparative purposes, production was calculated for the period of May to October for both 1977 and 1978. The two values, 19.23 and 20.53 g/m^2 for 1977 and 1978 respectively, were virtually identical. It may also be noted that these values are close to the value for yearly production, indicating the extremely low production during winter due to the low densities of *C. volutator* and low growth rate. Birklund (1977) calculated production of 2 to 4 g/m^2 for May to September for a low density population of *C. volutator* in Denmark. This would be much lower than the value of production for the same period in the present study.

The ratio of production to biomass was also determined for the period of November to October. The ratio of 2.64 compared favourably with the ratio of 2.7 (Yeo, 1978) and 3 to 4 (Birklund, 1977) for the same species. Winberg (1971) cited annual production to biomass ratios for a number of amphipod species in Russia: 2 and 3 for *Gammarus lactustris*, 1.6 and 2.9 for *Gmelinoidea fasciatus* and 1.9 and 3.44 for

Pontoporeia affinis. The lower of the pair of ratios for the first two species was due to a prolonged life cycle and for the third species was due to lower water temperatures. Peer (1970) noted that the production to biomass ratio became steadily lower through the life history of the polychaete *Pectinaria hyperborea*.

As a comparison between a spring and late summer cohort, production was also calculated using the Allen curve method (Neess and Dugdale, 1959; Peer, 1970), where the area under the curve, on a plot of density against mean weight through the life of the cohort (Figure 16), equals production. The Allen curves were constructed using points obtained from the regression lines of weight and length against time (Figure 18).

The values for production obtained by this method differed markedly from those obtained by the IBP method, although the differences may be explained by the presence of anomalies in the original data. For the spring cohort the IBP method gave a value of 7.80 g/m^2 whereas the Allen method gave a value of 9.90 g/m^2 . This difference was created by a much higher value, for the Allen method, for the mean weight of an individual in the cohort at ten weeks after recruitment. In the original data this was where the growth rate abruptly dropped off at the end of the cohort's life cycle. This alone caused about 70% of the difference between the two values. For the late summer cohort the

values obtained were 9.52 and 6.18 g/m² for the IBP and Allen methods, respectively. The difference was due almost entirely to much lower mean weights, by the Allen method, at 42 and 46 weeks after recruitment. These times correspond to the May and June samples where the growth rate of the cohort was greatly accelerated as the warmer spring weather arrived.

Biomass and cumulative elimination may also be calculated from the Allen curve (Table 4) and then plotted along with cumulative production to demonstrate accumulation of these factors through the life history of the cohort (Peer, 1970). Substantial differences were found to exist between the spring and late summer cohorts of *C. volutator* (Figure 19) mainly because of the variation in longevity of the two cohorts. The late summer cohort was present for approximately 46 weeks from mid-August to early July of the following year. The rate of production reached a peak between weeks 2 and 6, declining steadily thereafter. The rate at which biomass increased was also greatest between weeks 2 and 6. The amount of biomass, peaked at 2.75 g/m² at week 26, which corresponded to early February. At this point the rate of elimination began to gradually decrease. This decrease, and part of the preceding increase, was so gradual that the line for cumulative elimination appeared to be linear from week 14

to week 46. During this period the rate of elimination varied from 0.34 to 0.42 to 0.35g/m² for weeks 14, 26 and 46 respectively. From this it would seem that mortality, although fairly constant throughout the winter, was slightly greater in late autumn and early winter.

The duration of the life history of the spring cohort was only about 10 weeks from early June to the end of August in 1978. By the end of that period cumulative production, biomass and cumulative elimination were all increasing rapidly although the rates of biomass increase and cumulative production had peaked at weeks 4 and 6, respectively and were decreasing over the last few weeks of the cohort's brief life history. The rate of elimination increased from 0.35 g/m² between weeks 0 and 2 to 1.23 g/m² between weeks 8 and 10. This greatly increased elimination may be due to a great extent to the tens of thousands of shorebirds migrating through the area in late summer. They reached peak densities in early August this past year (J. S. Boates, pers. comm., Biology Dept., Acadia University). This period is the equivalent of weeks 8 and 10, when the peak in the rate of elimination was calculated.

FUTURE RESEARCH

Perhaps the most important missing link in the available data on *C. volutator* is the need to know the number of eggs produced by females of the species and how the size of the brood and the survival of the young are related to changes in water temperatures.

Due to the importance of *C. volutator*, in terms of its biomass and production, the amount of predation on the species by shorebirds, various fish species and other, as yet, undetermined predators must be known when energy flow values are determined for the Minas Basin-Bay of Fundy system.

SUMMARY

1. Transects were established at White Water, Kingsport, Starrs Point and Evangeline in the western Minas Basin and Scots Bay on the Minas Channel.

2. Samples were taken every four weeks from May 1977 to October 1978 at all but the first and last transects above. These were only sampled from May to August of both 1977 and 1978.

3. Substrate has long been regarded as one of the most important factors involved in determining the distribution of *C. volutator*. Deep silt deposits along intertidal streams have been associated with the greatest densities of the species. In this study the greatest densities in 1977 and 1978 at Avonport occurred at a station along a stream only from late August to October. For the remaining nine months the greatest densities were found at a station with only a thin (2 cm) layer of silt over firm clay, supposedly not optimum *C. volutator* substrate.

4. The density of *C. volutator* peaked at various times during the summer along the transects of Starrs Point, Evangeline and Avonport. In 1978 the densities peaked at 6,200/m² in late June at Starrs point, at 2,900/m² in late August at Evangeline and at 20,000/m² in early June and 22,000/m² in September at Avonport.

5. The percentages of males, females and females with eggs were recorded from samples taken at Avonport from November 1977 to October 1978. The percentage of males varied between 8.5% and 18% of the population. The percentage of females with eggs peaked at 56% in May and again in July at 19.2%. Egg-bearing females were present from April to October in 1978.

6. All of the *C. volutator* collected were placed into size classes and size-frequency histograms were constructed. Three cohorts per year were evident. The first two cohorts were produced by the overwintering population in early June and early July. These two cohorts produced a third cohort in August, which overwintered, reproducing the following spring and early summer.

7. The growth rate of the cohorts during the summer ranged from 0.38 to 1.45 mm/week. In winter the growth rate was considerably lower, 0.06 mm/week, but rose to 0.21 mm/week in spring as water temperatures in the Minas Basin increased. The overwintering cohorts attained greater mean lengths than the other cohorts. This may be due to a much slower growth rate in the former cohorts through their longer life span.

8. Yearly production was calculated by IBP method 2 for the period of November 1977 to October 1978. The production of 20.64 g/m² was more than twice the highest

value reported in the literature for the same species. The production to biomass ratio of 2.64 compared favourably with previous research.

9. The Allen method for the calculation of production was used to compare production for the spring cohort of 1978 and the late summer cohort of 1977. For the late summer cohort the rate of production was greatest during the first 6 weeks after recruitment and gradually decreased for the remainder of the 46 weeks for which the cohort was present, from August to July. The biomass and the rate of cumulative elimination was greatest at 26 weeks after recruitment. Elimination was in the range of 0.34 to 0.42 g/m² from week 14 to week 46. The spring cohort was present for only a 10 week period during the summer. In this cohort the rate of production was also greatest over the first 6 weeks after recruitment. The rate of production was much higher than that of the late summer cohort. Biomass continued to increase over the 10 weeks. The rate of elimination was greatest during the last 2 weeks of the cohort's life history.

The amount of predation on *C. volutator*, especially by fish and shorebirds, is very important in terms of the energy flow within the Minas Basin-Bay of Fundy system.

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TABLES

Table 1. Percentage of males, females and females with eggs from November 1977 to October 1978 at the Avonport transect.

Sampling date	Total number	% males	% females	% females with eggs
10/11	318	8.7	91.3	0
07/12	281	13.1	86.9	0
05/01	259	10.1	89.9	0
02/02	221	11.2	88.8	0
06/03	243	12.8	87.2	0
30/03	333	9.5	90.5	0
27/04	244	9.4	90.6	0.01
24/05	398	11.6	88.4	56.2
08/06	188	8.5	91.5	52.3
20/06	373	9.8	90.2	38.3
10/07	783	13.5	86.5	6.1
21/07	873	10.7	89.3	19.2
07/08	788	17.5	82.5	7.2
18/08	615	10.4	89.6	7.8
13/09	469	10.4	89.6	1.2
12/10	440	18.0	82.0	0

Table 2. Values used for the calculation of production (P) and biomass (B) by the IBP method 2 (Crisp, 1971) for all cohorts found during the study period. The cohorts are designated as: spring cohort, A; early summer cohort, A¹; late summer cohort, B.

Cohort	Sampling date	Year	N (/m ²)	\bar{N}	w (mg)	w	P (g/m ²)	B (g/m ²)
B	27/05	1977	2500		0.620			1.550
	09/06		1944	2222	0.921	0.301	0.667	1.790
	21/06		3004	2474	0.748	-0.173	-0.428	2.248
	07/07		1140	2074	1.885	1.137	2.357	2.150
			1164	1152	2.421	0.536	0.617	2.819
								total P 3.213
A	09/06		987	493	0.022	0.022	0.011	0.022
	21/06		5855	3421	0.055	0.033	0.113	0.322
	07/07		11391	8623	0.287	0.232	2.004	3.274
	21/07		8706	10049	0.714	0.426	4.285	6.215
	03/08		7667	8186	0.864	0.150	1.230	6.624
							total P 7.642	
A ¹	07/07		2775	1883	0.033	0.033	0.080	0.092
	21/07		3451	3113	0.065	0.032	0.100	0.224
	03/08		5551	4501	0.099	0.034	0.153	0.550
	17/08		3928	4739	0.680	0.581	2.753	2.670
	16/09		5004	4466	0.930	0.250	1.119	4.655
							total P 4.204	
B	17/08		9732	4866	0.054	0.054	0.263	0.526
	16/09		14847	12289	0.119	0.065	0.799	1.767
	12/10		8540	11694	0.385	0.266	3.105	3.284
	10/11		7660	8100	0.450	0.066	0.532	3.448
	7/12		4962	6311	0.410	-0.040	-0.253	2.035

Table 2 (cont'd)

Cohort	Sampling date	Year	N (/m ²)	\bar{N}	w (mg)	w	P (g/m ²)	B (g/m ²)
B	05/01	1978	5251	5106	0.375	-0.035	-0.177	1.971
	02/02		5289	5270	0.434	0.058	0.306	2.293
	06/03		2328	3808	0.493	0.060	0.227	1.148
	30/03		2847	2587	0.594	0.101	0.262	1.692
	27/04		3260	3053	0.666	0.071	0.217	2.169
	24/05		2821	3040	1.232	0.567	1.724	3.477
	08/06		1196	2008	1.455	0.223	0.417	1.740
	20/06		2668	1932	2.148	0.692	1.338	5.731
	10/07		1111	1890	2.170	0.023	0.043	2.411
								total P
A	08/06		49	24	0.015	0.015	0.000	0.001
	20/06		14847	7448	0.079	0.064	0.477	1.173
	10/07		12160	13503	0.345	0.266	3.593	4.196
	21/07		10017	11088	0.611	0.266	2.946	6.118
	07/08		7280	8648	0.670	0.059	0.509	4.875
	18/08		6668	6974	0.709	0.039	0.272	4.726
							total P	7.798
A ¹	10/07		2333	1667	0.036	0.036	0.060	0.084
	21/07		4285	3309	0.054	0.018	0.060	0.231
	07/08		5293	4789	0.060	0.006	0.029	0.318
	18/08		4540	4917	0.119	0.059	0.290	0.540
	13/09		5966	5253	0.954	0.845	4.385	5.690
	12/10		3583	4774	1.580	0.626	2.990	5.661
							total P	7.814
B	18/08		4770	2385	0.021	0.021	0.051	0.101
	13/09		16128	10449	0.102	0.081	0.846	1.648
	12/10		12064	14096	0.136	0.033	0.471	1.636
							total P	1.368

Table 3. Values used for the calculation of the linear regressions, by the least squares method (Mendenhall, 1975) of the logarithm of density (N) versus time (t) and the logarithm of weight (w) versus the logarithm of time (t) for the late summer cohort of 1977 (B) and the spring cohort of 1978 (A). Raw data are in Appendix II.

Line	Cohort	x	y	SS _x	SS _{xy}	SS _y	\bar{x}	\bar{y}	\hat{B}_1	\hat{B}_0	r
1	B	t	log N	143.0	-9.4194	0.7358	6.0	3.6939	-0.0659	4.0891	0.92
2	A	t	log N	10.0	-0.9187	0.0861	3.0	3.9890	-0.0920	4.2646	0.99
3	B	log t	log w	1.7804	1.6974	1.8878	0.6573	-0.3689	0.9534	-0.9957	0.93
4	A	log t	log w	0.3050	0.4236	0.6435	0.4158	-0.4204	1.3888	-0.9979	0.96

line 1 $y = 4.0891 - 0.0659 x$ $\log N = 4.0891 - 0.0659 t$

2 $y = 4.2646 - 0.0920 x$ $\log N = 4.2646 - 0.0920 t$

3 $y = -0.9957 + 0.9534 x$ $w = 0.1010 t^{0.9534}$

4 $y = -0.9979 + 1.3888 x$ $w = 0.1004 t^{1.3888}$

Table 4. Values used for the calculation of elimination (E), biomass (B) and cumulative production ($P_{Cum.}$) by the Allen method (Peer, 1970). The cohorts are designated as: late summer cohort of 1977, B; spring cohort of 1978, A.

Cohort	Time (weeks)	N (/m ²)	N	w (mg)	\bar{w}	$\frac{E}{N\bar{w}}$ (g/m ²)	$E_{Cum.}$	B $\frac{B}{N\bar{w}}$ (g/m ²)	B	$P_{Cum.}$ (g/m ²)	
B	0	12280		0							
	2	11380	900	0.052	0.052	0.047	0.047	0.594	0.594	0.641	
	6	9780	1600	0.149	0.101	0.161	0.208	1.454	0.860	1.662	
	10	8402	1378	0.242	0.195	0.269	0.477	2.033	0.579	2.510	
	14	7220	1182	0.334	0.288	0.340	0.817	2.408	0.375	3.225	
	18	6204	1016	0.424	0.379	0.385	1.202	2.629	0.221	3.831	
	22	5330	874	0.513	0.468	0.409	1.611	2.735	0.106	4.346	
	26	4579	571	0.602	0.557	0.419	2.030	2.755	0.020	4.785	
	30	3935	644	0.690	0.646	0.416	2.445	2.714	-0.041	5.160	
	34	3381	554	0.777	0.733	0.406	2.852	2.627	-0.087	5.479	
	38	2905	476	0.864	0.820	0.391	3.242	2.509	-0.118	5.752	
	42	2496	409	0.950	0.907	0.371	3.614	2.372	-0.137	5.986	
	46	2145	351	1.036	0.993	0.349	3.962	2.222	-0.150	6.184	
							total	$\frac{B}{\bar{B}}$ 27.052			
								$\frac{B}{\bar{B}}$ 2.081		$P_{Cum.} : \bar{B} = 2.97$	
A	0	18390		0							
	2	14890	3500	0.101	0.101	0.352	0.352	1.496	1.496	1.848	
	4	12040	2850	0.263	0.152	0.433	0.784	3.167	1.670	3.951	
	6	9740	2300	0.462	0.362	0.834	1.612	4.500	1.333	6.118	
	8	7882	1858	0.689	0.576	1.070	2.688	5.433	0.933	8.120	
	10	6377	1505	0.939	0.814	1.225	3.913	5.989	0.556	9.902	
						total	$\frac{B}{\bar{B}}$ 20.585				
							$\frac{B}{\bar{B}}$ 3.431		$P_{Cum.} : \bar{B} = 2.89$		

FIGURES

Figure 1

Figure 1. Map of Minas Basin and Scots Bay, Nova Scotia.

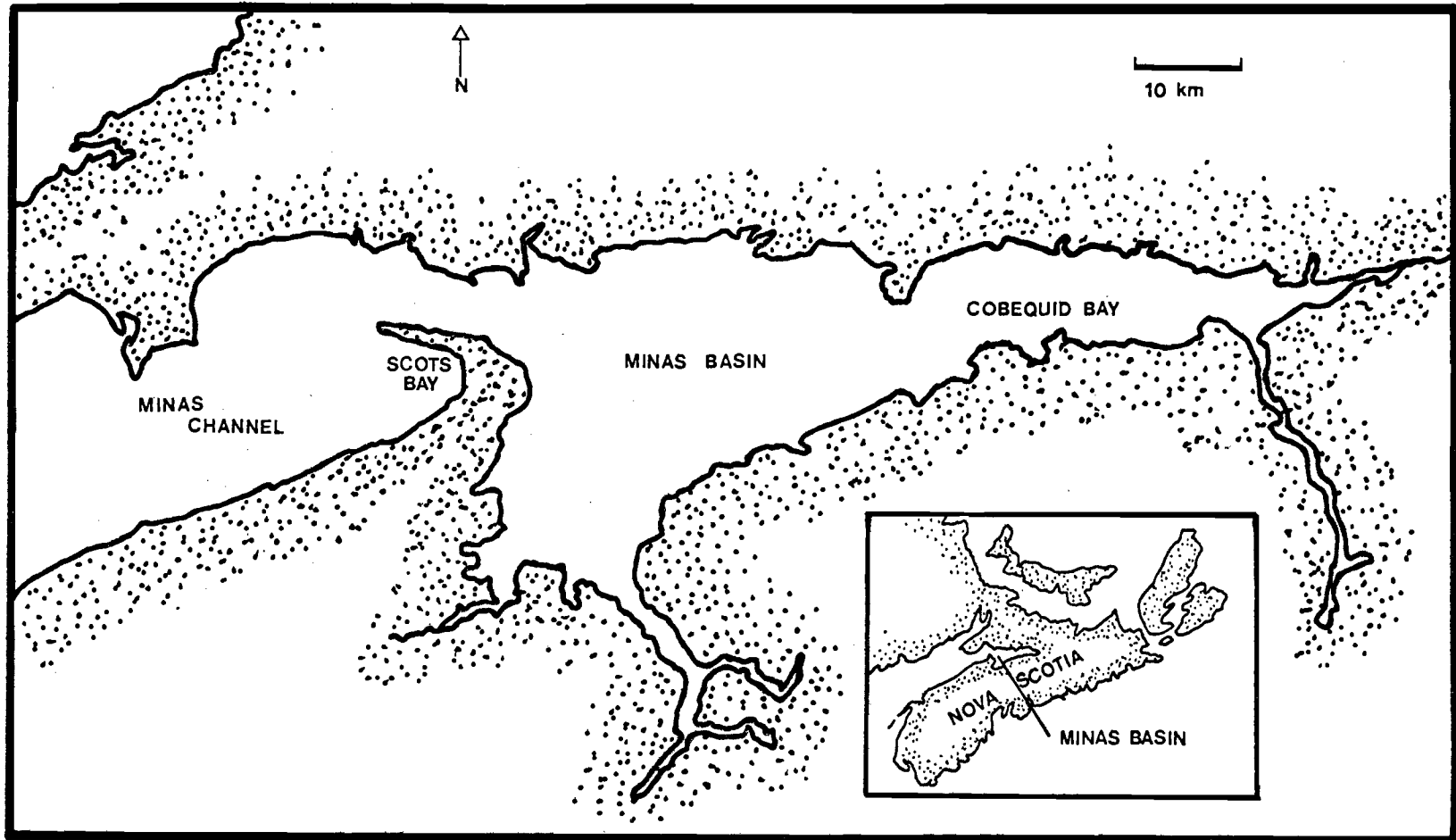
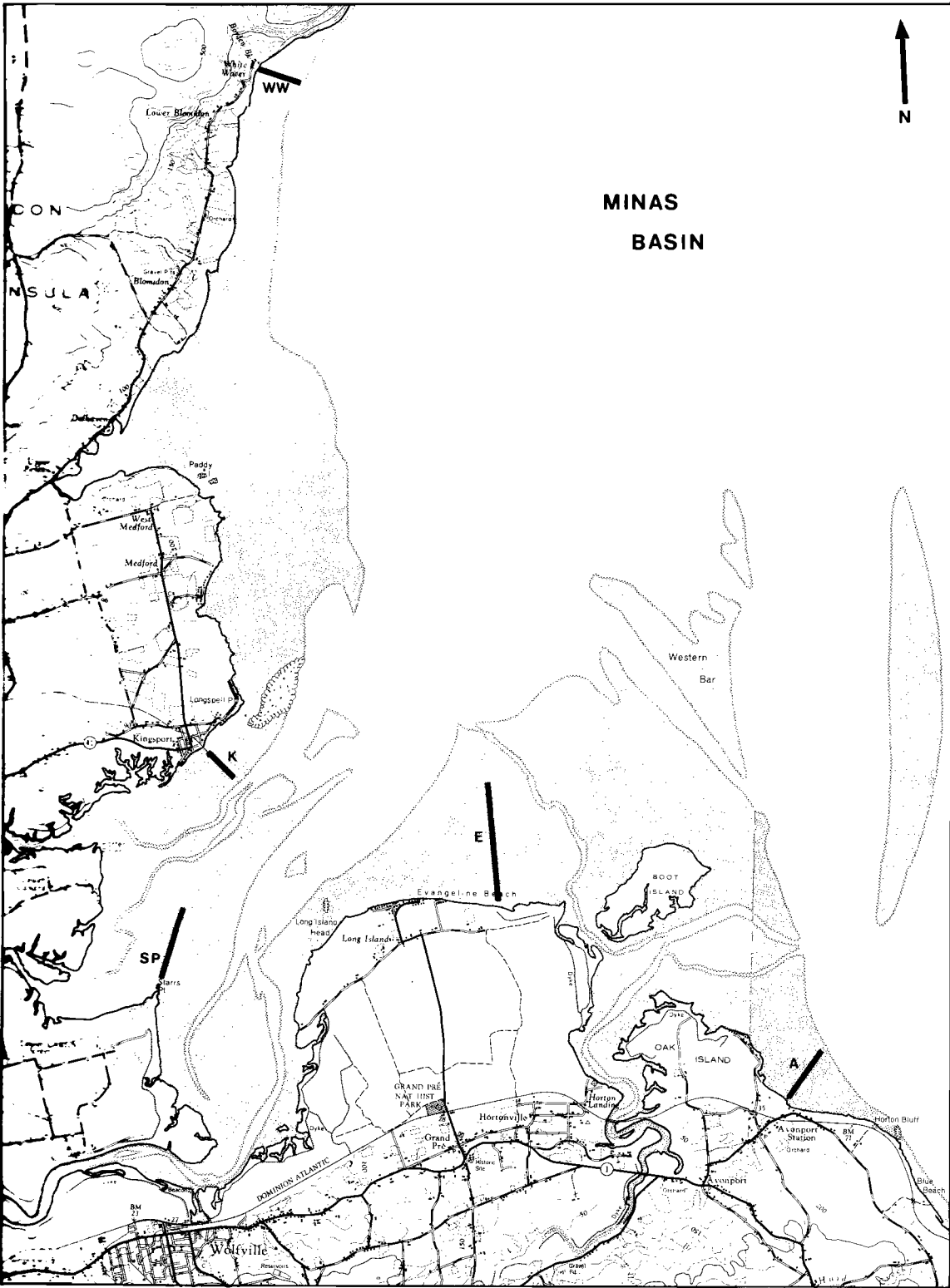


Figure 2

Figure 2. Map of western Minas Basin showing location of transects at White Water, Kingsport, Starrs Point, Evangeline and Avonport.

WW - White Water
K - Kingsport
SP - Starrs Point
E - Evangeline
A - Avonport

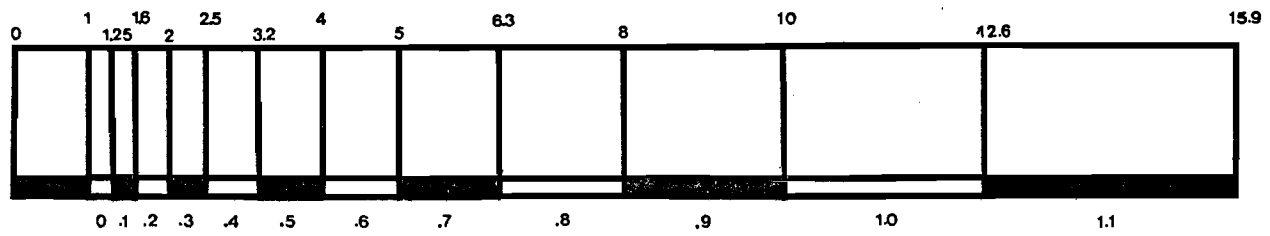


**MINAS
BASIN**

Figure 3

Figure 3. Logarithmic scale used to size-class
Corophium volutator.

LENGTH (mm)



SIZE CLASS

Figure 4

Figure 4. Average densities (/m²) of *C. volutator* each sampling period at Avonport from May 1977 to October 1978. The average densities (/m²) on an adjacent transect from June to December 1976 (Gratto, 1977) are also included.

--- - Gratto (1977)

— - May 1977 to April 1978

..... - May 1978 to October 1978

Range of values may be found in Appendix IV.

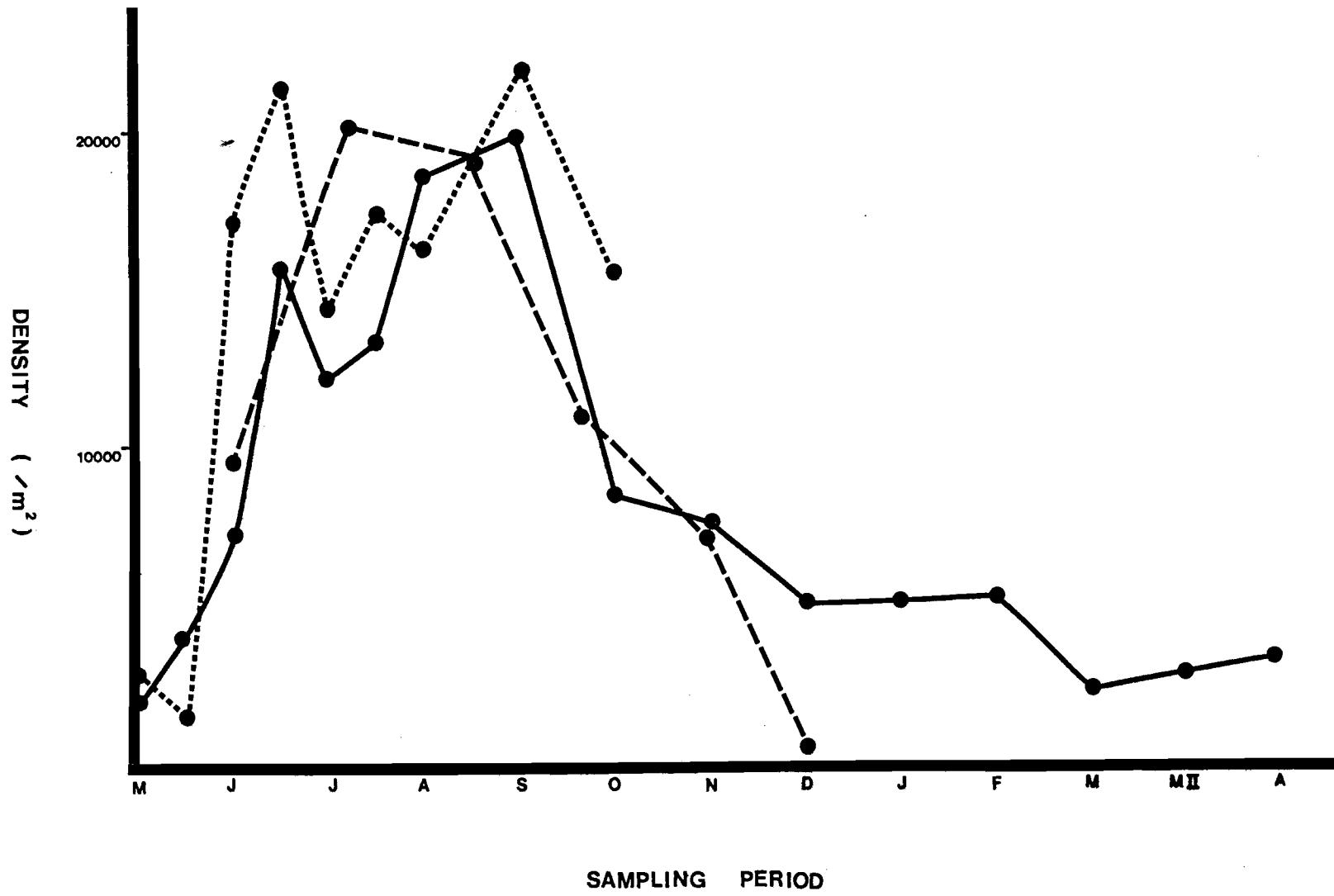


Figure 5

Figure 5. Average densities (/m²) of *C. volutator* each sampling period at Starrs Point from May 1977 to October 1978.

— - May 1977 to April 1978

..... - May 1978 to October 1978

Range of values may be found in Appendix IV.

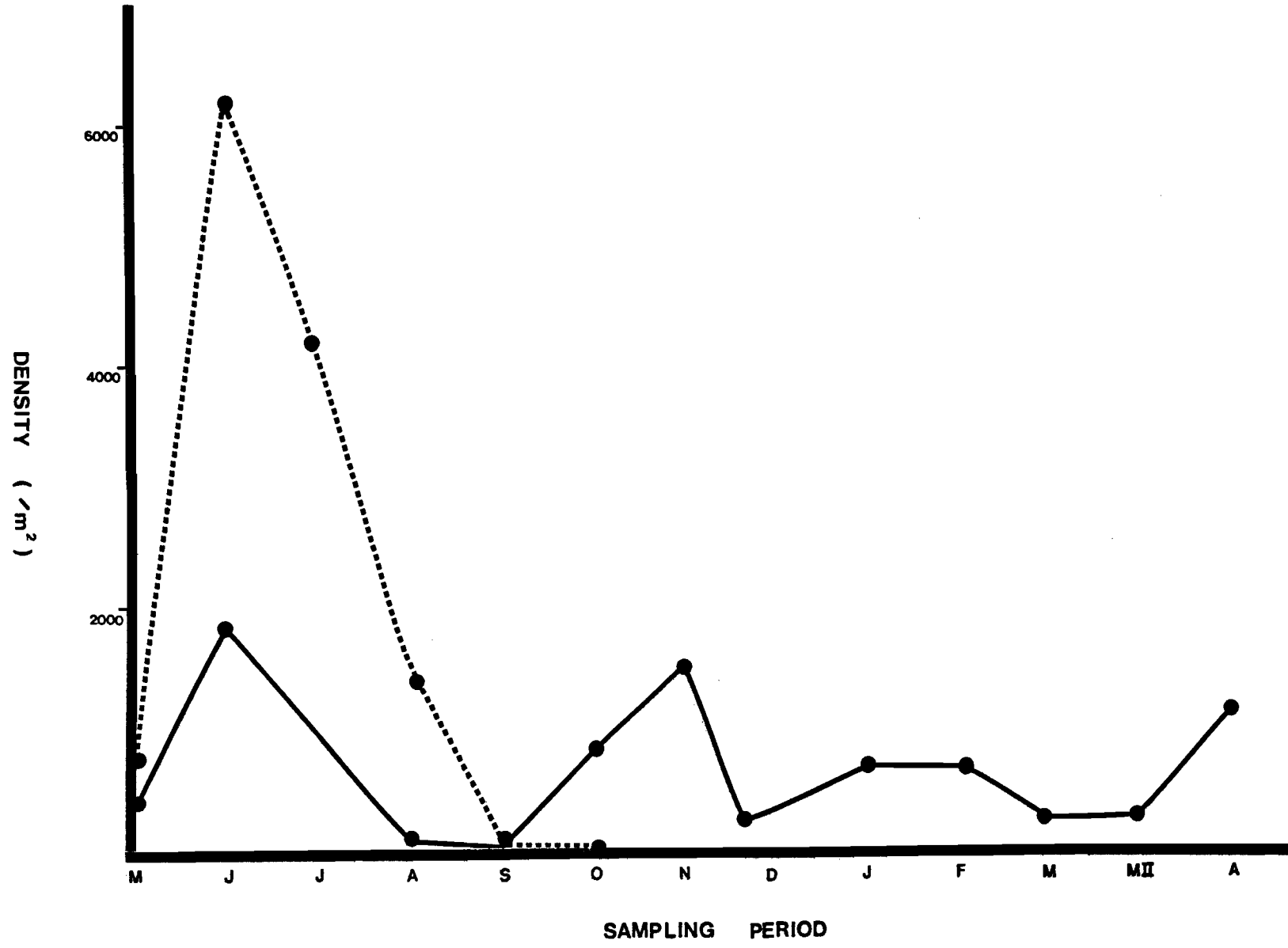


Figure 6

Figure 6. Average densities (/m²) of *C. volutator* each sampling period at Evangeline from May 1977 to October 1978.

— - May 1977 to April 1978

..... - May 1978 to October 1978

Range of values may be found in Appendix IV.

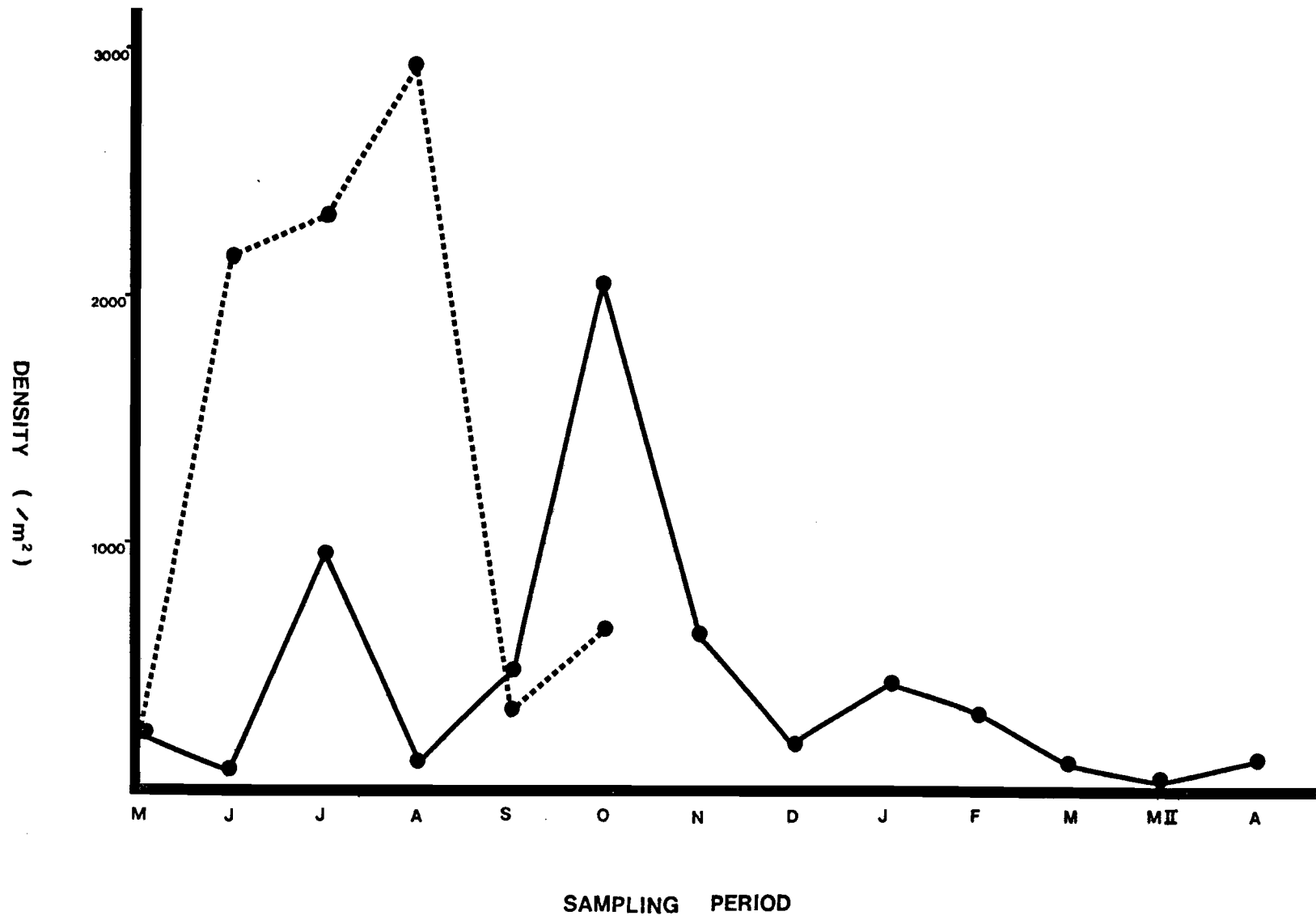


Figure 7

Figure 7. Average densities (/m²) of *C. volutator* each sampling period at Stations 5 and 6 at Avonport from May 1977 to October 1978.

..... - Station 5

———— - Station 6

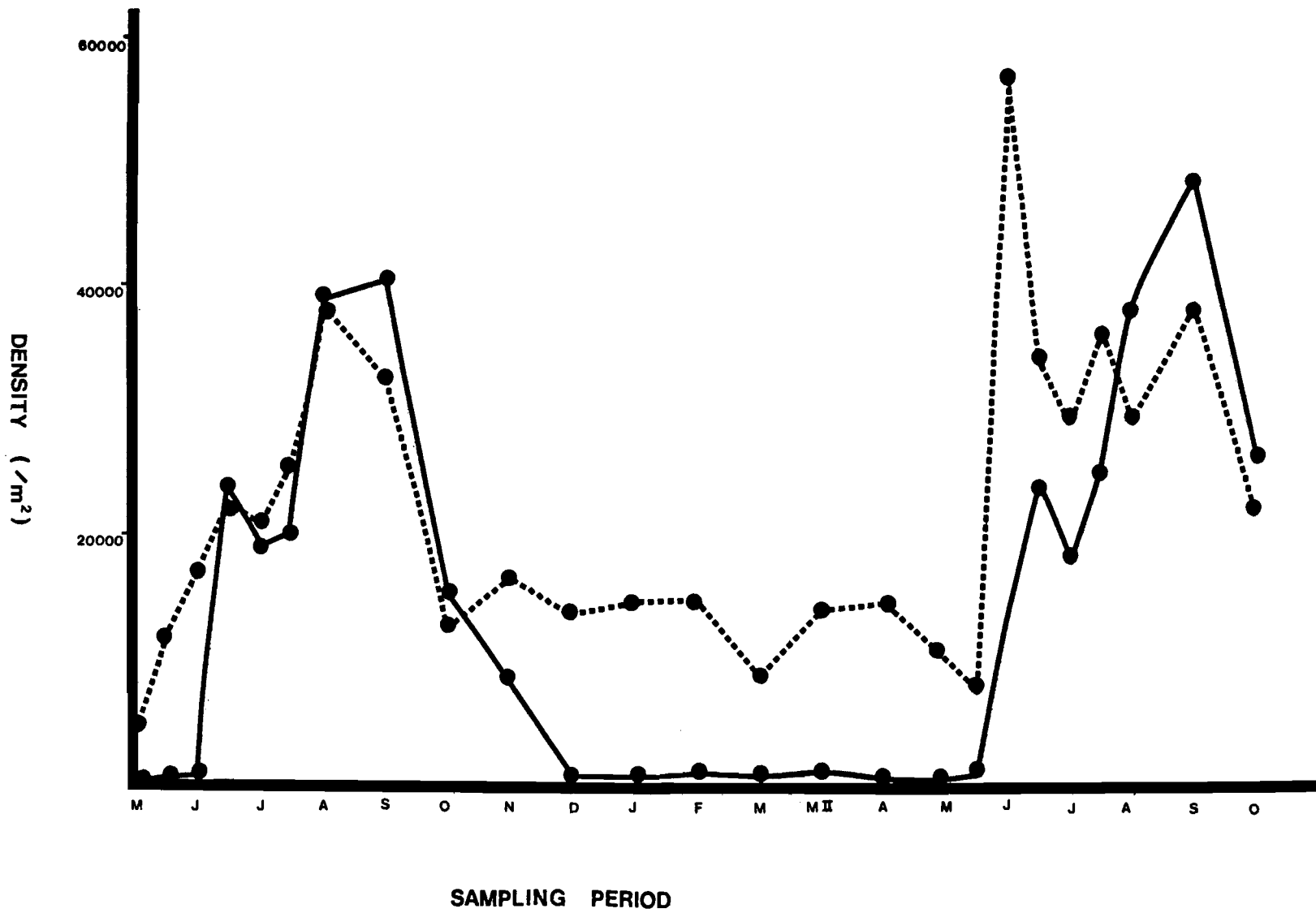


Figure 8

Figure 8. Percentage of female *C. volutator* with eggs or young in the brood pouch at Avonport from November 1977 to October 1978 and percentage of *C. volutator* with a fully developed brood pouch with eggs, from the Dovey estuary, North Wales, from January to November 1938 (Watkin, 1941).

..... - Watkin (1941)

— - this study

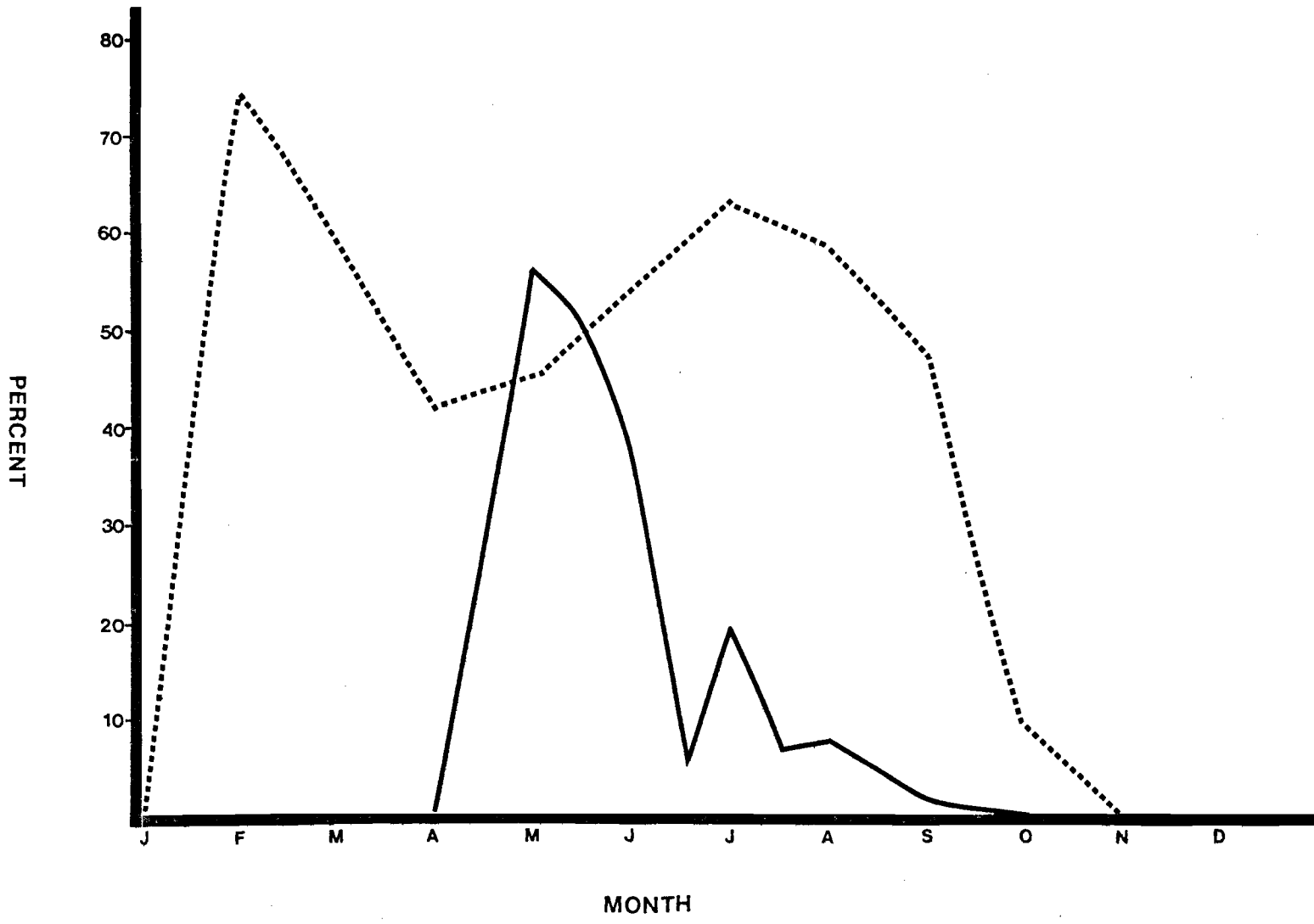
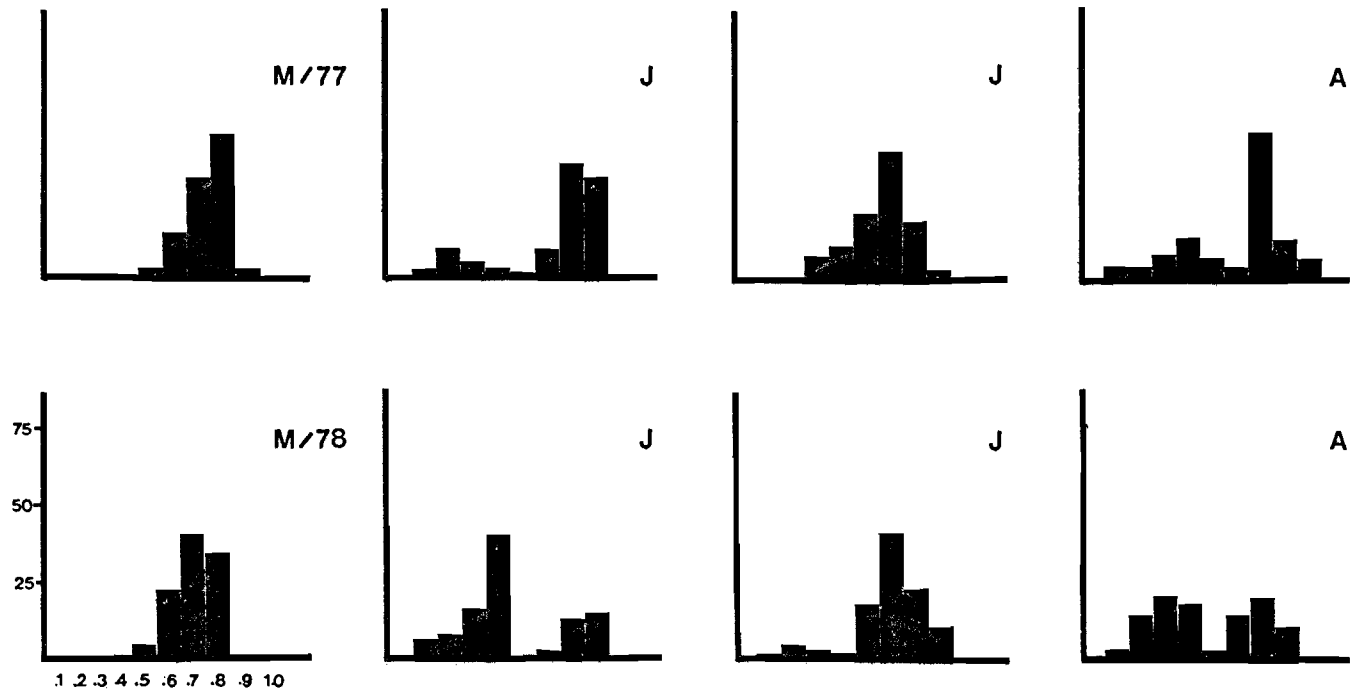


Figure 9

Figure 9. Size-frequency histograms of *C. volutator* for every sampling period at White Water from May to August, 1977 and 1978.

PERCENT



SIZE CLASS

Figure 10

Figure 10. Size-frequency histograms of *C. volutator* for every sampling period at Kingsport from May 1977 to October 1978.

PERCENT

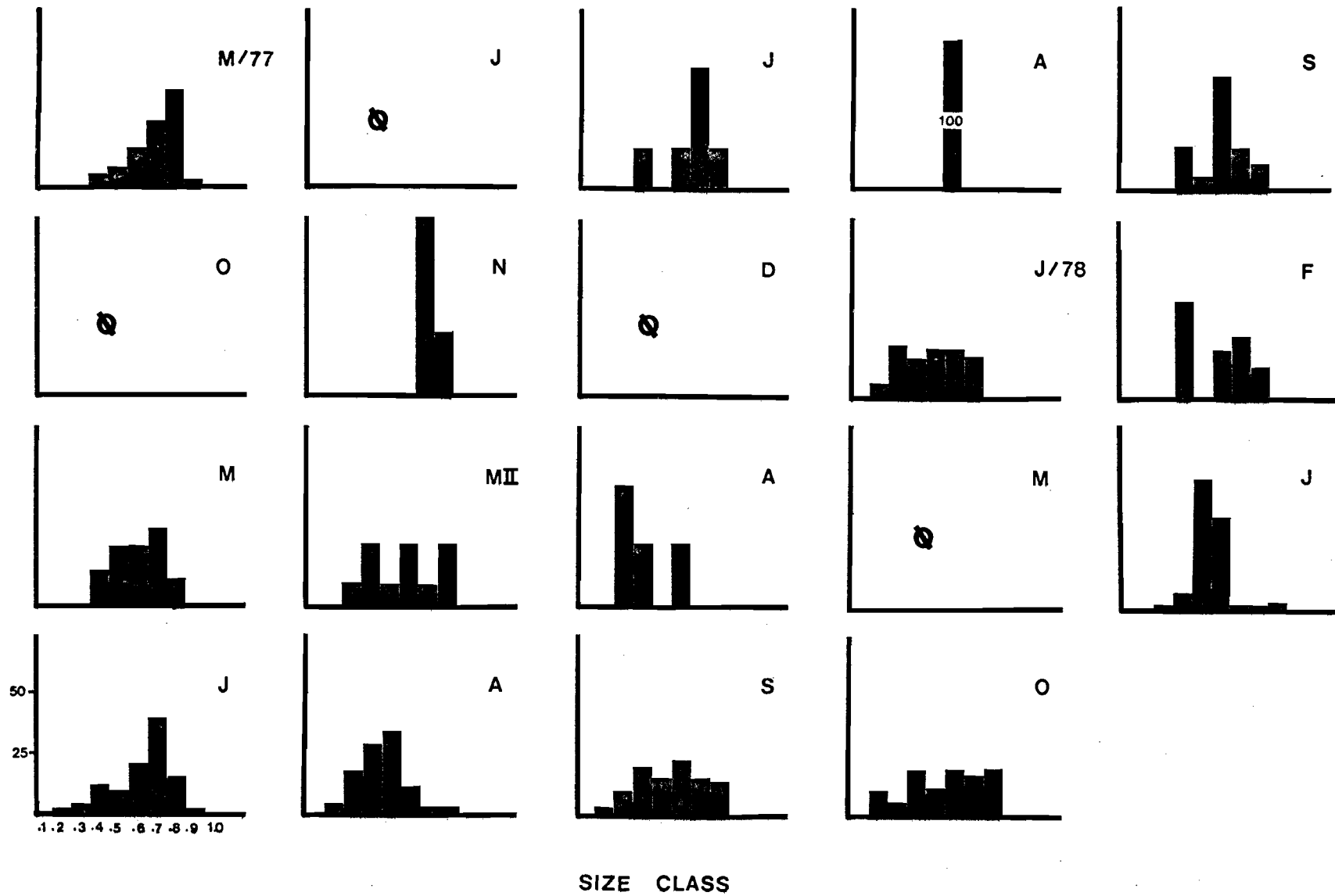


Figure 11

Figure 11. Size-frequency histograms of *C. volutator* for every sampling period at Starrs Point from May 1977 to October 1978.

PERCENT

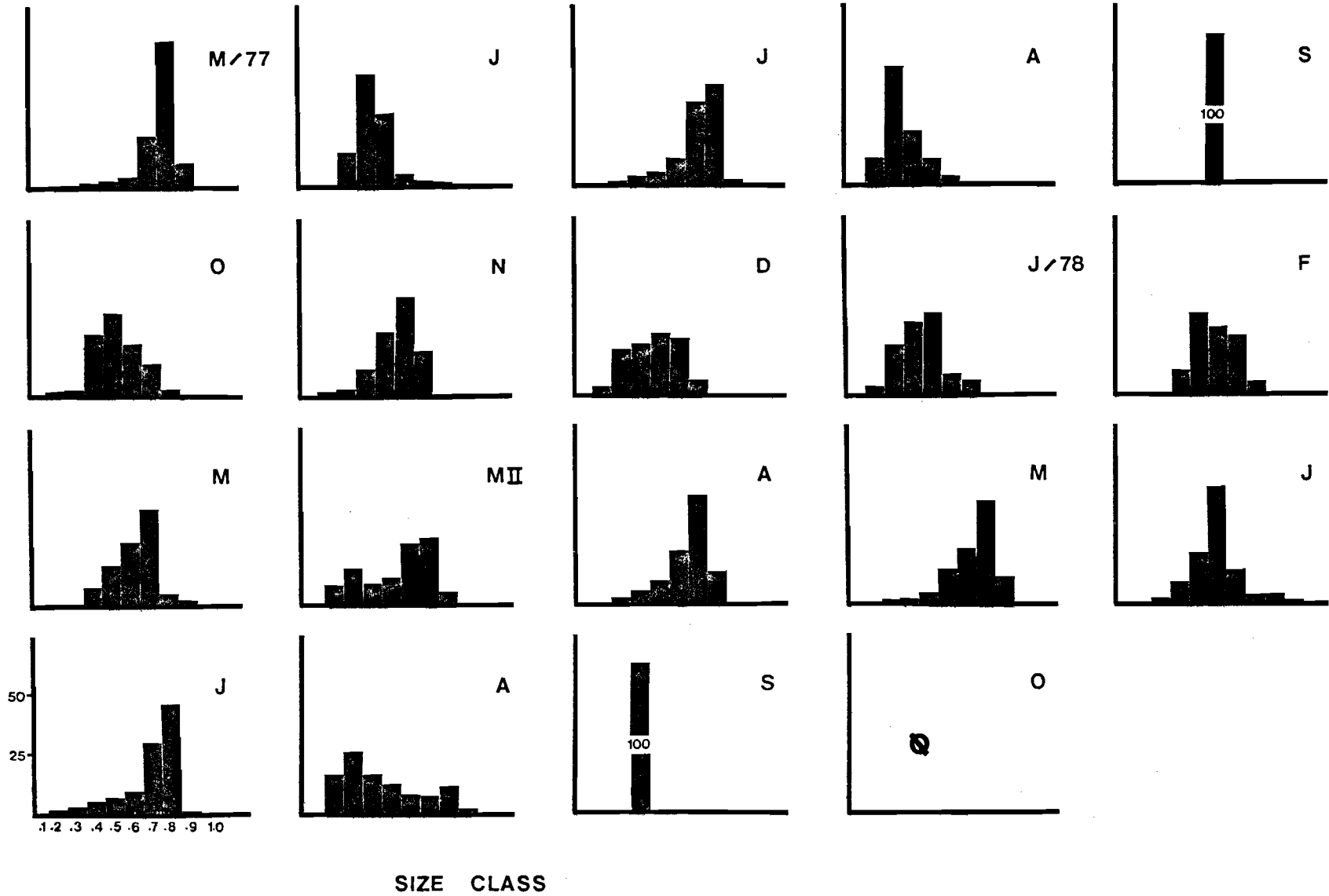
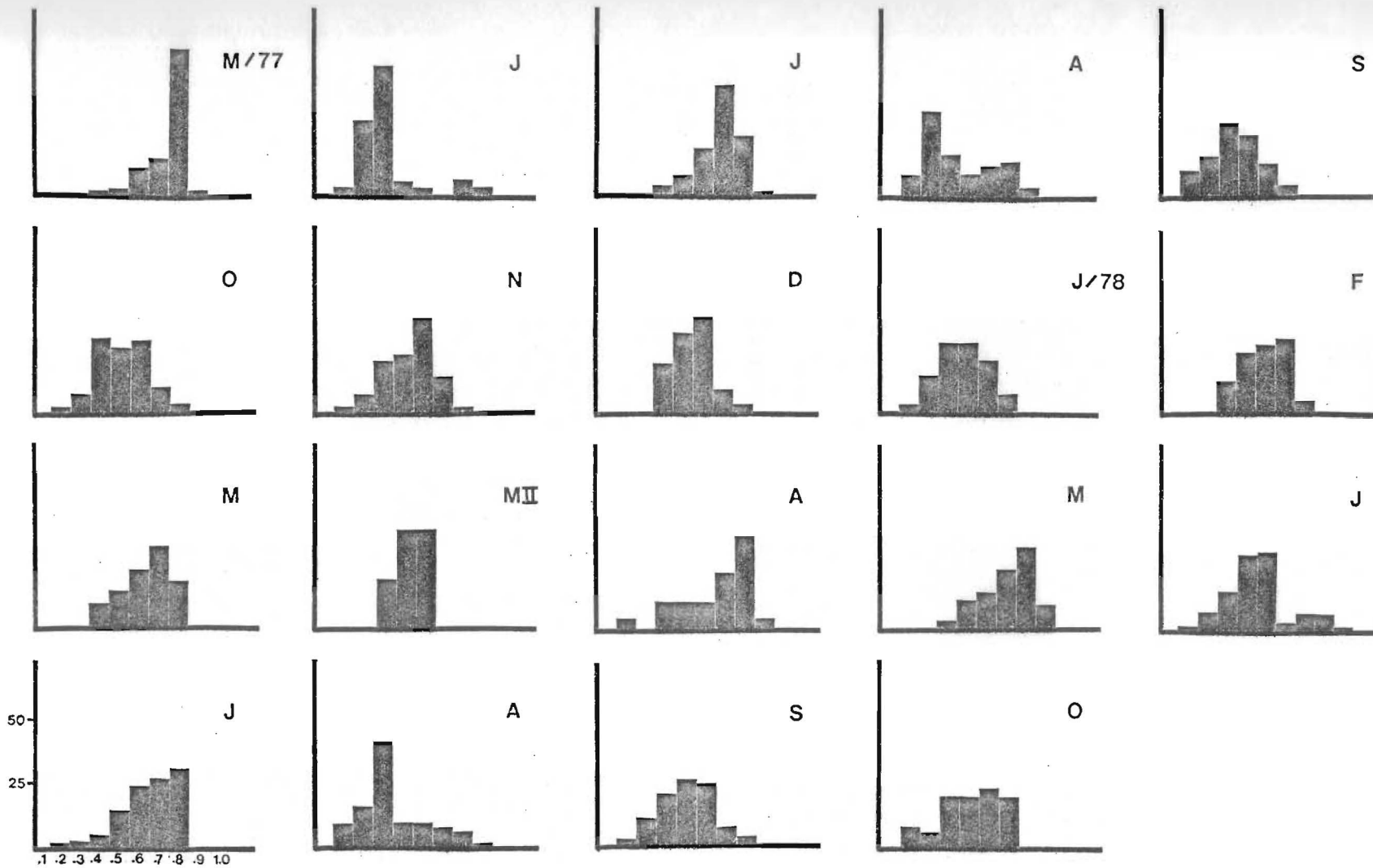


Figure 12

Figure 12. Size-frequency histograms of *C. volutator* for every sampling period at Evangeline from May 1977 to October 1978.

PERCENT



SIZE CLASS

Figure 13

Figure 13. Size-frequency histograms of *C. volutator* for every sampling period at Avonport from May 1977 to October 1978.

PERCENT

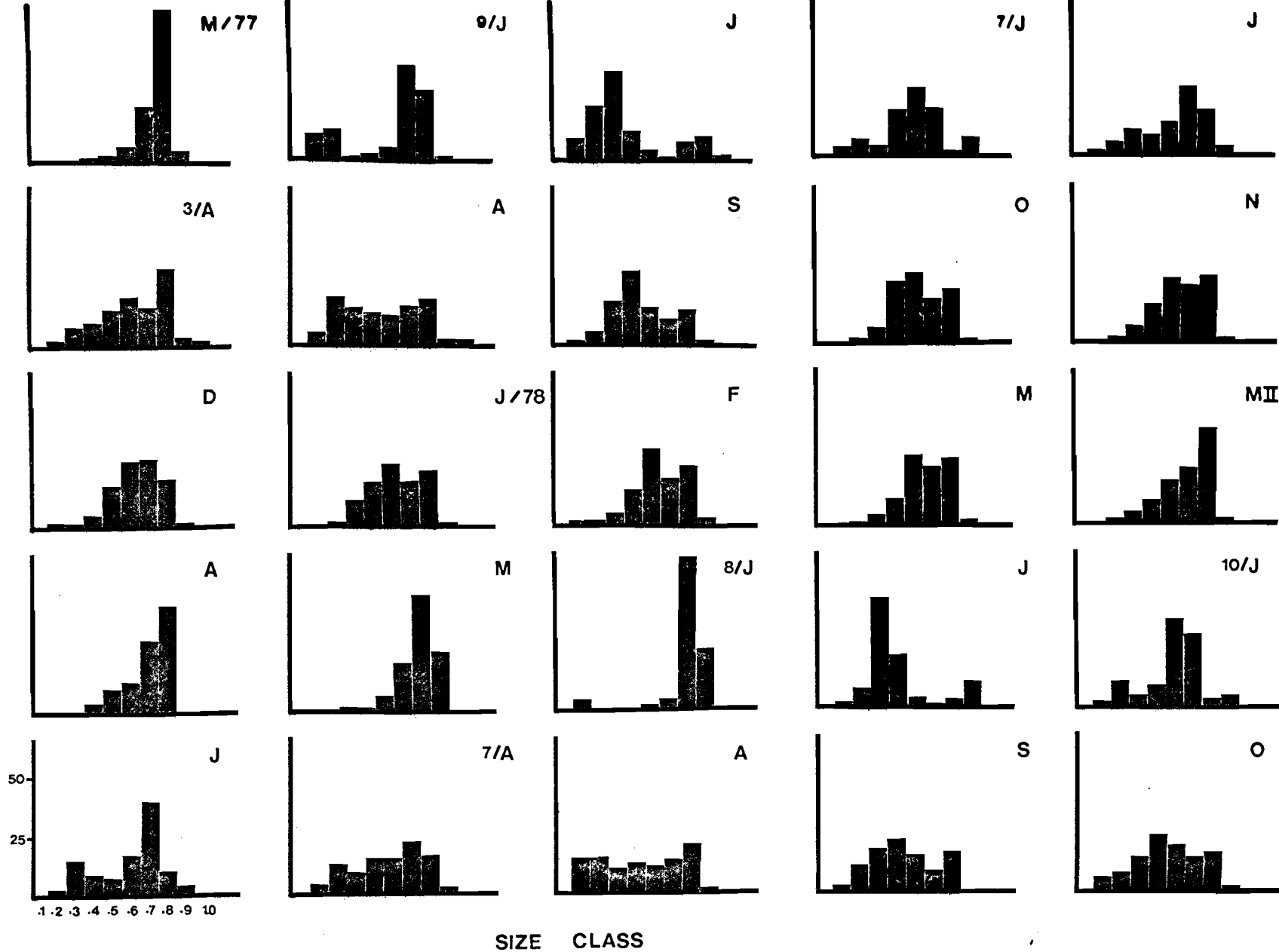


Figure 14

Figure 14. Mean length of *C. volutator* each sampling period at Avonport from May 1977 to October 1978.

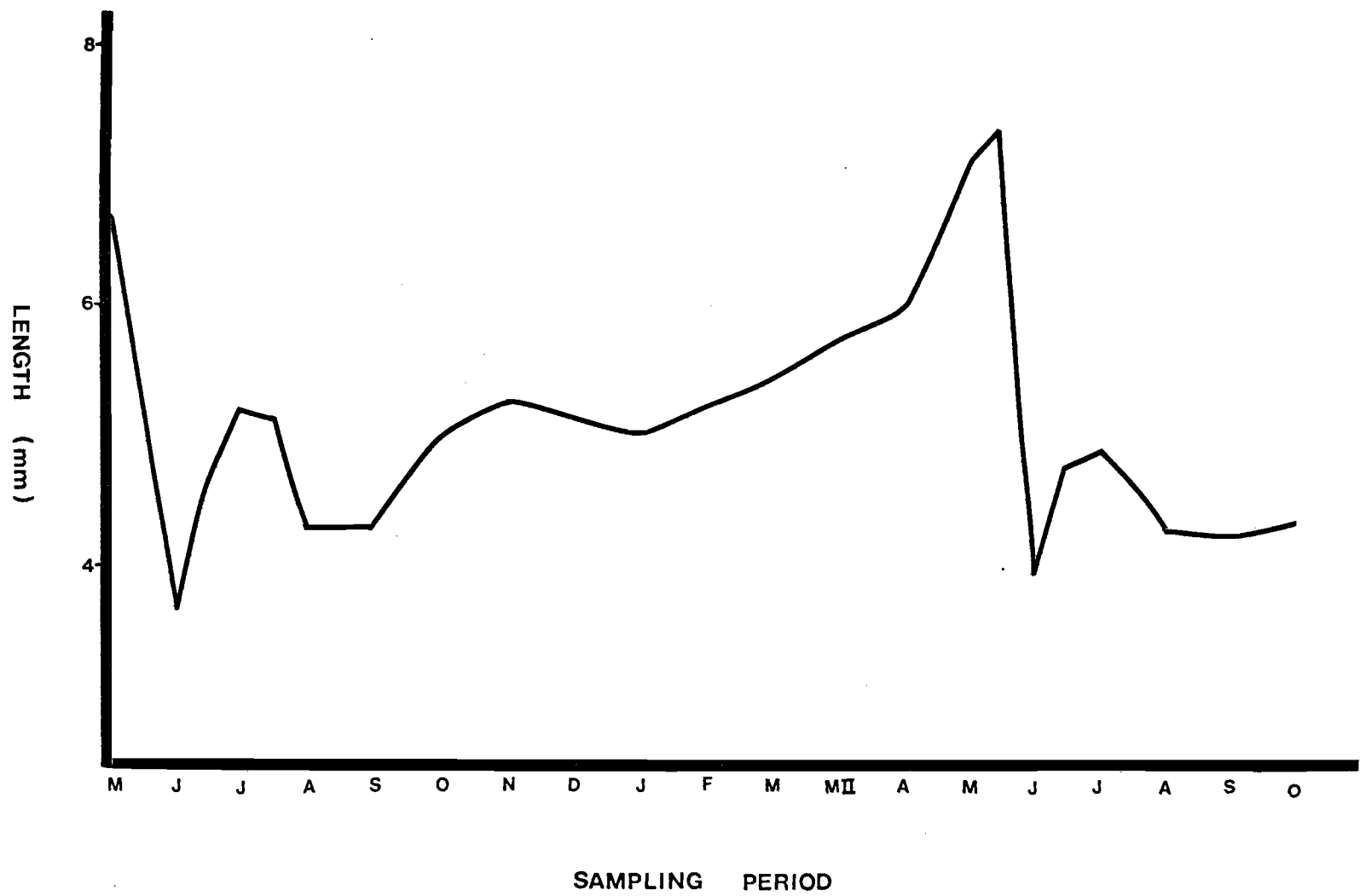


Figure 15

Figure 15. Growth in the cohorts of *C. volutator* present at Avonport from May 1977 to October 1978.

A - spring cohort

A¹ - early summer cohort

B - late summer cohort

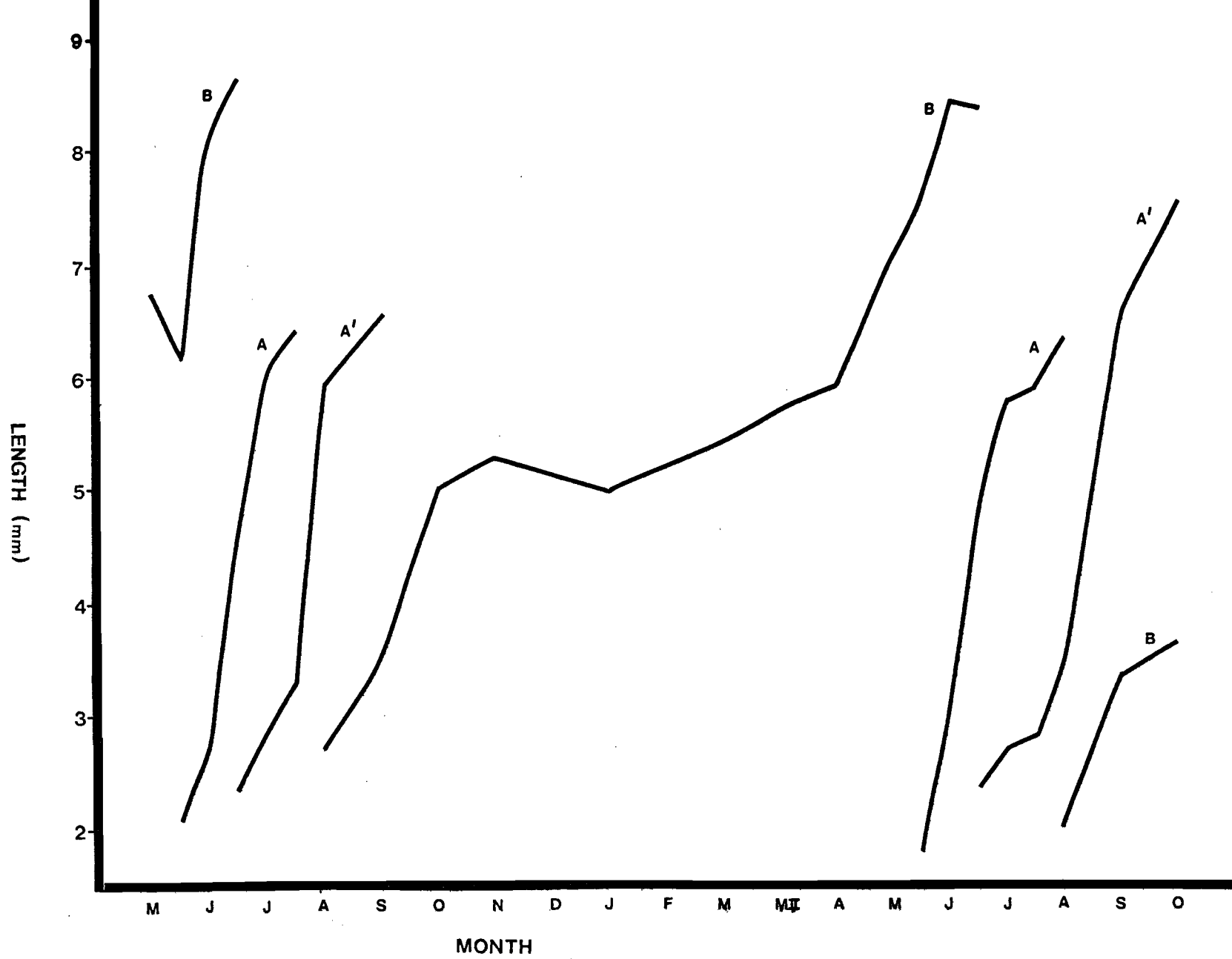


Figure 16

Figure 16. Linear regressions of weight (w) and number per m^2 (N) of *C. volutator* versus time for the late summer cohort of 1977 (subscript B) and the spring cohort of 1978 (subscript A).

- - actual data for late summer cohort
- - actual data for spring cohort

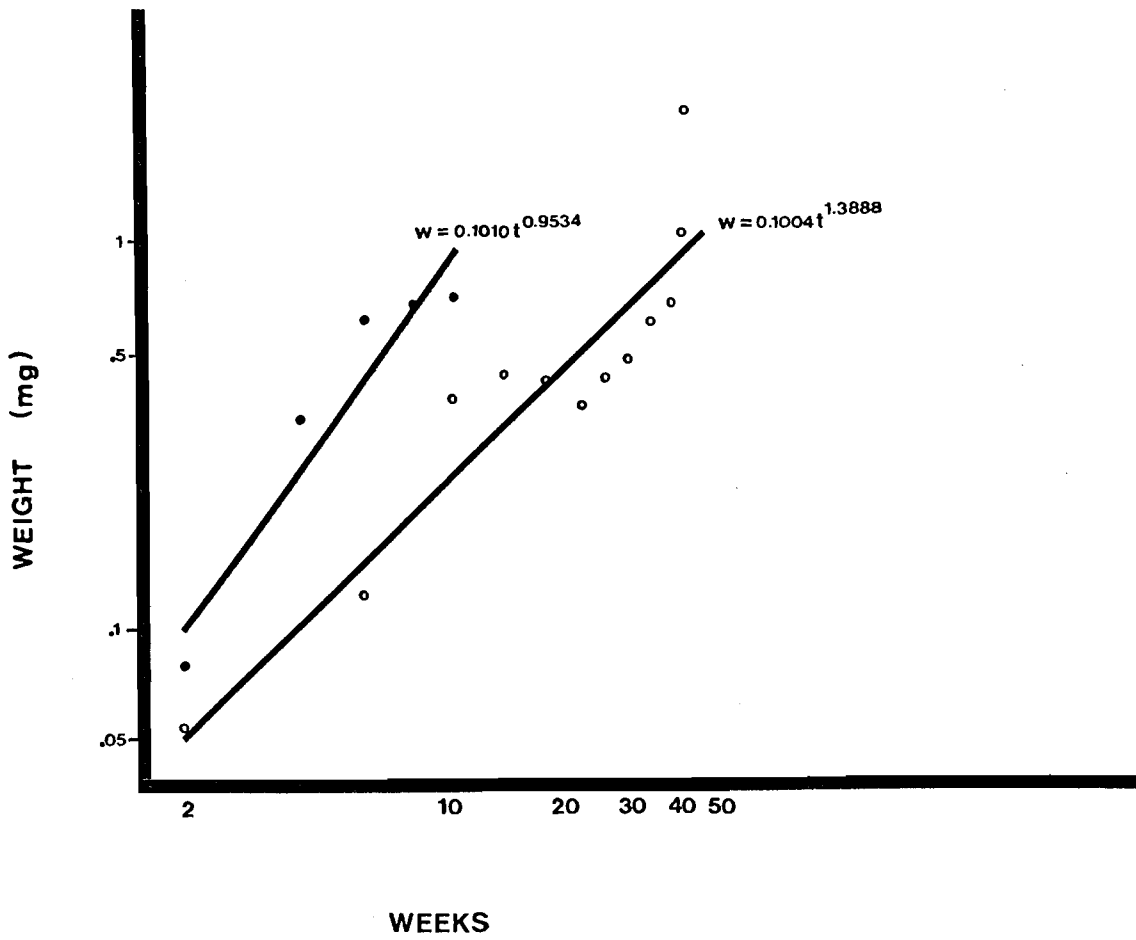
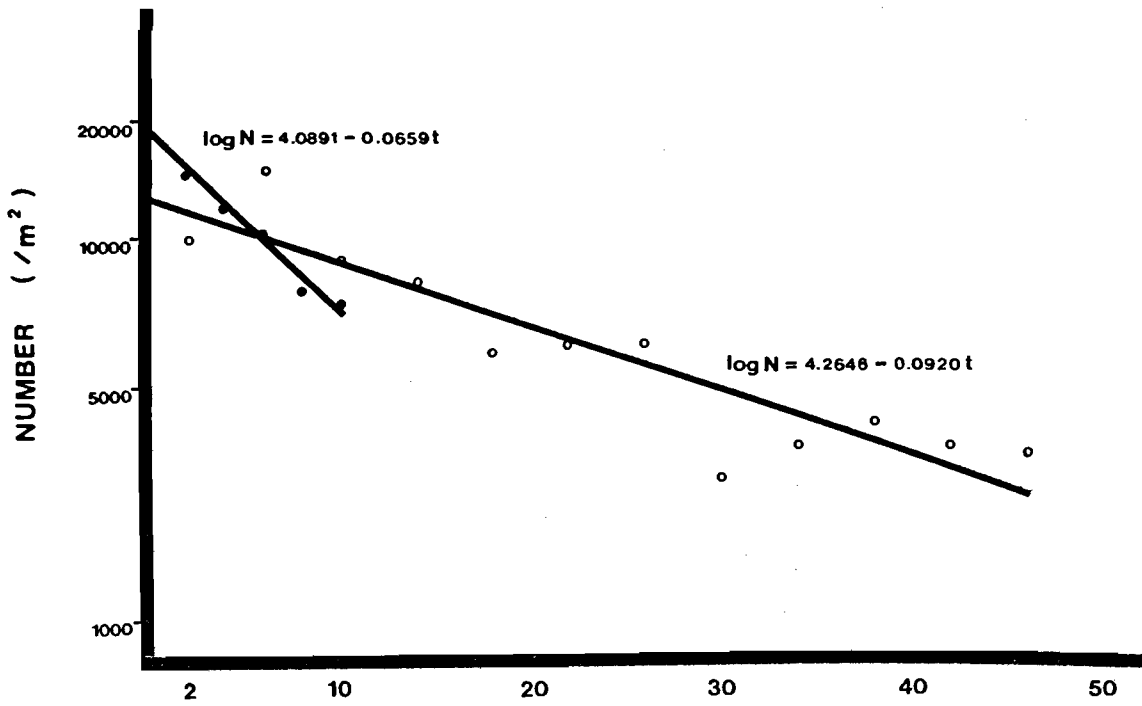


Figure 17

Figure 17. Method by which production (P) and elimination (E) within the time interval t_1 to t_2 and biomass (B) at time t_1 are calculated (Peer, 1970).

$P = \text{area of } t_1 w_1 w_2 t_2$

$B = \text{area of } n_1 o w_1 t_1$

$E = \text{area of } n_1 n_2 t_2 t_1$

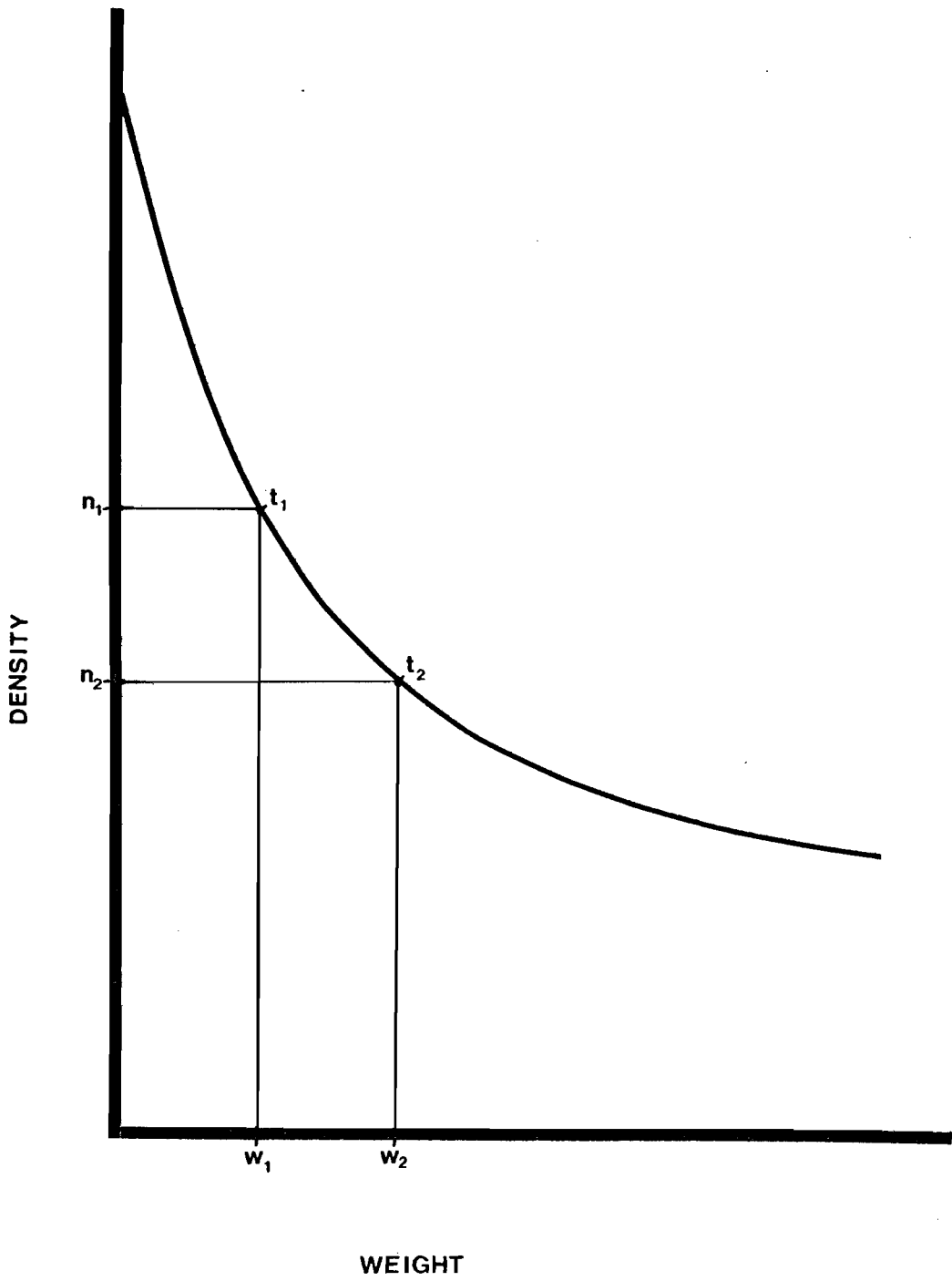


Figure 18

Figure 18. Allen curves of the late summer cohort of 1977 (subscript B) and spring cohort of 1978 (subscript A).

s_A - Allen curve for late summer cohort

s_B - Allen curve for spring cohort

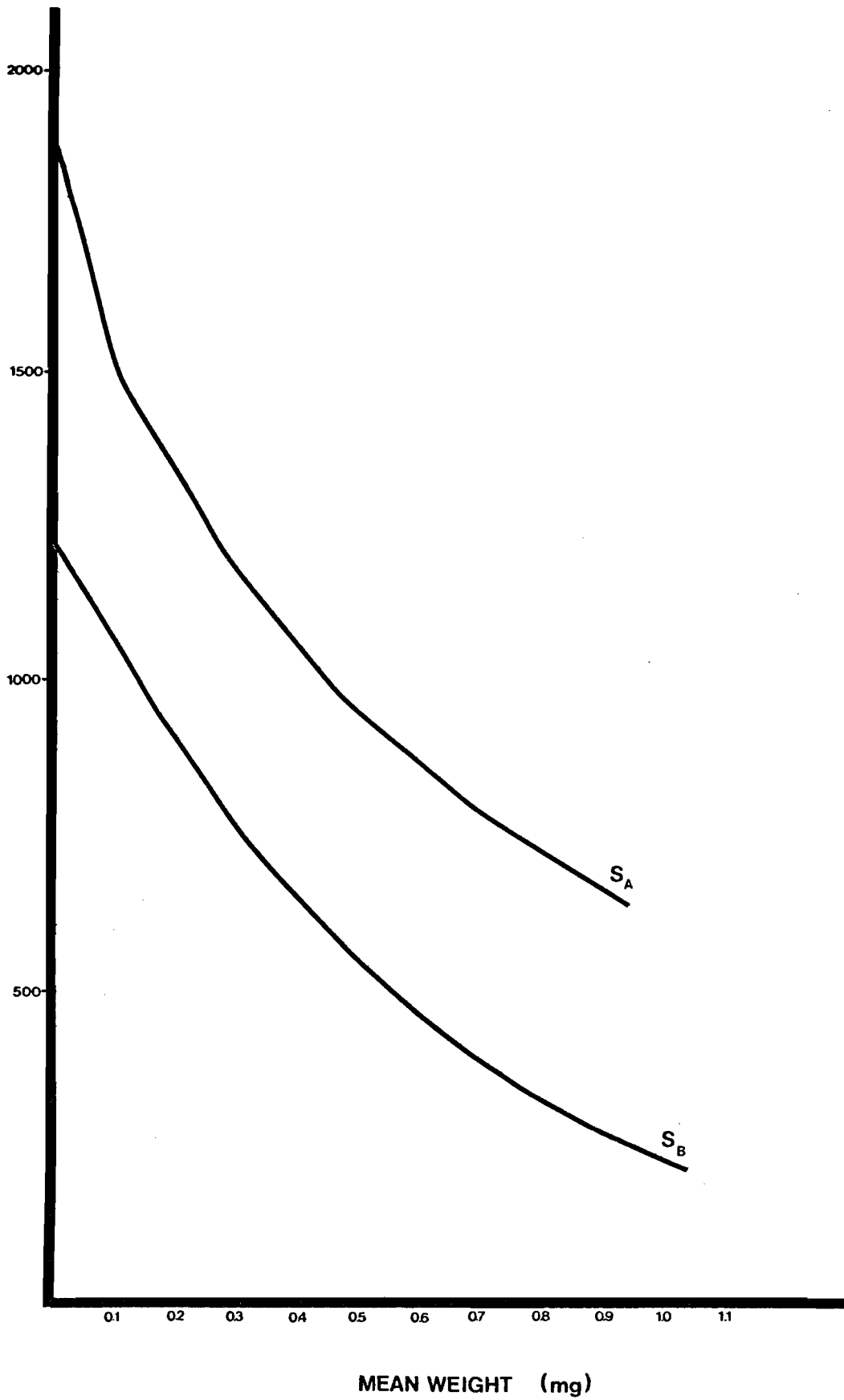
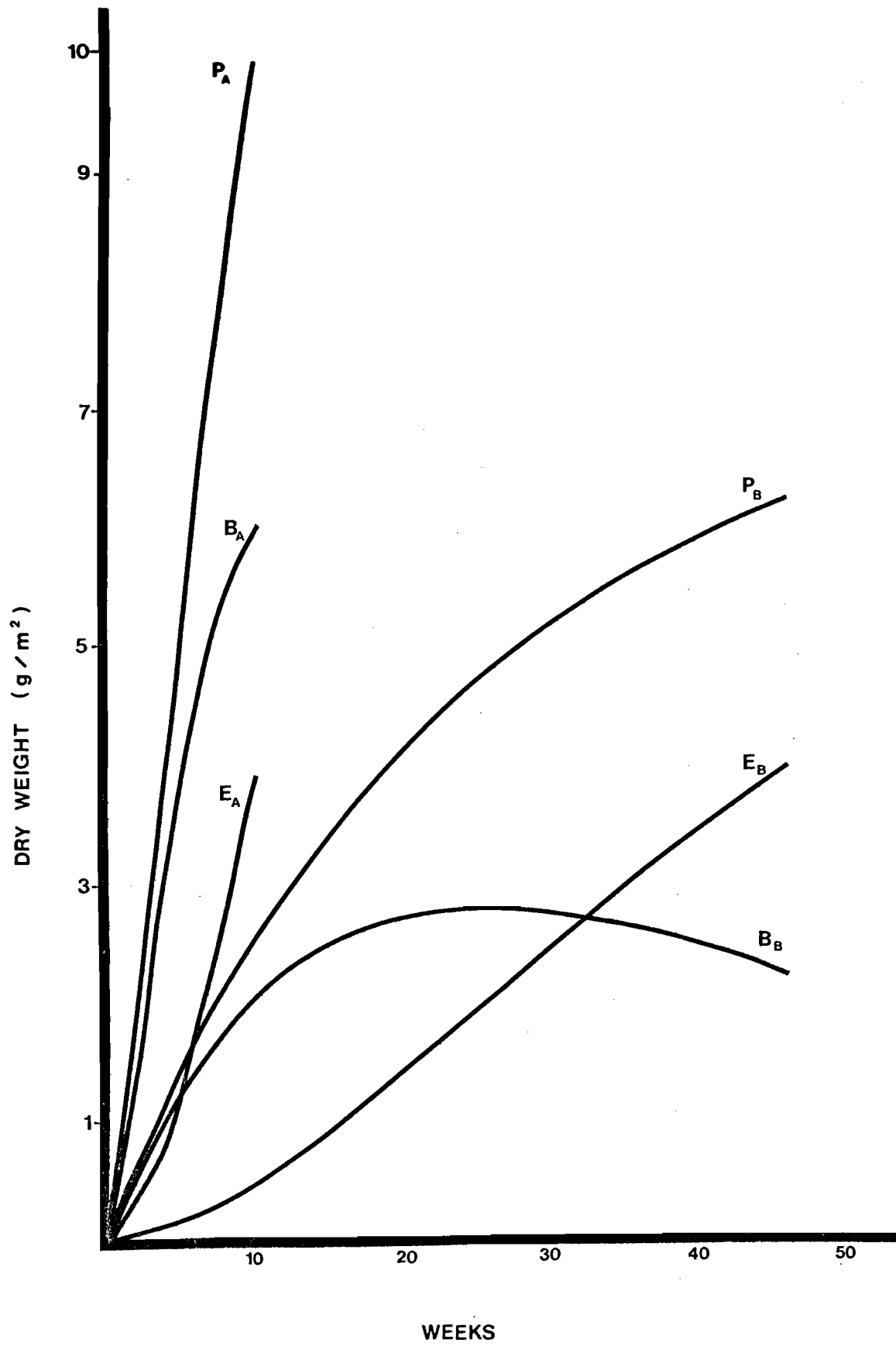


Figure 19

Figure 19. Changes with time of cumulative production (P), cumulative elimination (E) and biomass (B), during the life history of the late summer cohort of 1977 (subscript B) and spring cohort of 1978 (subscript A).



APPENDIX I

Number in each size-class, total number and density (/m²) of *C. volutator*
at each transect for each sampling period

Transect	Date	Size-Class								Total No.	Density (/m ²)	
		0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9			1.0
Scots Bay	26/05/77						1				1	2.12
	18/08			2	1						3	10.08
	14/08/78					1	1				2	6.72
White Water	26/05/77				2	10	22	34	2		70	148.15
	24/06	1	6	4	2	1	7	27	24		72	242.02
	22/07			6	9	19	37	17	2		90	302.52
	18/08	1	1	2	4	2	1	15	4	2	32	107.56
	26/05/78				1	7	12	11			31	104.20
	23/06	9	10	26	63	1	4	21	22		156	524.37
	20/07	1	13	10	6	73	169	95	41		408	1371.43
	14/08	3	15	22	19	2	14	22	10		107	359.66
Kingsport	24/05/77			4	8	13	23	33	2		83	204.94
	18/07			6	9	19	37	17	2		90	302.52
	18/08					1					1	3.92
	14/09			3	1	8	3	2			17	66.67
	09/11						3	1			4	15.69
	06/01/78		3	9	7	8	8	7			42	164.71
	03/02			6		3	4	2			15	58.82
	05/03			4	7	7	9	3			30	117.65
	29/03		1	3	1	3	1	3			12	47.01
	26/04		2	1		1					4	15.69
	19/06		1	8	64	45	1	1	2		122	478.43
	19/07	3	5	24	18	43	83	32	1		209	819.61
	17/08	5	24	40	43	16	4	4			136	533.33

APPENDIX I (cont'd)

Transect	Date	Size-Class									Total No.	Density (/m ²)
		0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0		
Kingsport	14/09	19	70	139	104	158	109	101			700	2745.09
	11/10	22	12	41	27	43	39	42			226	886.27
Starrs Pt.	25/05/77		2	7	11	60	170	28			278	457.61
	22/06		102	326	206	42	10	7	5		698	1824.84
	20/07		2	13	18	44	132	158	4		371	969.93
	16/08	3	13	6	3		1				26	67.97
	12/09				1						1	4.71
	11/10	2	5	45	61	39	25	2			179	842.35
	06/11	1	5	34	87	130	59	7			323	1520.00
	03/12	2	9	10	12	11	3				47	221.18
	03/01/78		3	30	43	47	10	8			141	663.53
	01/02			14	49	40	36	7			146	687.06
	08/03			4	9	15	22	3	1		54	254.12
	28/03	5	9	5	7	15	16	3			60	282.35
	25/04		5	14	26	55	113	32			245	1152.94
	22/06		43	192	499	1148	315	87	83	5	2372	6201.31
	17/07	4	22	85	119	155	461	735	8		1589	4154.25
	16/08	95	151	101	73	48	44	69	9		590	1542.48
11/09			1							1	4.71	
Evangeline	30/05/77			1	4	17	43	93	2		160	239.19
	23/06	1	10	18	2	1		2	1		35	74.87
	19/07		3	6	14	33	18	1			75	160.43
	15/08	3	13	6	3		1				26	67.97
	15/09		12	19	36	29	16	6			118	462.74
	14/10	3	32	152	131	141	49	11			519	2035.29
	07/11	1	11	32	36	60	22	2			164	643.14
	05/12			9	15	18	4	1			47	184.31
	04/01/78	2	15	29	29	22	8				105	411.76

APPENDIX I (cont'd)

Transect	Date	Size-Class									Total No.	Density (/m ²)
		0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0		
Evangeline	31/01			10	19	21	23	4			77	301.96
	09/03			2	3	5	7	4			21	82.35
	31/03					1	2	2			5	19.61
	24/04	1		3	3	3	6	10	1		27	105.88
	23/05			5	13	16	26	36	11		107	228.88
	21/06	6	74	157	301	313	27	67	68	1	1014	2168.98
	18/07	1	16	42	144	263	283	335			1084	2318.71
	15/08	131	222	566	134	129	98	82	5		1367	2924.05
	12/09	2	9	17	21	20	6	3			78	305.88
	10/10	11	9	29	29	33	28				139	654.12
Avonport	27/05/77			2	7	38	165	457	31		700	1944.45
	09/06	107	113	2	9	43	353	267	4		898	3991.11
	21/06	132	389	623	186	46	7	116	143	2	1644	6995.75
	07/07	115	184	152	508	783	560	55	202	5	2559	15747.69
	21/07	60	168	319	264	441	880	586	135	4	2857	12157.45
	03/08	21	250	296	415	534	455	952	50	1	2974	13217.76
	17/08	190	844	666	587	545	711	820	20	2	4385	18659.58
	16/09	41	179	925	1639	705	478	678	20		4665	19851.01
	12/10		4	106	495	581	361	442	18		2007	8540.43
	10/11		9	102	273	485	434	488	9		1800	7659.58
	07/12	3	7	56	205	318	336	240	1		1166	4961.70
	05/01/78		15	134	228	327	236	283	11		1234	5251.06
	02/02	2	9	65	187	401	253	305	21		1243	5289.36
	06/03		2	20	62	166	138	152	7		547	2327.66
	30/03		1	31	69	129	154	274	11		669	2846.81
	27/04			15	65	109	226	351			766	3259.58
	24/05			1	3	36	133	328	162		663	2821.28
	08/06	11				3	12	182	72		280	1723.08

APPENDIX I (cont'd)

Transect	Date	Size-Class								Total No.	Density (/m ²)
		0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9		
Avonport	20/06	44	343	1952	973	177	21	150	456	4116	17514.90
	10/07	31	352	142	314	1311	1111	79	161	3501	21544.61
	21/07	25	472	264	246	532	1361	342	119	3361	14302.13
	07/08	125	368	265	433	440	664	467	67	2829	17409.23
	18/08	563	558	399	458	420	543	814	42	3797	16157.45
	13/09	150	571	996	1234	839	507	884	11	5192	22093.62
	12/10	184	270	510	891	713	535	574	1	3678	15651.07

APPENDIX II

Number and density (/m²) of *C. volutator* at Stations 5 and 6 at Avonport from May 1977 to October 1978

Date	Station 5		Station 6	
	No.	No./m ²	No.	No./m ²
27/05/77	280	4148.1	0	0
09/06	390	12000.0	0	0
21/06	706	16611.8	13	305.9
07/07	729	22430.8	771	23723.1
21/07	871	20494.1	799	18800.0
03/08	1144	25422.2	900	20000.0
17/08	1616	38023.5	1626	38258.8
16/09	1379	32447.1	1719	40447.1
12/10	532	12517.6	643	15129.4
10/11	691	16258.8	336	7905.9
07/12	573	13482.4	18	423.5
05/01/78	613	14423.5	5	117.6
02/02	611	14376.5	17	400.0
06/03	360	8470.6	9	211.8
30/03	584	13741.2	27	635.3
27/04	620	14588.2	1	23.5
24/05	434	10211.8	1	23.5
08/06	234	7200.0	14	430.8
20/06	2421	56964.7	574	13505.9
10/07	1117	34399.2	784	24123.1
21/07	1235	29058.8	746	17552.9
07/08	1185	36461.5	814	25046.2
18/08	1245	29294.1	1641	38611.8
13/09	1641	38611.8	2062	48517.6
12/10	919	21623.5	1108	26070.6

APPENDIX III

Data used for the calculation of regression lines of number per m² (N) and weight (w) versus time (t) for the late summer cohort of 1977 (B) and spring cohort of 1978 (A)

Cohort	x t	y log N	x ²	xy	y ²	t (weeks)	N (/m ²)
B	0.5	3.9882	0.25	1.9441	15.9057	0	12280
	1.5	4.1720	2.25	6.2580	17.4056	2	11380
	2.5	3.9315	6.25	9.2878	15.4567	6	9780
	3.5	3.8842	12.25	13.5947	15.0870	10	8402
	4.5	3.6956	20.35	16.6302	13.6575	14	7220
	5.5	3.7204	30.25	20.4622	13.8414	18	6204
	6.5	3.7234	40.25	24.2021	13.8637	22	5330
	7.5	3.3671	56.25	25.2532	11.3374	26	4579
	8.5	3.4545	72.25	29.3632	11.9336	30	3935
	9.5	3.5131	90.25	33.3745	12.3419	34	3381
	10.5	3.4504	110.25	36.2292	11.9053	38	2905
	11.5	3.4263	132.25	39.4024	11.7400	42	2496
	<u>72.0</u>	<u>44.3267</u>	<u>575.00</u>	<u>256.5426</u>	<u>164.4758</u>	46	2145
A	1.0	4.1717	1.00	4.1717	17.4031	0	18390
	2.0	4.0853	4.00	8.1706	16.6900	2	14890
	3.0	4.0008	9.00	12.0024	16.0064	4	12040
	4.0	3.8620	16.00	15.4480	14.9150	6	9740
	5.0	3.8240	25.00	19.1200	14.6230	8	6377
	x log t	y log w	x ²	xy	y ²	t (weeks)	w (/m ²)
B	-0.3010	-1.2676	0.0906	0.3815	1.6068	0	0.0000
	0.1761	-0.9245	0.0310	-0.1628	0.8547	2	0.0522
	0.3979	-0.4151	0.1583	-0.1652	0.1723	6	0.1487

APPENDIX III (cont'd)

Cohort	x log t	y log w	x	xy	y	t (weeks)	w (/m ²)
B	0.5441	-0.3467	0.2960	-0.1886	0.1202	10	0.2420
	0.6532	-0.3871	0.4267	-0.2529	0.1498	14	0.3335
	0.7404	-0.4372	0.5482	-0.3237	0.1911	18	0.4237
	0.8129	-0.3630	0.6608	-0.2951	0.1318	22	0.5131
	0.8751	-0.3071	0.7658	-0.2687	0.0943	26	0.6016
	0.9294	-0.2259	0.8638	-0.2100	0.0510	30	0.6897
	0.9777	-0.1767	0.9559	-0.1728	0.0312	34	0.7770
	1.0212	0.0917	1.0428	0.0936	0.0084	38	0.8638
	1.0607	0.3319	1.1251	0.3520	0.1102	42	0.9504
	<u>7.8877</u>	<u>-4.4273</u>	<u>6.9651</u>	<u>-1.2125</u>	<u>3.5219</u>	46	1.0360
A	0.0000	-1.1024	0.0000	0.0000	1.2153	0	0.0000
	0.3010	-0.4621	0.0906	-0.1391	0.2135	2	0.1005
	0.4771	-0.2142	0.2276	-0.1022	0.0459	4	0.2630
	0.6021	-0.1740	0.3625	-0.1048	0.0303	6	0.4620
	0.6990	-0.1495	0.4886	-0.1045	0.0224	8	0.6893
	<u>2.0792</u>	<u>-2.1022</u>	<u>1.1694</u>	<u>-0.4506</u>	<u>1.5273</u>	10	0.9392

APPENDIX IV

Range of densities (station with lowest and station with highest density) and mean densities of *C. volutator* along the transect for each sampling period at Starrs Point, Evangeline and Avonport.

Transect	Date	Density (/m ²)		
		Low	Mean	High
Starrs Point	25/05/77	0	457.6	1087.2
	22/06	0	1824.8	9717.3
	20/07	0	969.9	3906.0
	16/08	0	68.0	612.0
	12/09	0	4.7	23.4
	11/10	0	842.4	4165.2
	06/11	0	1520.0	7599.6
	03/12	0	221.2	1106.1
	03/01/78	0	663.5	3317.4
	01/02	0	687.1	2988.0
	08/03	0	254.1	846.9
	28/03	0	282.4	964.8
	25/04	0	1152.9	4376.7
	22/05	0	865.4	7670.7
	22/06	0	6201.3	15976.8
	17/07	0	4154.2	7694.1
	16/08	0	1542.5	13694.4
	11/09	0	4.7	23.4
	11/10	0	0	0
	Evangeline	30/05/77	0	239.2
23/06		0	74.9	256.8
19/07		0	160.4	1309.2
15/08		0	68.0	538.8
15/09		0	462.7	2798.4
14/10		0	2035.3	7008.0
07/11		0	643.1	3747.6
05/12		0	184.3	718.8
04/01/78		0	411.8	2181.6
31/01		0	302.0	1591.2
09/03		0	82.4	462.0
31/03		0	19.6	51.6
24/04		0	105.9	168.0
23/05		0	228.9	820.8
21/06		0	2169.0	17377.2
18/07		0	2318.7	12013.2
15/08		0	2924.0	24776.5

APPENDIX IV (cont'd)

Transect	Date	Density (/m ²)		
		Low	Mean	High
Evangeline	12/09	0	305.9	1206.0
	10/10	0	654.1	3567.6
Avonport	27/05/77	0	1944.4	4148.1
	09/06	0	3991.1	12646.2
	21/06	329.4	6995.8	16611.8
	07/07	492.3	15747.7	23723.1
	21/07	5247.1	12157.4	20494.1
	03/08	30.8	13217.8	25422.2
	17/08	47.1	18659.6	38258.8
	16/09	870.6	19851.0	40447.1
	12/10	23.5	8540.4	21647.1
	10/11	0	7659.6	18023.5
	07/12	23.5	4961.7	13482.4
	05/01/78	70.5	5251.1	14423.5
	02/02	400.0	5289.4	14376.5
	06/03	211.8	2327.7	8470.6
	30/03	117.6	2846.8	13741.2
	27/04	23.5	3259.6	14588.2
	24/05	23.5	2821.3	10211.8
	08/06	153.8	1723.1	7200.0
	20/06	23.5	17514.9	56964.7
	10/07	2707.7	21544.6	34399.2
21/07	23.5	14302.1	29058.8	
07/08	30.8	17409.2	36461.5	
18/08	0	16157.4	38611.8	
13/09	2305.9	22093.6	48517.6	
12/10	6682.4	15651.1	26070.6	