



The life history of the amphipod, *Corophium volutator*: the effects of temperature and shorebird predation

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Abstract

The life cycle of the amphipod, *Corophium volutator* (Pallas), is described from an intertidal mudflat in Maine, near the southern limit of the species' range in the western Atlantic Ocean. This population has two generations per year, with one generation born in May to mid-June and growing to reproduce and give rise to a second generation in August. The individuals born in August form the over-wintering generation. Comparison to sites in the Bay of Fundy, where different populations of *C. volutator* display one and two generations per year, rejects the hypothesis that episodic predation by shorebirds selects for the life history with two generations per year. Water temperatures during the summer may control the number of generations per year for *C. volutator* in the western Atlantic.

Keywords: Amphipoda; Life history; Macrofauna; Shorebird predation; Soft-sediment habitat; Temperature

1. Introduction

The amphipod crustacean, *Corophium volutator* (Pallas), is an abundant member of the intertidal infauna in the North Atlantic Ocean. Ranging from southern Norway throughout the North Sea to the Bay of Biscay and the Adriatic along the European coast and from Nova Scotia south to southern Maine in North America (Hart, 1930; Muus, 1967; Bousfield, 1973; Larsen et al., 1983; Larsen and Doggett, 1991), this species frequents sedimentary habitats consisting of fine sand mixed with silts and clays (Meadows, 1964).

Corophium volutator is a major prey item for a number of migratory shorebirds

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on both sides of the North Atlantic (Bengtson and Svensson, 1968; Goss-Custard, 1977a,b,c; Boates and Smith, 1979; Hicklin and Smith, 1979; Gratto et al., 1984; Raffaelli and Milne, 1987; Wilson, 1989, 1990a). *Corophium volutator* also figures prominently in the diet of a number of demersal fishes (Imrie and Daborn, 1981; Dadswell et al., 1984; Mattila and Bonsdorff, 1989). The polychaetes, *Glycera dibranchiata* and *Nereis virens* (Commito, 1982; Ambrose, 1984; Commito and Schrader, 1985) and the nemertean *Tetrastemma melanocephalum* (Bartsch, 1973) consume *C. volutator* in significant numbers. Given the importance of *C. volutator* as a prey species, it is not surprising that a considerable literature exists on the population ecology of this species (Hart, 1930; Watkin, 1941; McLusky, 1968; Birklund, 1977; Fish and Mills, 1979; Mills and Fish, 1980; Möller and Rosenberg, 1982; Gratto et al., 1983; Hawkins, 1985; Murdoch et al., 1986; Olafsson and Persson, 1986; Peer et al., 1986; Jensen and Kristensen, 1990; Flach, 1992). These studies reveal two distinct life history patterns. In portions of the species' range, two generations are produced per year while in other populations a single generation has been observed. For all populations studied, females usually die after release of one or two broods and rarely live to reproduce the following season. As a result, populations of *C. volutator* have barely overlapping generations.

The present research was designed to shed light on the striking divergence of life history of *C. volutator* between the upper and lower Bay of Fundy in the Maritime Provinces of Canada. In the upper Bay of Fundy, *C. volutator* has two generations per year. A summer generation born in late May reproduces in late July or early August; these offspring grow through the fall as the overwintering generation which reproduces in May, completing the annual cycle of two generations (Gratto et al., 1983; Peer et al., 1986; Wilson, 1988, 1989). In contrast, *C. volutator* in the lower Bay of Fundy has a single generation per year with most reproduction occurring in June (Gratto et al., 1983). Two explanations for this pattern suggest themselves. First, the waters of the lower Bay of Fundy are colder (by 6–10°C) than the waters of the upper Bay (Gratto et al. 1983; Greenberg, 1984). Presuming that *C. volutator* does not show any sort of thermal compensation in the lower Bay (Davenport, 1992), then growth of lower Bay populations would be expected to be slower than growth of upper Bay populations and hence, a single generation per year might be expected. Second, Wilson (1989) showed that the heavy predation on adult amphipods by migratory shorebirds in the late summer ameliorates competition between newly released juveniles and post-reproductive adults, resulting in higher overwintering populations. Wilson (1989) provided no data to indicate that the observed life history pattern of two generations per year evolved in response to the episodic predation, but could not rule out the possibility. To attempt to separate these two possible explanations for the life history variation, we monitored the reproductive patterns of *C. volutator* at Lowes Cove, Walpole, Maine for a year. Lowes Cove has relatively warm temperatures (McAlicee, 1993) like the upper Bay of Fundy, but receives very little shorebird use, like the lower Bay of Fundy. Elucidation of the reproductive pattern at Lowes Cove (warm temperatures, no shorebird predation) should allow one of the two possible explanations to be rejected.

2. Materials and methods

The study site was at Lowes Cove, an embayment in the Damariscotta River, in Walpole, Maine (43° 57' 43" N, 69° 33' 21" W), adjacent to the Darling Marine Center of the University of Maine. Lowes Cove empties on low tides lower than 0.0 m. The area is dug by commercial clam diggers although the particular site we chose had few of these commercially valuable species and was not disturbed by the diggers. Mean seawater temperatures range from 1.0°C in January to 17.2°C in August (Fig. 1).

A small bed of *C. volutator* on the north side of the cove at a tide level of 0.12 m above MLW served as the study population. The sediment consisted mostly of fine sand, silt and clay. Broken bivalve shells and pebbles comprised the fraction of larger sediment particles.

The population was sampled 14 times between June 10, 1991 and July 2, 1992 (see Fig. 2, Fig. 3, Fig. 4 for dates). At each sampling, five cores (10 cm in diameter) were taken to a depth of 10 cm. Each core was placed in a separate plastic bag and sieved within an hour of sampling by washing the sediment in seawater through a 500- μ m stainless steel sieve. This screen size retains virtually all of the *C. volutator*, even newly released juveniles (Wilson, 1988, 1989). The residue was placed into jars and preserved with 5% formalin in seawater.

Sorting was accomplished by first washing the residue with freshwater. To facilitate sorting, a beaker containing the residue was placed on a sieve and a stream of water from the tap was directed into the beaker with sufficient velocity to suspend lighter particles of the residue, including *C. volutator*, while leaving larger sediment particles behind. Nearly 100% of the *C. volutator* could be separated from the sediment in this fashion. The remaining material in the residue was searched for additional *C. volutator* to insure that all of the specimens had been separated.

Once all the *C. volutator* were separated from the residue, all individuals were placed on their sides in a Petri dish. Each sample was photographed using Ektachrome film with a cm scale in the field of view. The transparencies were then projected from above onto a digitizing pad using a lens with a right-angle mirror.

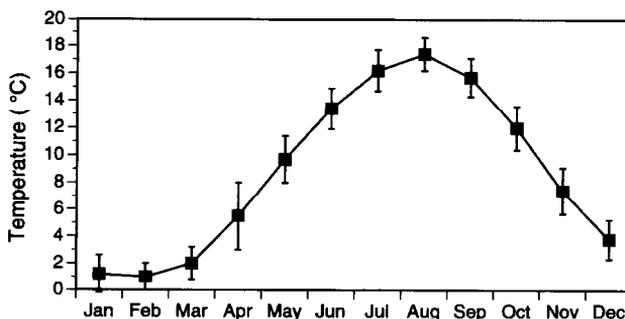


Fig. 1. Average seawater temperature in the Damariscotta River estuary for the period 1970–1977. Error bars represent 1 SE. Data taken from McAlice (1993).

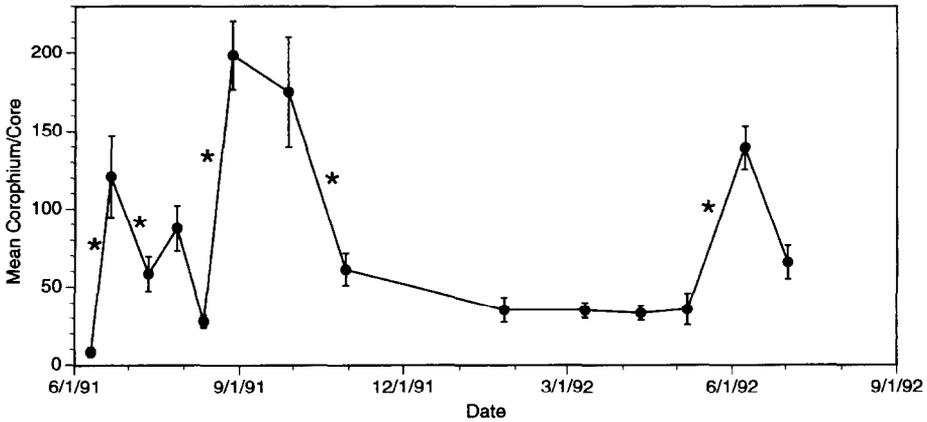


Fig. 2. Population dynamics of *C. volutator* at Lowes Cove. Error bars represent 1 SE. An asterisk indicates that a significant change in abundance ($p < 0.05$, Scheffé test) occurs between the two consecutive dates.

Length is an excellent predictor of body mass ($r^2 > 0.98$) and, therefore, provides a meaningful and easily obtained measure of size (Boates and Smith, 1979). Using the software SigmaScan (Jandel Corporation), the length of each amphipod (from base of antennae to the apex of the telson) was determined.

Abundance data were analyzed for significant changes in abundance over time by one-way ANOVA using Statview II software (Abacus Concepts). Differences in abundance between successive sampling periods were tested for significance using Scheffé post hoc comparisons. A significance level of $p \leq 0.05$ was used for all tests.

To examine changes in size-frequency across sampling periods, the replicates at each sampling were combined. For some samplings when density was low, pooling of data was necessary to have an adequate sample size. For samples where density was high, the size-frequency distributions of each replicate were concordant (G -tests, $p < 0.05$ in all cases) and therefore no measure of inter-replicate variability was lost by pooling.

3. Results

The changes in population abundance over the course of this study are given in Fig. 2. Scheffé contrasts show that significant differences exist between consecutive samplings for June 10 to June 28, June 28 to July 14, July 28 to August 28, September 30 to October 30 and May 7 to June 8.

Fig. 3 and Fig. 4 present data on the change of size-frequency of the populations at each sampling period. The initial distribution (June 10) was dominated by individuals in the smaller size-classes with a few large adults present. However, there were very few juveniles (0–1 mm size-class), indicating

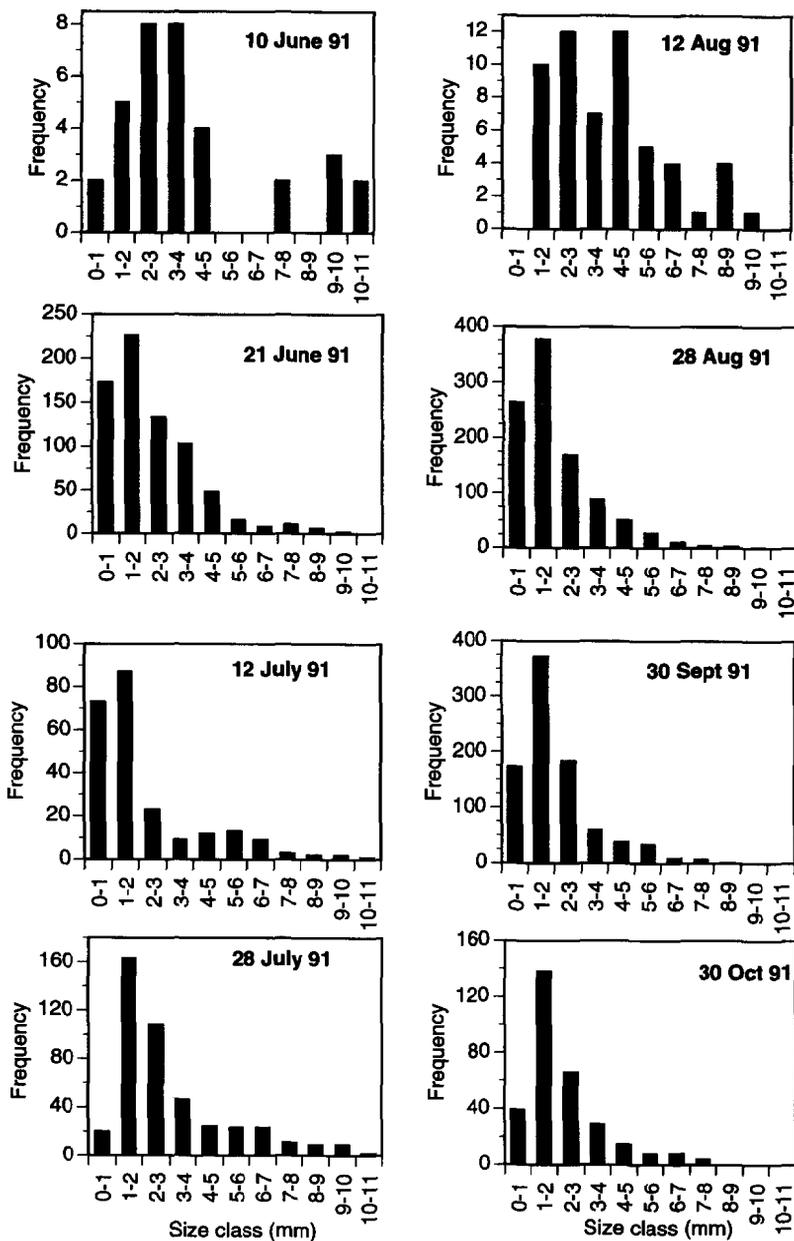


Fig. 3. Size-frequency distributions of *C. volutator* at Lowes Cove for the period June 10, 1991 to October 30, 1991. The distributions for each sampling period represent five pooled replicates.

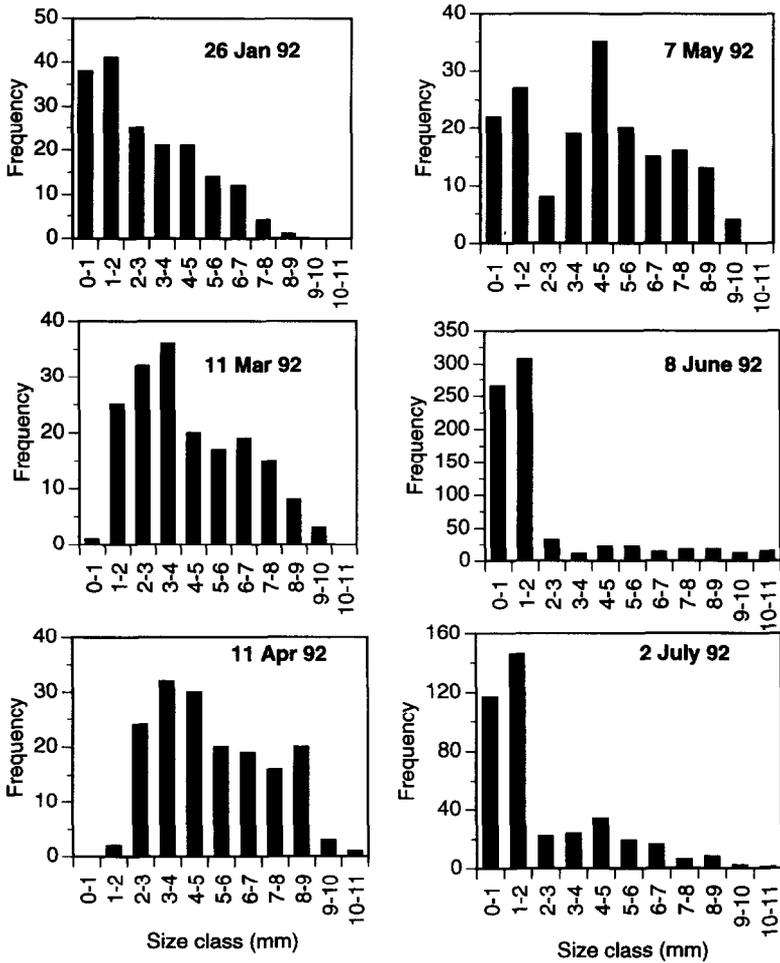


Fig. 4. Size-frequency distributions of *C. volutator* at Lowes Cove for the period January 26, 1992 to July 2, 1992. The distributions for each sampling period represent five pooled replicates.

that reproduction was minimal. By June 21, the significant rise in abundance is largely explained by births. Additional births were detected in the July 12 samples. By July 28, recruitment had essentially ceased and growth of recently released juveniles into the 1–2 and 2–3 mm intervals can be seen. No births were seen in August 12 samples, although a second bout of reproduction was discerned from the August 28 samples. This reproduction continues through September and even into October. Reproductive females were not found in the October samples so the persistence of young in the smallest size-class merely indicates slow growth of the amphipods. In fact the September 30 and October 30 distributions are virtually identical although densities are significantly lower. By January, the

size-frequency distribution has changed with mortality falling most heavily on the 1–2 mm long amphipods. The 0–1 mm long amphipods apparently failed to grow between October 30 and January 26. Between January and March, there was no significant change in abundance and, as no ovigerous females were observed after October, the change in distribution over the winter of smaller *Corophium* probably indicates growth into larger size-classes. The growth of these smaller *Corophium* continues into April. Some reproduction has clearly occurred in May. This reproduction is even more evident in the June samples.

4. Discussion

Two life history patterns have been described for *C. volutator*. In some populations, a single generation per year has been noted. In other populations, two generations per year, usually of unequal duration, have been described. Table 1 provides a compendium of the life histories of *C. volutator* at different geographic localities.

Variation can be noted in populations that are reasonably close to each other. Although *C. volutator* are known to leave their burrows and swim, it is not likely that individuals disperse for great distances. Meadows and Reid (1966) indicate that *C. volutator* begin to sink a few seconds after beginning swimming. Hughes (1988) suggests that *C. volutator* swim only two or three times in their lives with each swimming bout lasting no longer than 3 h. Essink et al. (1989) found that less than 0.06% of the individuals in a *C. volutator* population were found in the plankton. Therefore, populations separated by hundreds of km can probably be considered isolated. Striking divergence in the life history of *C. volutator* has been

Table 1
Compendium of life history patterns for *Corophium volutator*

(a) One generation per year	
Location	Reference
Inner Baltic Sea	Segerstråle, 1940
Holbæk Fjord, Zealand, Denmark	Birklund, 1977
Ythan Estuary, Scotland	McLusky, 1968
St. Andrews, New Brunswick, Canada	Gratto et al., 1983
(b) Two generations per year	
Location	Reference
Western coast of Sweden	Möller and Rosenberg, 1982
Dovey Estuary, England	Watkin, 1941; Fish and Mills, 1979
Whitby Harbor, England	Hart, 1930
Cumberland Basin, New Brunswick	Murdoch et al., 1986
Chignecto Bay, Nova Scotia	Peer et al., 1986
Starrs Point, Nova Scotia	Boates and Smith, 1979
Avonport, Nova Scotia	Gratto et al., 1983; Wilson, 1988; Wilson, 1989
Lowes Cove, Maine	Present study

noted by Gratto et al. (1983) in the upper Bay of Fundy. In the lower Bay of Fundy, a single generation per year is reported while in the upper Bay of Fundy, there are two generations per year (see also Peer et al., 1986; Wilson, 1988, 1989). These differences were attributed to differences in water temperature. The late summer temperature in the lower Bay of Fundy is 11°C while the upper Bay ranges between 17 and 21°C (Greenberg, 1984). However, the work of Wilson (1989, Wilson, 1991) suggests a possible alternative explanation. In the upper Bay of Fundy, intertidal mudflats are used by several million migratory shorebirds, mostly Semipalmated Sandpipers (*Calidris pusilla*). *Corophium volutator* is the major prey item for most shorebirds as well as demersal fishes (Imrie and Daborn, 1981). By excluding fish and shorebird predators, Wilson (1989) showed that *C. volutator* densities declined. This apparently anomalous result is explained by the fact that predators removed larger *C. volutator* from the population which ameliorated competition between newly born and adult amphipods. Predator-exclusion areas had significantly higher numbers of adults and proportionately few juveniles whereas control areas were dominated by small individuals. If the predators did not remove the post-reproductive adults, then one would expect the young *Corophium* to be forced to disperse to suboptimal habitats, resulting in a smaller population size after the post-reproductive adults died. The question addressed here is: is the good fit between prey life history and predator size-selection and intensity serendipitous or has the prey evolved its life history in direct response to the episodic predation of sandpipers?

The present data suggest that temperature (or temperature-dependent resources, like food) rather than predation rate determines the life history of *C. volutator* in the two parts of the Bay of Fundy. Lowes Cove, Maine, has a temperature regime that is similar to the upper Bay of Fundy (Gratto et al., 1983). However, the restricted distribution of *C. volutator* and its relatively low densities result in virtually no use by migratory shorebirds in the late summer. The fact that the Lowes Cove population has essentially the same life history as the upper Bay of Fundy *C. volutator* population is sufficient to reject the hypothesis that size-selective predation has selected for the two-generation/year life history in the upper Bay of Fundy. The present data are consistent with the notion that temperature may have a direct influence on the life history. A rigorous test of this remaining hypothesis is not possible with the present data. However, comparisons to other amphipod species make a compelling argument for the influence of temperature on life history. Donn and Croker (1986) show that the number of amphipod species with multiple generations per year increases as one proceeds southward along the eastern coast of the United States. Fish and Preece (1970) showed that two species of *Bathyporeia* reproduce year-round in England, but cease reproduction in the winter in more northerly habitats. A similar pattern occurs in *Ampelisca brevicornis* in which two generations per year are observed on the southern French coast but only one in the North Sea (Hastings, 1981). Wildish (1984) showed that *Casco bigelowi* has two generations per year in the Bay of Fundy, but only one at deepwater stations offshore.

The likely effects of temperature on *C. volutator* life history can be discerned

from Table 1. The European populations with one generation per year come from northerly habitats with colder waters. Populations with two generations per year are more southerly. An exception to the latitudinal pattern in Europe is the Swedish populations; however, summer temperatures at that site exceed 20°C, with extremes of 25°C. These temperatures are warmer than those observed in Lowes Cove, Maine, where the population has two generations per year.

There are some differences in the life history of *C. volutator* between the upper Bay of Fundy and Lowes Cove. The Lowes Cove population appears to begin reproducing somewhat earlier in May than the Bay of Fundy population (Fig. 3). The summer generation at Lowes Cove reproduces for a longer period of time, reproducing into September when the Bay of Fundy amphipods have ceased reproduction. Nevertheless, the overall similarity of the life history between the two populations is evident.

Although the Lowes Cove data reject the hypothesis that shorebird predation determines the life history pattern of *C. volutator*, it is possible that predation by shorebirds has influenced other aspects of the life history. Matthews et al. (1992) compared the timing of reproduction of *C. volutator* at two sites within 15 km of each other in the upper Bay of Fundy. One of these Nova Scotian sites (Starrs Point) has heavy use by shorebirds while a second site (Blomidon) is avoided by shorebirds. Although both populations of *C. volutator* have two generations per year, the amphipods at Starrs Point showed much more synchrony of reproduction. The authors argue that the episodic predation by shorebirds at Starrs Point narrows the window of time in which successful reproduction can occur (Wilson, 1989). Shorebird predation at Starrs Point may also contribute to apparent synchrony by removing ovigerous females before they reproduce, resulting in a hiatus in reproduction not observed at Blomidon where shorebirds are nearly absent.

The present data reinforce Wilson's assertion that marine infaunal communities appear to be loosely organized communities in which there is little evidence to suggest that one species has a direct influence on the life history or behavior of a second (Wilson, 1990b). The fact that the two-generation/year life history of *C. volutator* is observed in the upper Bay of Fundy is fortuitous for both this species and its major predators. The predators, by removing post-reproductive adults, are in essence 'managing' the population for future growth. If the predation were to fall when the adult population was high but before reproduction had occurred, it is doubtful that the *C. volutator* population could survive the intense predation. Certainly, a net positive increase on the population would not be observed.

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