

Autecology of an intertidal Alaskan harpacticoid copepod *Apolethon* sp.

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Abstract

The life history and ecology of a harpacticoid copepod, *Apolethon* sp., were investigated for one year in the intertidal zone of a subarctic bay in southeastern Alaska. Core samples were collected biweekly at the 0 m tidal level from March, 1992 through March, 1993; zonation and vertical distribution were determined from additional samples. Large seasonal variations in density of *Apolethon* sp. paralleled that of the total harpacticoid community, with highest densities (124.3 ± 12.5 10 cm⁻²; mean \pm standard error) in March and lowest densities in May and October (7.6 ± 4.5). The sex ratio of *Apolethon* sp. varied directly with population density, varying from <0.1 to 1.2 (male:female) during the study period. The species was restricted to a relatively narrow vertical band within the intertidal zone, having its greatest density at -1 m and being rare above $+1$ m tidal height. Adult *Apolethon* sp. bear conspicuous ovoid mucin structures located laterally on the genital double-somite. The mucin structures are unique to the species; several putative functions are discussed.

Introduction

The ecology and life history of copepods, particularly meiofaunal harpacticoid copepods, are poorly known. Most species have been described from preserved material collected from one or a few sampling periods. Commonly in those few species for which autecological data are available, information on distribution and seasonal changes in density must be gleaned from community structure analyses. In North America, the life histories of few harpacticoid copepods have been detailed (Lasker *et al.*, 1970; Harris, 1972; Coull & Vernberg, 1975; Feller, 1977; Fleeger, 1979; Palmer, 1980; Lonsdale & Levinton, 1985, 1986), and even fewer subarctic copepods have been studied (Jewett & Feder, 1977).

In the present study we address life history traits and ecology of *Apolethon* sp. which has unique morphological characteristics. The harpacticoid copepod fauna of southeastern Alaska is not well known (Fleeger & Shirley, 1990). However, a number of new copepods have been described recently from Auke Bay (Gee, 1988; Gee & Fleeger, 1990; Schizas & Shirley, in press). The genus *Apolethon*, which now includes four

species: *A. fumator*, *A. trigonus*, *A. bilobatus* and the recently described *Apolethon* sp., has not previously been reported from North America.

Material and methods

The study site was a single location in Auke Bay ($58^{\circ}22'N$, $134^{\circ}40'W$), approximately 19 km north of Juneau, Alaska (Fig. 1). The biota and hydrography of Auke Bay were reviewed by Coyle & Shirley (1990). An intertidal mudflat, approximately 60 m wide, was sampled from March, 1992 to April, 1993. The beach has a low gradient and is characterized by a barnacle-*Fucus* zone in the high intertidal, which changes to a *Mytilus trossulus* zone in the mid intertidal, and eventually to the mudflat which begins just above mean low tide level. The seagrass *Zostera marina* is present in patches throughout the mudflat. Sediments are silty sands and the depth of the redox zone is approximately 1 cm. Four replicate cores were collected at randomly selected sites along a transect paralleling the 0 m tidal level. Only the upper 2 cm of the sediment within the hand-held, piston corer (50 cc syringe; 2.6 cm

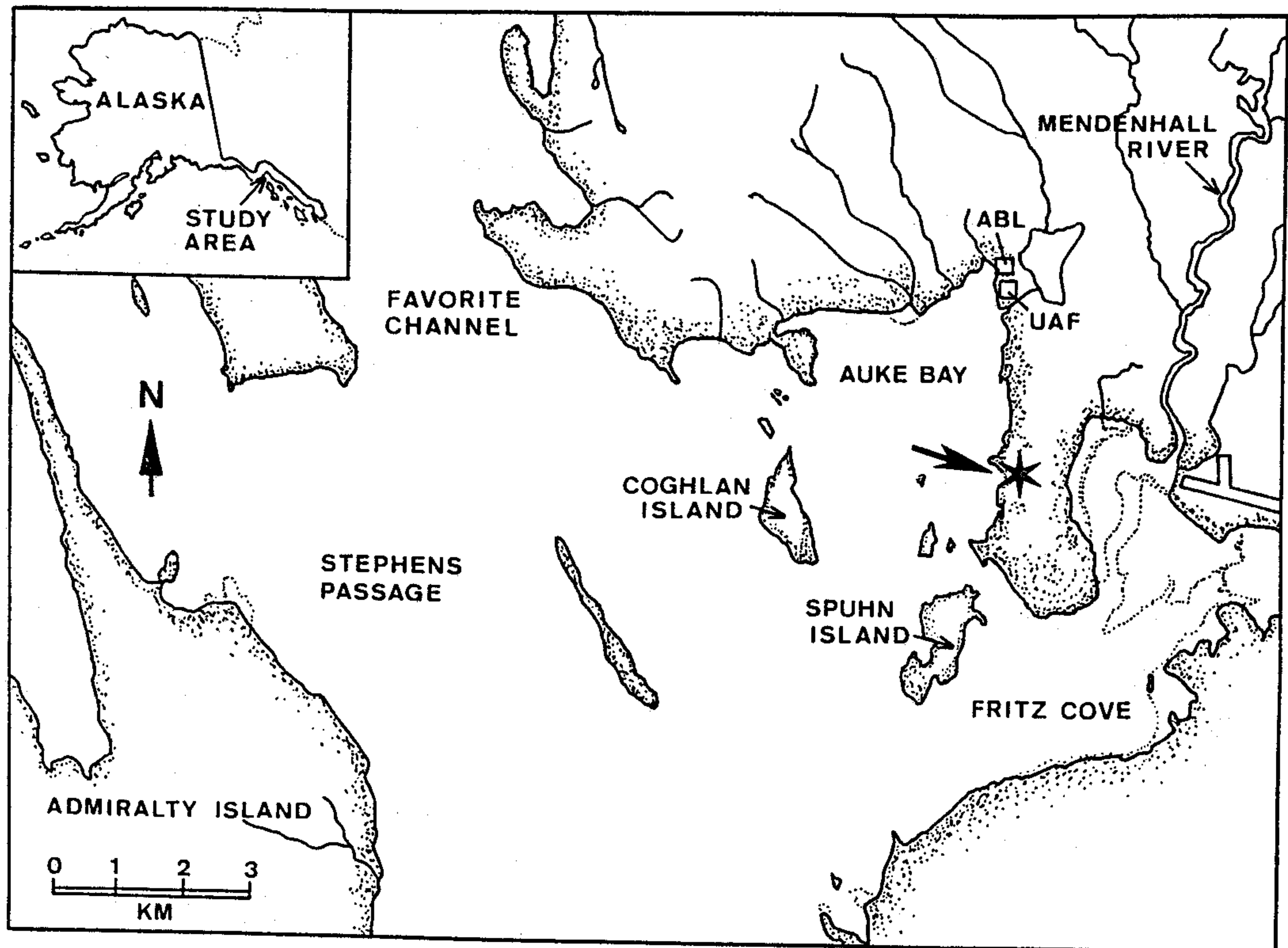


Fig. 1. Map of Auke Bay, Alaska. Asterisk denotes the sampling area.

diameter) were processed since >90% of the harpacticoids occur in the upper 10 mm of substrate (Shirley *et al.*, 1990). Sediments were washed through 0.500 and 0.063 mm sieves to separate macrofauna from meiofauna. This lower sieve size retains all life history stages of harpacticoid copepods. Meiofauna were stained with rose bengal to facilitate sorting and were preserved in 10% buffered formalin. Observations of living *Apolethon* sp. were made from specimens collected in additional samples.

Dr John McCall (of Livingston University) graciously permitted us to use unpublished data from core samples he collected at our site to study distribution of copepods vertically by tidal height and within the sediment (McCall, 1992). Six replicate cores were collected on July 20, 1989 at the +3, +2, +1, 0 and -1 m tidal heights along a transect through the type habitat. Each core was separated into six vertical sections: five 2 mm thick sections from 0–10 mm depth, and one 10 mm section from 10–20 mm depth. Additional cores were collected subtidally at -8 m, -12 m, -25 m and -55 m on the same date and sectioned with the same techniques, except core samples were collected from ship with a multiple corer (Chandler *et al.*, 1988).

Samples were not successfully collected at -3 m due to the nature of the substrate (little sediment with many shells). Meiofauna samples were also collected weekly for 4–12 months/year for 5 years (1985–89) at -25 m and -55 m immediately offshore of the type habitat (Fleeger *et al.*, 1989; Fleeger & Shirley, 1990).

Results

The intertidal *Apolethon* sp. experienced a broad range of air (minimum of -11.5 °C to maximum of 20.6 °C in August; average = 4.2 °C) and water (-1.0 °C in January to 15.8 °C in August; average = 6.5 °C) temperatures in Auke Bay; sea ice rarely occurs in Auke Bay and was not observed in the study area during the sampling period. Salinity varied from 20.5 ppt in July to >35 ppt in April. Glacial and snow meltwater results in decreased salinity during summer when the temperatures are higher. The maximum tidal range in the study area is 7 m. The photoperiod varies from 18L:6D (hours light:hours dark) in June to 6L:18D in December.

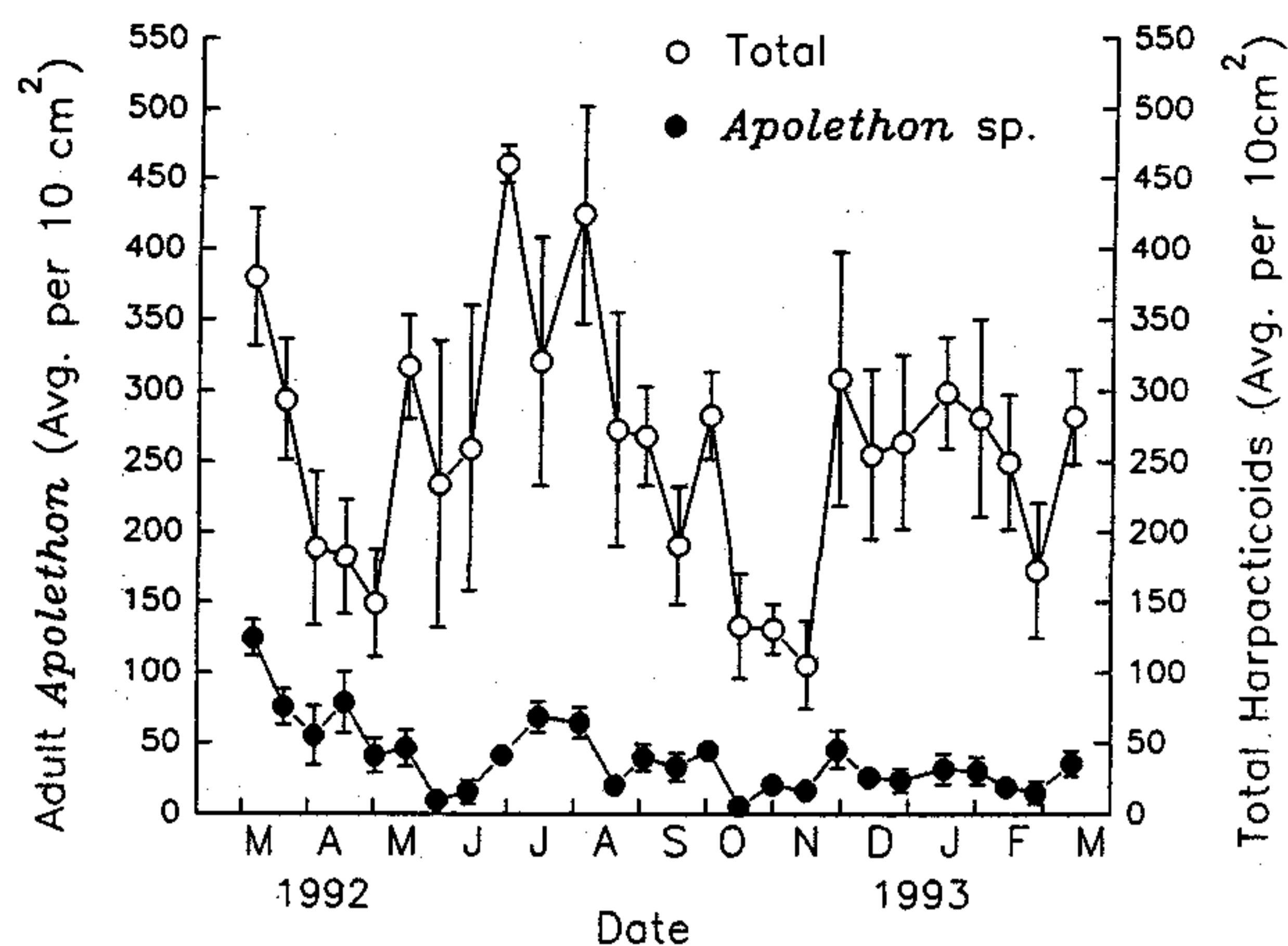


Fig. 2. Adult *Apolethon* sp. and total harpacticoid copepod densities 10 cm^{-2} (average \pm standard error) from March 1992 to March 1993.

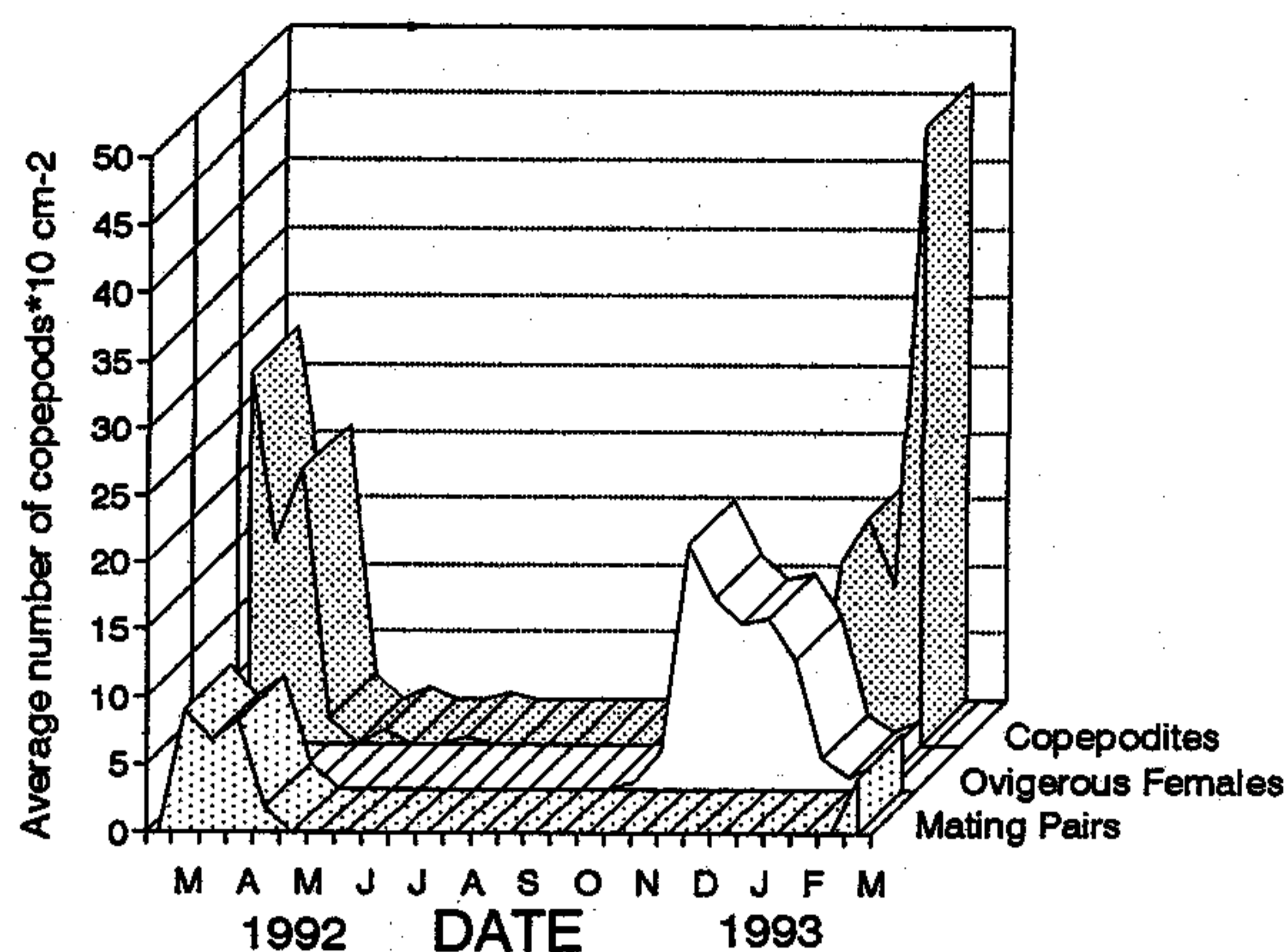


Fig. 4. Average densities 10 cm^{-2} of mating pairs, ovigerous females and copepodites of *Apolethon* sp. from March 1992 to March 1993.

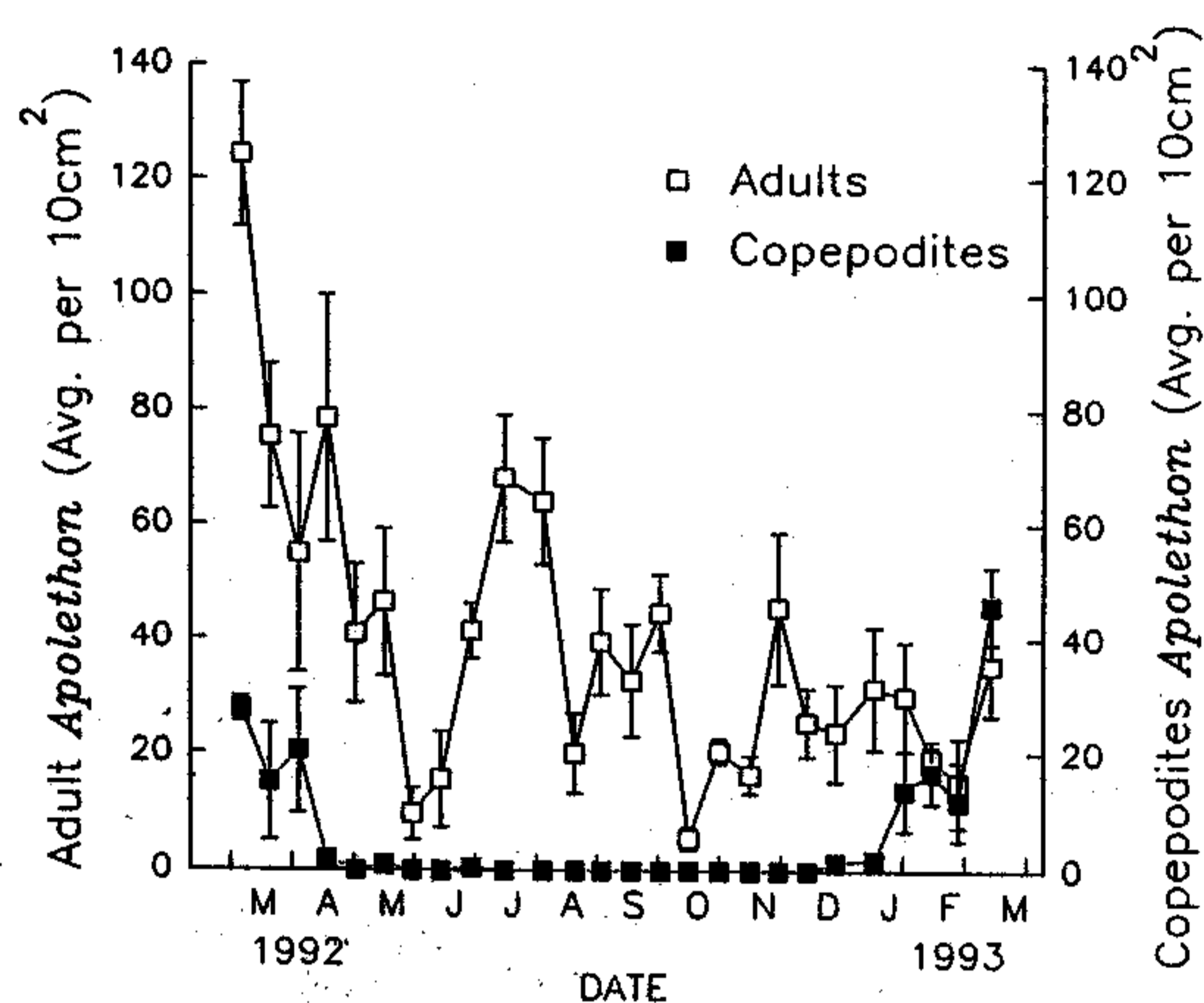


Fig. 3. Adult and copepodite *Apolethon* sp. densities 10 cm^{-2} (average \pm standard error) from March 1992 to March 1993.

Apolethon sp. attained highest densities ($124.3 \pm 12.5\ 10\text{ cm}^{-2}$; average \pm standard error) in March 1992 and lowest densities ($5.5 \pm 1.9\ 10\text{ cm}^{-2}$) in October 1992 (Fig. 2). Secondary peaks were observed in July, September and November (Fig. 3). Densities of *Apolethon* sp. paralleled and were significantly correlated ($r=0.689$, $p<0.05$, $n=26$) with those of the harpacticoid community (Fig. 2).

Copepods in precopulatory pairing were observed in March and April in densities that varied from 9.1 ± 1.3 to $1.8 \pm 1\ 10\text{ cm}^{-2}$ (Fig. 4). Ninety-three percent of the mating pairs in 1992 were found from March 6 through April 3. Adult males were attached to fourth and fifth copepodid stage females. The first ovigerous female (a single individual) was reported in late October and the last in early March; maxi-

imum densities occurred in late November ($18.2 \pm 6.1\ 10\text{ cm}^{-2}$). Seventy-six percent of the ovigerous females were collected from November 25 to January 11. The minimum time between collection of mating pairs and ovigerous females indicates that eggs were extruded by the females at least six months after mating occurred.

Nauplii were not identified to species but naupliar development probably occurred during winter, as the first copepodites of *Apolethon* sp. appeared in low densities ($1.4 \pm 0.4\ 10\text{ cm}^{-2}$) in December, attained maximum densities ($45.8 \pm 6.8\ 10\text{ cm}^{-2}$ for 1993 and $27.7 \pm 2.2\ 10\text{ cm}^{-2}$ for 1992) in March and declined ($1.8 \pm 0.6\ 10\text{ cm}^{-2}$) in April (Fig. 3). Thereafter, copepodites were present in low numbers sporadically in May and June. Different stages of copepodites were present synoptically in the same sample. High variability was observed in the density of copepodites of *Apolethon* sp. from year to year. While copepodites comprised 18.2% of the total population of *Apolethon* sp. in March 1992, they outnumbered (56.4% of the total population) the adults during March 1993 (Fig. 3).

The sex ratio of adult *Apolethon* varied from (male:female) $<0.1:1$ to $1.2:1$, with highest male ratios occurring usually during peak mating periods (Fig. 5). The proportion of males for the sampling period March 1992–93 was significantly less than 50% of adult *Apolethon* ($p<0.01$, one-tail t -test, $n=26$). We collected more males than females only on March 9, 1993. The increase in males was significantly correlated with total adult density ($r=0.938$, $p<0.001$, $n=26$) (Fig. 5).

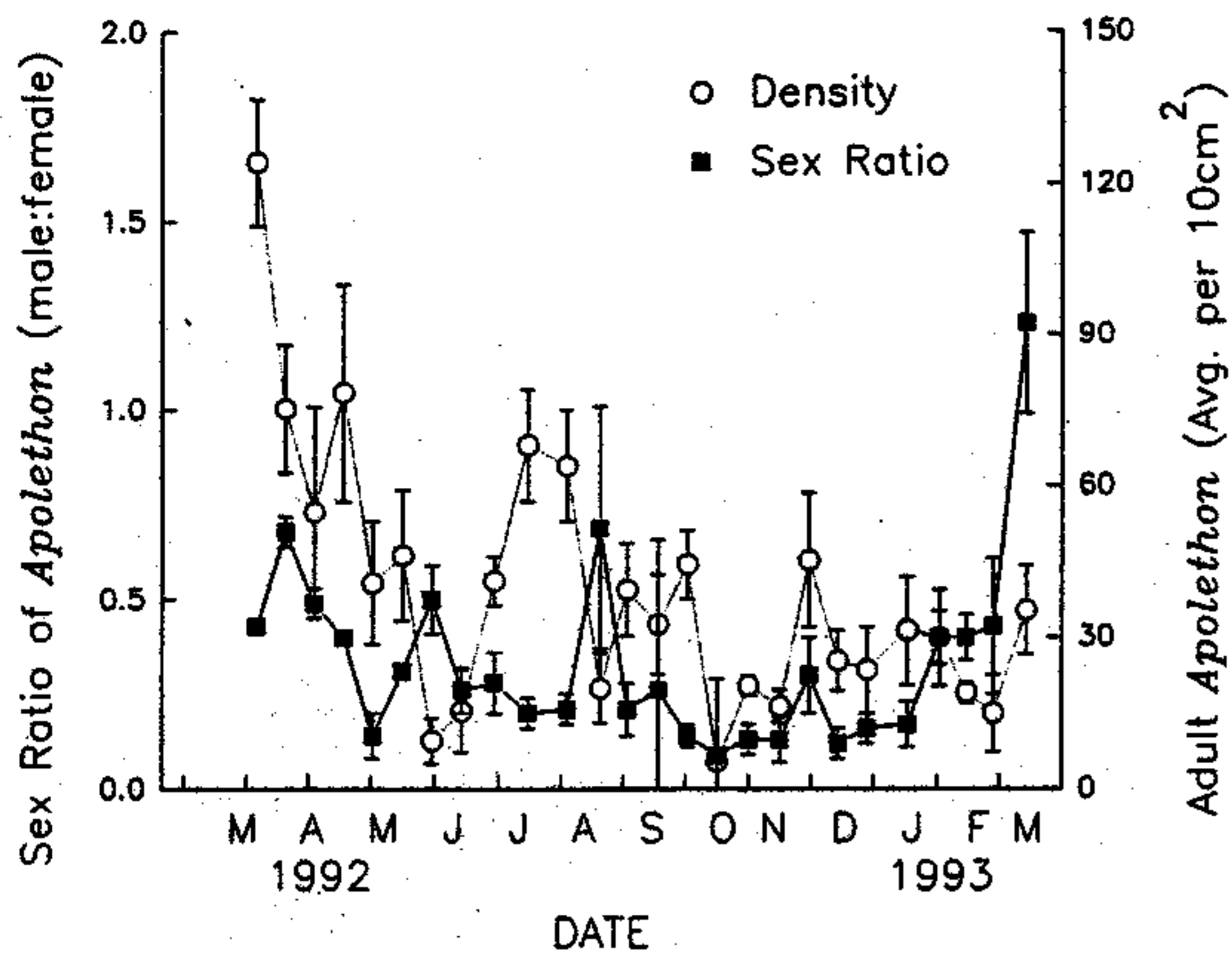


Fig. 5. Adult *Apoletthon* sp. densities 10 cm^{-2} (average \pm standard error) vs sex ratio (male:female) from March 1992 to March 1993.

Apoletthon sp. were significantly more abundant ($p < 0.001$, $n = 4$) at the tidal height of -1.0 m than at other tidal heights, rare at $+1.0\text{ m}$ and absent at higher levels during 1987–88 (Fig. 6A). Within the sediment, *Apoletthon* sp. were uniformly distributed to 10 mm depth, a deeper distribution than most other species (McCall, 1992) but entirely absent deeper (Fig. 6B).

Discussion

Apoletthon sp. was the fifth most numerically abundant species for 1992–93 at the 0 m tidal level in the subarctic embayment we studied. During April 1992, *Apoletthon* sp. adults comprised 43.1% of the harpacticoid community, while in late May of 1992 they constituted only 4.1% of the copepods (Fig. 2). *Halectinosoma* sp., *Amphiascoides dimorphus*, *Microarthidion* cf. *littorale*, *Mesochra* sp. and *Stenhelia peniculata* are the other predominant species of the muddy intertidal. The present copepod assemblage of the numerically predominant species has the same rank order that was recorded during a 1987–88 study on the same intertidal beach (McCall, 1992). The similarity of rank order of harpacticoid copepods in the same location from the 1987–88 study (McCall, 1992) and the present study implies a stable harpacticoid community.

Adult *Apoletthon* sp. attain their highest densities just before the temporally predictable phytoplankton bloom of Auke Bay. Food availability for subtidal harpacticoid copepods increases substantially during the phytoplankton bloom which consists primarily of the diatoms *Thalassiosira aestivalis*, *Skeletonema*

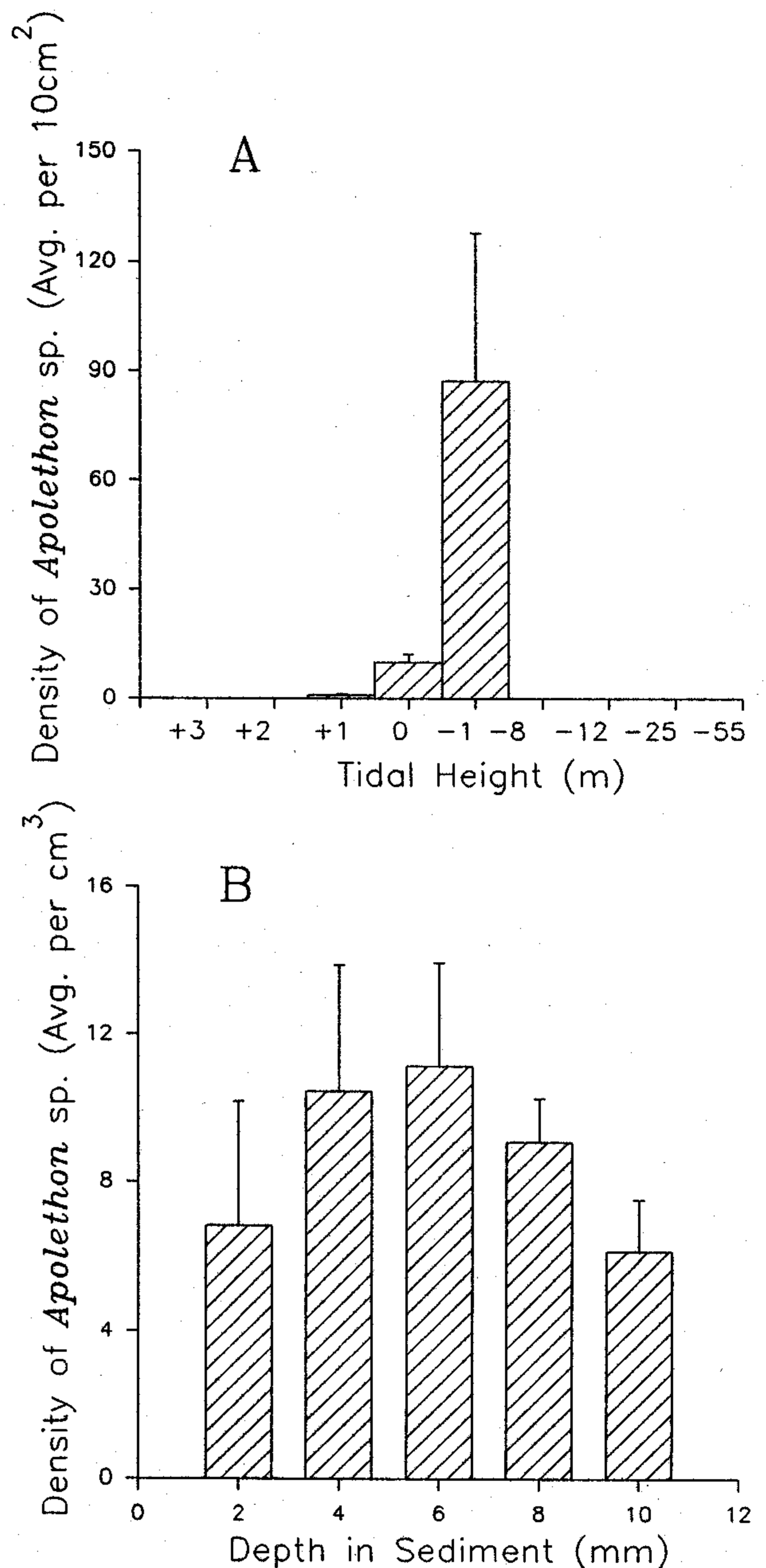


Fig. 6. A. Tidal height distribution of *Apoletthon* sp. 10 cm^{-2} (average \pm standard error). B. Vertical distribution within sediment of *Apoletthon* sp. 10 cm^{-3} (average \pm standard error).

costatum and *Chaetoceros compressus* (Ziemann *et al.*, 1991). Benthic diatoms, protozoa and bacteria serve as food for many intertidal harpacticoids (Hicks & Coull, 1983), but were not studied here. The timing of their spring production may have offered a better understanding of *Apoletthon* sp. population dynamics.

Recruitment of copepodites to the adult population occurs mainly during March and April (Fig. 3). Secondary peaks of adult *Apolethon* sp. observed in June, September and November cannot be explained by recruitment of copepodites. Immigration from different tidal heights or nearby beaches are plausible explanations. Seasonal and tidal movements of copepods were not investigated since all samples were collected during low tides.

Copepodites were also present in substantial numbers during March 1992 and 1993, and thereafter were absent or occurred sporadically in low numbers. All copepodite stages were found in samples in January, February and March, suggesting that hatching within the population is not synchronous or that development of the later copepodid stages requires longer time. These copepods hatch and develop during the winter months when food availability is relatively low in the subarctic marine environment, where most benthic organic material originates from sedimentation immediately following the sharply pulsed spring phytoplankton bloom (Fleeger & Shirley, 1990).

Sex biased ratios towards females have been reported from many harpacticoid copepod populations, both subtidal and intertidal (Hicks & Coull, 1983), but authors rarely have data to examine seasonal changes in sex ratios. Skewed sex ratios and seasonal fluctuations of the sex ratio of several subtidal harpacticoids were reported during an extensive study (1985–1989) in Auke Bay (Fleeger *et al.*, 1989; Fleeger & Shirley, 1990). In this study, we report similar seasonal changes in sex ratio *Apolethon* sp., which is found in the lower intertidal community of Auke Bay. The positive correlation between the numbers of males and total adults of *Apolethon* sp. suggest that males are short-lived and that a density dependent mechanism for the observed sex ratio may exist. We have noticed that in extended laboratory cultures, males die before females, supportively the suggestion that males are short-lived. Similar relationships between sex ratio and population density were reported for several subtidal harpacticoid species from nearby sites (Fleeger & Shirley, 1990). Alternatively, the skewed sex ratio may be explained by more rapid developmental rates of males or higher mortality due to differential predation on males. In the same intertidal beach, differential predation rates were recorded for males and females of *Microarthridion* cf. *littorale* by the starry flounder *Platichthys stellatus* (McCall, 1992).

Water temperature may influence the sex ratio of harpacticoid copepods (Takeda, 1950; Ginsburger-

Vogel, 1975). Takeda (1950) suggested that temperature may affect the sex ratio of *Tigriopus japonicus*, and variations in temperature may cause the seasonal variation of sex ratio observed in nature. The proportion of male *Apolethon* sp. increased during March, late June and early August when the water temperature varied from 6.5 to 15.8 °C. Salinity is also known to affect the sex ratio of copepods (Igarashi, 1969; Gaudy *et al.*, 1982). Male ratio was highest when salinity varied from >35 to 22 ppt. No obvious relationships exist between sex ratio of *Apolethon* sp. and water temperature or salinity fluctuations in Auke Bay.

Mating in *Apolethon* sp. probably occurs once a year during March and April. The first ovigerous females appeared in the population approximately nine months after mating began. A female *Apolethon* sp. may reach the egg-bearing stage in seven to nine months. Adult females were observed with one spermatophore at a time; mating with multiple partners probably does not occur. Ovigerous females, with a single egg sac, were found from late October through March. It is impossible to conclude from our data whether female *Apolethon* sp. are semelparous. However, when developmental rates at lower temperatures are considered, it seems unlikely that they are multivoltine. Jewett & Feder (1977) reported that females of Alaskan populations of *Harpacticus uniremis* seem to have a single brood a year in the field, although Sibert (1979) reported up to 11 broods for *Harpacticus uniremis* in a laboratory study.

The life pattern of *Apolethon* sp. is similar to that of the Alaskan population of *Harpacticus uniremis* whose clasping pairs appeared from December through May and ovigerous females were found from December and January (Jewett & Feder, 1977). Egg production was much higher in *Harpacticus uniremis* (Jewett & Feder, 1977) than *Apolethon* sp. (83 to 155 eggs vs 8 to 20 eggs). *Harpacticus uniremis* began mating earlier in the year and ovigerous females are present for a shorter period of time than *Apolethon* sp.

Development time of naupliar and copepodid stages is unknown for *Apolethon* sp. We infer from the presence of ovigerous females and copepodites (late October to March and December to June, respectively) that development occurs between October and June when the water temperature varies from -1.0 to 11 °C. However, the majority of ovigerous females and copepodites were collected in winter and early spring, respectively. From November through mid-April we recorded temperatures less than 5 °C (except February 21).

Apolethon sp. was restricted to a narrow zone within the deep subtidal within Auke Bay. It was collected primarily at the -1 m and 0 m intertidal stations, as only two specimens were found at +1 m and none were found at the six other intertidal and subtidal depths. No specimens of *Apolethon* sp. were found in subtidal samples collected intensely over a five year period in Auke Bay (Fleeger & Shirley, 1990). The species may have been present in the shallow subtidal which was not tidally exposed and could not be sampled with remote corers from vessels. The intertidal zone in which *Apolethon* sp. is restricted is not characterized by any abrupt change in sediment characteristics, increased detritus or flotsom. Most of the other harpacticoid copepod species in our study area are similarly restricted to relatively narrow vertical zones within the intertidal zone (McCall, 1992; unpublished data).

Within the sediment, *Apolethon* sp. was found deeper in the sediment than most harpacticoid species present at the site. It was almost uniformly distributed to 10 mm depth, but none were found below 10 mm depth. The three numerically predominate harpacticoid species in the samples had their highest densities within the upper 4 mm of sediment (McCall, 1992), in marked contrast to the more deeply distributed *Apolethon* sp. In a study of fine-scale vertical distribution of harpacticoid copepods in an intertidal sandflat in England, Joint *et al.* (1982) reported 83% of the species occurred in the top 20 mm and that only four species were rarely present below that depth. The more shallow distribution of our copepods is undoubtedly related to the finer grain size at our beach.

Copepods of the genus *Apolethon* have been sampled from strikingly different habitats and locations around the world. *Apolethon fumator* was collected from detritus and sand of the Island of Inhaca, in Indian Ocean (Wells, 1967). *Apolethon trigonus* and *A. bilobatus* were discovered in the Pearl River and Pacific River respectively, Guangdong Province, China (Shen & Tai, 1973). *Apolethon* sp. was studied in a muddy habitat in Auke Bay, Alaska, where salinity varied from 22 to 37 ppt and sea surface temperature varied from 2.3 to 12.1 °C. The occurrence of the genus in rivers and intertidal areas suggests a euryhaline distribution of *Apolethon*.

The paired mucin structures in the adults of *Apolethon* sp. of both sexes are present throughout the year on freshly collected specimens. The mucous is not an artifact of preservation since it was detected in most live specimens we examined. The mucin does

not stain with Rose Bengal and fluoresces a bright red when exposed to an ultraviolet light source (Leitz Laborlux 12 microscope, 50 W ultra high pressure mercury lamp). No copepodites were observed with these structures. In laboratory cultures, the mucin structures that had been present disappeared after two months, suggesting that the structures may be used for energy storage or that the artificial laboratory diet was insufficient for their secretion or maintenance. An alternate explanation of their function is that because these structures are found only on adults, they may be associated with some aspects of reproduction.

Mucous secretions have been associated with tube-building copepods (Chandler & Fleeger, 1984; Williams-Howze & Fleeger, 1987; Williams-Howze *et al.*, 1987) and encystment (Coull & Grant, 1981), however, no tube-building species has been reported to have mucin structures like *Apolethon* sp. We have found several *Stenhelia peniculata* nauplii inside tubes, but have not found tubes with any other species. *Apolethon* sp. may construct very delicate tubes that break up during sieving. We have not observed tube production in cultures of *Apolethon* sp. maintained in cultures with small amounts of fine sand for approximately 10 weeks, and therefore the use of the secretions for cultivation of bacteria or fungus is improbable. Our cultures did not persist long enough for production of a new generation, although we observed clasping pairs. The nature of the function of the mucin structures remains speculative and warrants more detailed study.

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