

Seasonal changes in structure of an Alaskan intertidal meiofaunal assemblage

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ABSTRACT: A subarctic, intertidal meiofaunal assemblage in Auke Bay, Alaska, USA, was sampled throughout one year at 3 intertidal heights; mean low water (0 m) and 1 m above and below this level (+1 m, -1 m). Samples were taken twice a month at 0 m and approximately every other month at -1 and +1 m intertidal heights. Nematodes predominated numerically (31 to 77%), followed by harpacticoid copepods (adults and copepodites combined 10 to 35%, nauplii 5 to 32%). Meiofaunal densities fluctuated significantly throughout the sampling period. The demography of the 6 numerically predominant species of copepods was examined. In order of abundance, they were *Halectinosoma* sp., *Amphiascoides dimorphus* Lang 1965, *Microarthridion* cf. *littorale* Poppe 1881, *Apolethon* sp., *Mesochra* sp. and *Stenhelia* (*Stenhelia*) *peniculata* Lang 1965. Densities of the adults, ovigerous females and copepodites of these species changed significantly throughout time. The peak densities of ovigerous females and copepodites were well separated temporally (whereas those of adults overlapped) and tended to occur in months from November to March. Only *M.* cf. *littorale* displayed a high abundance of ovigerous females and copepodites in the summer months. Reproductive patterns varied among the harpacticoid species, from discrete (*Apolethon* sp.) to continuous reproductive periodicity (all other species).

KEY WORDS: Meiofauna · Harpacticoid copepods · Alaska · Intra-annual variability

INTRODUCTION

Although the ecological importance of meiofauna (mobile benthic invertebrates that pass through a 0.500 mm sieve but are retained on a 0.063 or 0.045 mm sieve) has been established, ecological studies of meiofaunal communities of the subarctic waters are scarce. Meiofauna are an important link in the benthic food web. Harpacticoid copepods, a significant component of the meiobenthos, prey on microalgae and bacteria, bioturbate the sediment (with burrowing activities), enhance recycling of bacterial material, and return accumulated nutrients to the benthos when they die (Giere 1993). Harpacticoid copepods are also important prey of invertebrate species and for a short time during the early life history of several fish species the importance of these copepods to the survival of

their predators may be crucial (see reviews by Gee 1989, Coull 1990, Webb 1991, McCall 1992, Aarnio & Bonsdorff 1993, Keats & Steele 1993, Keats et al. 1993, Nilsson et al. 1993, Toepfer & Fleeger 1995). Seasonal and annual variation in abundance of harpacticoid copepods may be related to growth and survival of populations of commercially important species (Healy 1979, Sibert 1979). Additionally, meiofauna may be resource competitors with the juveniles of macrofaunal invertebrates (Zobrist & Coull 1992, 1994). A better understanding of meiofaunal dynamics requires detailed studies of nematode and harpacticoid assemblages.

Our study site, in Auke Bay, Alaska, USA, has been the focus of several ecological (Sturdevant 1987, McGregor 1991, McCall 1992) and taxonomic (Schizas & Shirley 1994a) meiobenthic studies. Previous investigators have gathered information on seasonal changes of meiofauna (McGregor 1991), prey selectivity of postmetamorphic flatfish for harpacticoid copepods (Sturdevant 1987, McGregor 1991), and species and

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sex-specific predation on copepods by postmetamorphic flatfish (McCall 1992) from the same field site. Fleeger & Shirley (1990) studied the population composition of Auke Bay subtidal harpacticoid fauna for 4 yr, but intertidal harpacticoid copepods have not been studied intensively as a distinct ecological group. There is no information on interannual variability of intertidal meiofauna in southeast Alaska. The objectives of this study were: (1) to examine seasonal changes in density and composition of meiofauna; and (2) to describe the demography of the numerically predominant harpacticoid copepods.

MATERIALS AND METHODS

An intertidal mudflat located in Auke Bay (58° 22' N, 134° 40' W), approximately 19 km north of Juneau, Alaska, was sampled from March 1992 to April 1993. The biota and hydrography of Auke Bay has been reviewed by Coyle & Shirley (1990). The intertidal region was approximately 60 m wide with a low gradient and was characterized by a barnacle-*Fucus* zone in the high intertidal, which changed to a *Mytilus trossulus* Gould zone in the mid-intertidal zone, and eventually to a mudflat which extended below the mean low intertidal level. The seagrass *Zostera marina* L. was present in sparse patches on the mudflat.

Samples were collected during aerial exposure of the mudflat with a hand-held, piston corer (50 cc syringe; 2.65 cm in inner diameter). Four replicate core samples were collected randomly along the mean lower low water (0 m) and 1 m above and below this level (+1 m, -1 m) during each sampling period. The 0 m intertidal level was sampled approximately every 15 d, whereas the other 2 intertidal levels were sampled less frequently (5 sampling dates throughout the year for each intertidal level) as tidal amplitude permitted. The intertidal level of +1 m was more accessible to sampling than 0 and -1 m, but not all 3 intertidal levels could be sampled during each collection date. Only the upper 20 mm of the sediment was retained since >90% of the harpacticoids occurred in the upper 10 mm of substrate in the mud of Auke Bay (Fleeger et al. 1995). Temperature was measured with a digital thermometer (Digi-Sense®) and salinity was measured with a refractometer *in situ*. Meiofauna were stained with rose bengal to facilitate sorting and were preserved in 10% buffered formalin.

Identification of the copepods was confirmed from their dissected parts. The parts were prepared by dissection under a low-power dissecting microscope, by mounting the dissected copepod parts in Hoyer's mounting medium or lactophenol and by examining the parts under oil immersion magnification (×1000).

We assumed that loss of egg sacs was similar for all copepod species and that clasping pairs of harpacticoids remained intact after the sorting and handling processes. The latter is supported by Kern et al. (1984), who found that the majority of clasping pairs remained attached during processing.

Statistical tests were performed using Statistical Analysis System (SAS) for a PC (SAS Institute Inc. 1990). Mean densities of meiofauna and demographic groups of harpacticoid species were compared among sampling dates using 1-way analysis of variance (ANOVA). The General Linear Modeling (GLM) procedure of SAS was used to perform all ANOVA tests. A 1-factor (sampling date) ANOVA model $Y_i = \mu + D_i + \varepsilon_i$ was used, where Y_i was the average density of the meiobenthic taxa and harpacticoid copepods examined, μ was the constant, D_i was the fixed effect of sampling date, and ε_i was the error term with $i = 1, \dots, 26$. Type III sums of squares (partial sum of squares) were used in interpreting the ANOVA results. Statistics with a probability <0.05 were considered significant.

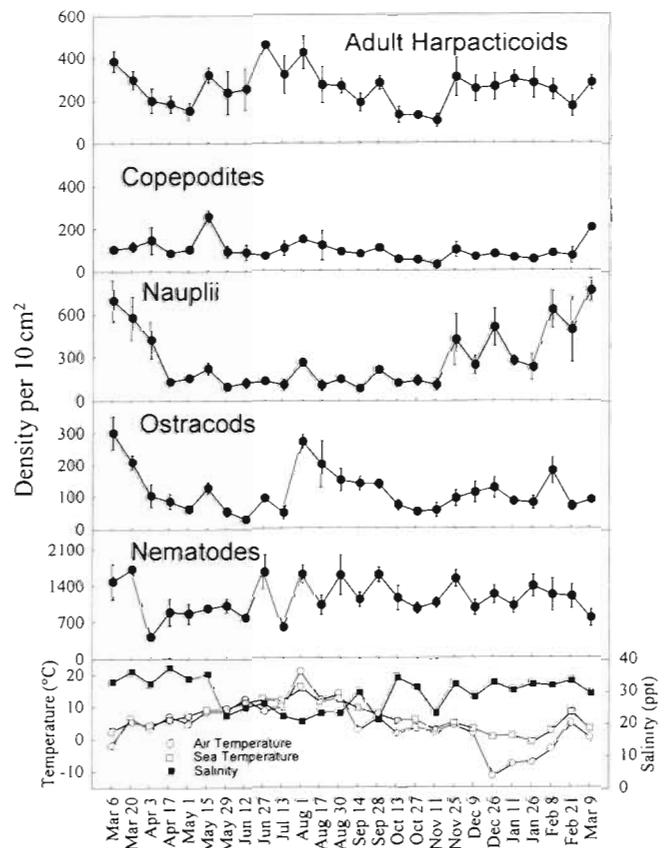


Fig. 1 Density (average \pm 1 standard error) of meiofauna at 0 m. Scale of ordinate varies with taxon. Temperature and salinity recorded in bottom graph.

RESULTS

The intertidal meiofauna of Auke Bay experienced a wide range of air and water temperatures (Fig. 1). Despite the cold temperatures, sea ice rarely occurs in Auke Bay and was not observed at the study site during this project. Salinity varied from 20.5‰ in July to >35‰ in April. However, surface salinities in Auke Bay rarely exceed 31‰ (Bruce et al. 1977). The Mendenhall River, primarily Mendenhall Glacier meltwater and snow meltwater, discharges freshwater just outside Auke Bay resulting in decreased salinity during the summer when temperatures are higher. The maximum intertidal range in the study area is 7 m. The photoperiod varies from 18 h light:6 h dark in June to 6 h light:18 h dark in December.

Meiofaunal taxa

Nematodes, followed by harpacticoid copepods (adults and copepodites combined), harpacticoid nauplii, and ostracods, were the most abundant meiofaunal taxon throughout most of the year (Fig. 1; Table 1). Other meiofaunal taxa present in lower densities were cyclopoid copepods, halacarid mites, hydroids, nemerteans, oligochaetes, rotifers, and turbellarians. Kino-

rhynchs and tardigrades were represented by single specimens. The temporary meiobenthos consisted primarily of polychaete larvae, juvenile bivalves, and gastropods.

The density of nematodes, ostracods, and harpacticoid copepods fluctuated significantly over the year at the 0 m intertidal height (Fig. 1; see Table 3). No patterns were apparent for nematodes except randomly occurring density peaks, whereas ostracods had consistently low densities during April–June. Ostracods attained maximum densities during March and August 1992 (but not in 1993), suggesting 2 annual recruitment periods or perhaps density maxima of 2 different species. Neither nematodes nor ostracods were identified to lower taxonomic levels; therefore, possible seasonal changes in species abundance or composition were undetected. Densities of ostracods and nematodes at the –1 and +1 m levels were similar to those of the 0 m intertidal level (Table 1).

Generally, the adults of harpacticoid species reached their highest densities during the summer. Harpacticoid nauplii had significantly higher densities from November through March (Tukey's Studentized Range Test) than during most of the rest of the year (Fig. 1). Oviparous females, copepodites and nauplii of all copepod species combined were present at all sampling dates, indicating continuous reproduction by

Table 1. Averages, maxima, and minima of densities of predominate meiofaunal taxa given as average \pm 1 standard error of the mean per 10 cm². Adult copepod values also encompass oviparous females. Averages from the 0 m intertidal level are based on means of 4 cores from 26 sampling dates, while averages from +1 and –1 m are based on 4 cores from 5 sampling dates. Percent composition of individual taxa is based on the density of taxa relative to the density of all meiofaunal taxa

Taxon	Average	Maximum	Minimum	% Composition	Tidal level
Nematoda	1461.9 \pm 228.2	2080.2 \pm 382.3	850.8 \pm 215.1	76.0%	–1
	1148.2 \pm 67.7	1703.4 \pm 81.64	408.4 \pm 60.6	59.6%	0
	1437.7 \pm 87.4	1768.8 \pm 573.1	1255.3 \pm 391.8	68.9%	+1
Adult harpacticoid copepods	210.3 \pm 41.5	318.3 \pm 45.6	95.8 \pm 48.7	10.5%	–1
	257.6 \pm 17.0	460.1 \pm 13.6	105.3 \pm 31.0	13.5%	0
	270.4 \pm 60.1	409.1 \pm 100.8	72.6 \pm 34.3	10.8%	+1
Oviparous harpacticoid females	31.3 \pm 8.8	52.2 \pm 17.9	8.6 \pm 6.3	1.3%	–1
	29.4 \pm 3.9	48.1 \pm 9.6	0.91 \pm 0.5	2.6%	0
	27.0 \pm 4.7	41.3 \pm 12.0	15.4 \pm 10.0	1.1%	+1
Harpacticoid copepodites	75.0 \pm 8.2	99.0 \pm 32.9	52.7 \pm 17.9	4.0%	–1
	100.5 \pm 9.4	206.91 \pm 17.6	31.8 \pm 11.4	5.4%	0
	153.9 \pm 61.4	371.8 \pm 205.1	17.3 \pm 14.3	6.0%	+1
Harpacticoid nauplii	106.8 \pm 37.2	248.3 \pm 79.6	42.7 \pm 13.7	4.7%	–1
	283.84 \pm 40.6	763.7 \pm 81.8	83.5 \pm 5.5	14.0%	0
	134.2 \pm 48.8	277.9 \pm 142.0	20.9 \pm 15.5	6.7%	+1
Ostracoda	75.3 \pm 19.1	119.4 \pm 26.1	23.6 \pm 17.1	3.7%	–1
	116.5 \pm 13.4	298.57 \pm 51.4	27.2 \pm 12.3	5.8%	0
	93.9 \pm 19.9	148.9 \pm 34.6	37.7 \pm 6.1	5.2%	+1
All meiofauna	1471.5 \pm 238.7	1940.8 \pm 294.3	615.0 \pm 126.6	–	–1
	1633.8 \pm 348.8	1938.8 \pm 105.5	693.0 \pm 176.0	–	0
	1337.3 \pm 205.8	2140.2 \pm 139.2	970.3 \pm 233.7	–	+1

Table 2. Species of harpacticoid copepods collected on -1, 0, and +1 m intertidal levels from Auke Bay, Alaska

Family	Species
Ectinosomatidae	<i>Halectinosoma</i> sp. <i>Pseudobradya</i> sp. Ectinosomid sp. 1
Tachidiidae	<i>Microarthridion</i> cf. <i>littorale</i> (Poppe 1881) <i>Danielssenia typica</i> Boeck 1872
Laophontidae	<i>Apolethon</i> sp. <i>Echinolaophonte horrida</i> (Norman 1876) <i>Paralaophonte perplexa</i> (T. Scott 1898) <i>Heterolaophonte</i> sp. <i>Laophonte</i> sp.
Canthocamptidae	<i>Mesochra</i> sp.
Diosaccidae	<i>Amphiascoides dimorphus</i> Lang 1965 <i>Amphiascus</i> sp. <i>Stenhelia</i> (<i>Stenhelia</i>) <i>peniculata</i> Lang 1965 <i>Stenhelia</i> (<i>S.</i>) sp.
Cletodidae	<i>Acrenhydrosoma maccalli</i> Schizas & Shirley 1994 <i>Stylicletodes</i> sp. <i>Cletodes</i> sp.
Huntemannidae	<i>Huntemannia jadensis</i> Poppe 1884
Harpacticidae	<i>Harpacticus</i> sp.
Tisbidae	<i>Tisbe</i> sp. <i>Zaus</i> sp.
Ameiridae	<i>Ameira parvuloides</i> Lang 1965
Thalestridae	<i>Dactylopodia vulgaris</i> Sars 1905

harpacticoids. Densities of harpacticoid adults at +1 and -1 m intertidal heights were generally lower than those at 0 m except for the 11 January 1993 sample at +1 m (409.1 ± 100.8 per 10 cm^2), which was the highest density recorded of that intertidal level during the year (Table 1).

The densities of copepodites were similar among the 3 intertidal heights with the exception of 15 May (371.8 ± 205.1 per 10 cm^2) and 1 August (17.3 ± 14.3 per 10 cm^2) at +1 m, when the highest and the lowest densities were recorded, respectively (Table 1). Copepodite densities twice attained >200 per 10 cm^2 concentrations in our samples, following maximal densities of nauplii. For example, the maximum copepodite density followed the 1992 maximum density of nauplii by approximately 2 mo.

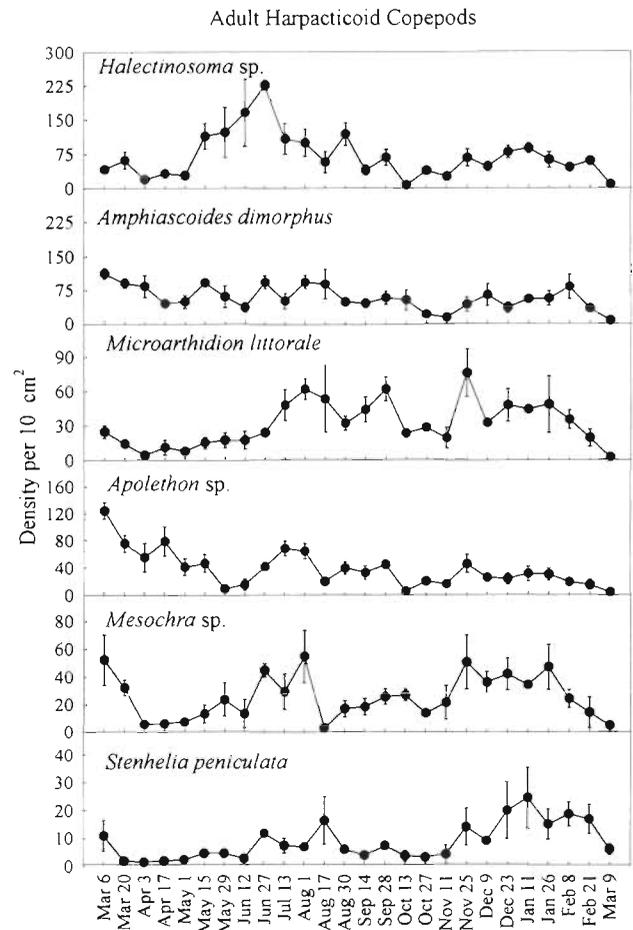


Fig. 2. Density (average \pm 1 standard error) of adults of 6 species of harpacticoid copepods at the 0 m intertidal height

Harpacticoid copepods

Twenty-five species of harpacticoid copepods were identified in the meiofaunal community (Table 2) but 6 copepod species frequently made up $>90\%$ of total harpacticoid fauna. The 6 numerically predominant species examined were: *Halectinosoma* sp., *Amphiascoides dimorphus* Lang 1965, *Microarthridion* cf. *littorale* Poppe 1881, *Apolethon* sp., *Mesochra* sp. and *Stenhelia* (*S.*) *peniculata* Lang 1965.

Densities of all 6 species varied significantly with the time of year (Fig. 2, Table 3). *Halectinosoma* sp. reached maximum densities during May and June 1992. *Halectinosoma* sp., the most abundant copepod in our study, had the greatest increase in density of all copepod species during May and the subsequent summer months of 1992. *Halectinosoma* sp. was also the predominant copepod in the +1 m samples but second in abundance to *Amphiascoides dimorphus* in the -1 m samples. Densities of *A. dimorphus* fluctuated with no apparent seasonal pattern. *Microarthridion* cf. *littorale*

was most abundant during summer and fall 1992. *Apolethon* sp. was most abundant during spring and summer. *Mesochra* sp. increased in density during summer and winter. Densities of *Stenhelia* (*S.*) *peniculata* were low (<25 copepods per 10 cm²) throughout most the year (Fig. 2).

Ovigerous females of *Halectinosoma* sp., *Microarthridion* cf. *littorale*, *Mesochra* sp. and *Stenhelia* (*S.*) *peniculata* were found generally throughout the sampling period (Fig. 3). Only *M.* cf. *littorale* displayed a high abundance of ovigerous females in the summer months. No ovigerous females of *Amphiascoides dimorphus* were present during the summer. Ovigerous females of *Halectinosoma* sp. and *Mesochra* sp. increased in density at the same time (30 August), whereas *A. dimorphus* increased during late fall (25 November) at 0 m. Ovigerous females of *Apolethon* sp. were present from November to March at the 0 m samples. Seventy-six percent of the ovigerous females of *Apolethon* sp. appeared from 25 November to 11 January at 0 m (Schizas & Shirley 1994b). Similarly, 43% of the ovigerous females of *S. (S.) peniculata* were collected in less than 1 mo (11 January to 8 February) at 0 m. Reproductive activity of harpacticoid copepods was similar at each of the intertidal levels.

Copepodites of the 6 predominant harpacticoid species at the 0 m intertidal height were at maximum densities during different times of the year (Fig. 4). *Halectinosoma* sp. copepodites were most abundant during May and June. *Amphiascoides dimorphus* copepodites were most abundant during spring. *Microarthridion* cf. *littorale* copepodites were most abundant during summer, whereas *Apolethon* sp. copepodites were present from January to April. *Stenhelia* (*S.*) *peniculata* copepodites were present mostly from September through March. Copepodites of all 6 copepod species were present at the -1 and +1 m intertidal heights.

Precopulatory pairs of *Halectinosoma* sp. and *Apolethon* sp. were

Table 3. Summary of the SAS output of ANOVA tests for among date variation of the predominant meiofauna taxa and 6 harpacticoid copepod species at the 0 m intertidal height in a muddy beach of Auke Bay, Alaska. The model $Y_i = \mu + D_i + \epsilon$, was used, where Y_i is the average density of the meiobenthic taxa examined, D_i is the fixed effect of sampling date (Date), and ϵ_i is the error term

	Source	df	Type II SS	F	p > F
Nematodes	Date	25	141035.01	4.44	0.0001
	Error	78	1270.61		
Ostracods	Date	25	3683942.15	2.34	0.0024
	Error	78	4909305.50		
Adult harpacticoids	Date	25	228726.97	1.69	0.0413
	Error	78	421371.25		
Gravid harpacticoids	Date	25	39718.62	5.10	0.0001
	Error	78	24300.00		
Copepodites	Date	25	62201.50	3.36	0.0022
	Error	78	82348.00		
Nauplii	Date	25	1300936.12	3.98	0.0001
	Error	78	1019444.5		
<i>Halectinosoma</i> sp. adults	Date	25	71717.12	3.46	0.0001
	Error	78	64729.50		
<i>Halectinosoma</i> sp. gravids	Date	25	5731.00	5.41	0.0001
	Error	78	3302.50		
<i>Halectinosoma</i> sp. copepodites	Date	25	19837.24	4.03	0.0001
	Error	78	15363.75		
<i>Amphiascoides dimorphus</i> adults	Date	25	19279.46	1.80	0.0266
	Error	78	33464.50		
<i>A. dimorphus</i> gravids	Date	25	3274.46	6.84	0.0001
	Error	78	1494.00		
<i>A. dimorphus</i> copepodites	Date	25	7466.96	3.10	0.0001
	Error	78	7503.50		
<i>Microarthridion</i> cf. <i>littorale</i> adults	Date	25	10521.65	2.15	0.0057
	Error	78	15300.00		
<i>M.</i> cf. <i>littorale</i> gravids	Date	25	1967.51	1.88	0.0185
	Error	78	3262.25		
<i>M.</i> cf. <i>littorale</i> copepodites	Date	25	46801.88	3.98	0.0001
	Error	78	36727.00		
<i>Apolethon</i> sp. adults	Date	25	21055.47	4.82	0.0001
	Error	78	13631.75		
<i>Apolethon</i> sp. gravids	Date	25	884.54	6.15	0.0001
	Error	78	448.50		
<i>Apolethon</i> sp. copepodites	Date	25	7257.50	8.45	0.0001
	Error	78	2680.50		
<i>Mesochra</i> sp. adults	Date	25	6993.12	1.78	0.0286
	Error	78	12255.50		
<i>Mesochra</i> sp. gravids	Date	25	1376.28	2.43	0.0016
	Error	78	1769.25		
<i>Mesochra</i> sp. copepodites	Date	25	469.59	2.40	0.0018
	Error	78	610.25		
<i>Stenhelia</i> (<i>S.</i>) <i>peniculata</i> adults	Date	25	1423.66	1.84	0.0222
	Error	78	2415.25		
<i>S. (S.) peniculata</i> gravids	Date	25	337.63	1.28	0.2062
	Error	78	824.75		
<i>S. (S.) peniculata</i> copepodites	Date	25	790.04	2.39	0.0019
	Error	78	1031.50		

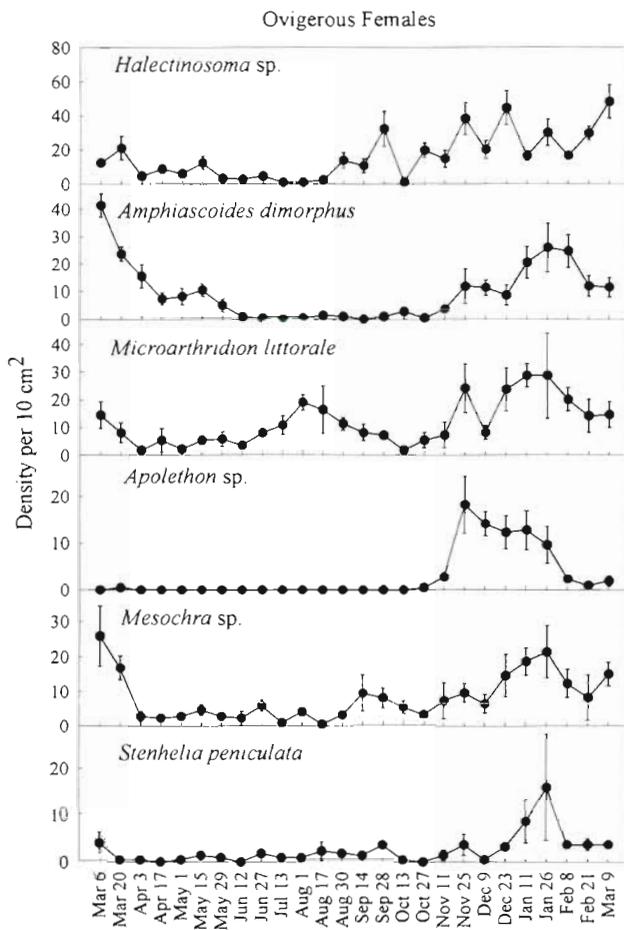


Fig. 3. Density (average \pm 1 standard error) of ovigerous females of 6 species of harpacticoid copepods at the 0 m intertidal height

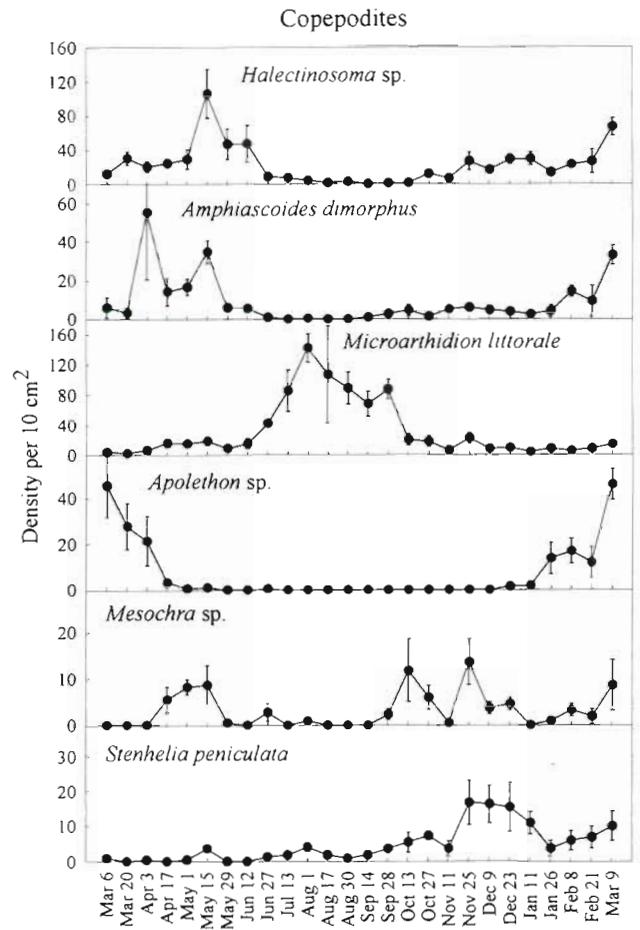


Fig. 4. Density (average \pm 1 standard error) of copepodites of 6 species of harpacticoid copepods at the 0 m intertidal height

present from February to June, and March to April, respectively (Fig. 5). No precopulatory pairs occurred in the 0 m samples for *Stenhelia* (*S.*) *peniculata* and *Mesochra* sp., but 2 pairs of *Amphiascoides dimorphus* and 3 pairs of *Microarthridion* cf. *littorale* were found.

DISCUSSION

Meiofauna attain highest densities on estuarine intertidal mudflats and lowest densities in the sediments of deeper waters (>200 m) (Coull 1988). Average densities of meiofauna were similar among the 3 intertidal levels sampled in Auke Bay (Table 1) and were within the ranges reported for other intertidal mudflats (Table 4).

A 1987-88 study (McGregor 1991) at the same sampling site in Auke Bay, Alaska, reported higher average densities of meiofauna and harpacticoid copepods than those reported herein (Table 4). The differences

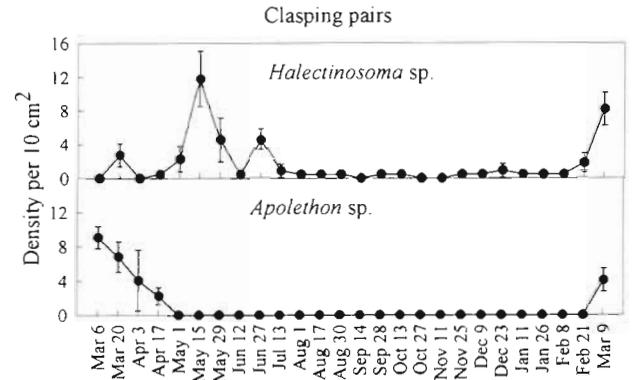


Fig. 5. Density (average \pm 1 standard error) of claspings pairs of 2 species of harpacticoid copepods at the 0 m intertidal height

in densities between those 2 studies may be partially explained by the sampling method employed. McGregor (1991) sampled the upper 5 cm of the sediment

Table 4. Summary of density ranges with ± 1 standard error (in some studies) of meiofauna taxa per 10 cm² from studies in the Alaskan mudflats. NE: not examined

Citation	Area	Meiofauna	Nematodes	Copepods	Nauplii
McGregor (1991) ^a	Auke Bay	1525 \pm 191 to 7043 \pm 699	857 \pm 299 to 2496 \pm 686	218 \pm 5 to 2573 \pm 251	<50 ^c to 2684 \pm 638
Cordell (1986) ^b	Auke Bay (Spuhn Is.)	NE	NE	49800 to 478800	NE
Fleeger et al (1989)	Auke Bay (subtidal)	2600 to 5400	2546 to 5339	NE	NE
Feder & Paul (1980)	Port Valdez	442 to 4682	307 to 3426	26 to 1248	NE
This study ^a	Auke Bay	693 \pm 176 to 1939 \pm 105	408 \pm 61 to 1703 \pm 82	105 \pm 31 to 460 \pm 14	83 \pm 5 to 764 \pm 82

^aSamples were collected from the same intertidal mudflat. ^bDensities were calculated per 10 m³ ^cExtrapolation from graph

while we sampled only the upper 2 cm of the sediment. Nematodes, which can inhabit deeper layers of sediment (Carman et al. 1987, Heldelberg & Jensen 1993), may contribute to density differences found in these 2 studies. Another possible source of the differences in meiofaunal densities is that interannual variability can be greater than seasonal variability (Coull 1985).

On a nearby intertidal site in Auke Bay, Cordell (1986) reported that harpacticoid copepods were the most abundant taxon, followed by nematodes and ostracods. However, Cordell sampled only the epibenthic fauna with a diver-operated suction pump during high tides. If his sampling techniques were biased towards the surface fauna, copepods would be expected to be the predominant faunal group since harpacticoid copepods are more abundant at the sediment-water interface.

Copepod nauplii were present throughout the year but were most abundant from December to April. Similarly, McGregor (1991) found that copepod nauplii attained highest densities in April of 1987 and 1988 but declined subsequently. In both McGregor's and our study the majority of harpacticoid nauplii and copepodites were found during late winter and early spring, when nutrients in the Auke Bay water-column are in low concentrations (Zeimann et al. 1990). Densities of nauplii decreased sharply during March and April of 1992 (Fig. 1), prior to the initiation of the spring diatom bloom in Auke Bay. Perhaps intertidal benthic primary production is uncoupled from water column production or begins earlier in the year. Although nauplii were not identified to species, density maxima of nauplii co-occurred with density maxima of ovigerous females of the 6 most abundant copepods. In every sample, more than 85% of the copepods were these 6 species, so it is reasonable to assume that the majority of nauplii belong to these 6 species as well.

On all sampling dates, there were more adults than copepodites. A similar numerical predominance of adult harpacticoids over copepodites was observed at

the same site in Auke Bay, during 1987-88 (McGregor 1991). The duration of the life history stages of harpacticoid copepods increases during later stages (Fleeger 1979), so the duration of the adult stage of a harpacticoid copepod is considerably longer than the copepodite and naupliar stages (Hicks & Coull 1983). Therefore, the numerically predominant adults probably represent several cohorts, whereas the copepodites represent but 1 cohort.

Halectinosoma sp. and *Amphiascooides dimorphus* numerically dominated the harpacticoid assemblage at our sampling site. These species were also the numerically most abundant copepods in the same site in a prior study (McCall 1992). Harpacticoid communities of intertidal mudflats are typically dominated by one or only a few copepod species (Coull & Fleeger 1977, Feder & Paul 1980, Fleeger 1980, 1985), with the species of the genus *Halectinosoma* commonly being the predominant copepods (Hicks & Coull 1983).

Five of the 6 species (all except *Apolethon* sp.) bred continuously (sensu Hicks & Coull 1983) throughout the sampling period, although all of the species had periods of increased reproductive activity through winter and early spring. In a temperate situation, Coull & Vernberg (1975) reported temporal separation of reproductive activities of taxonomically related harpacticoid copepods in a South Carolina mudflat and suggested the de facto result may be resource partitioning. Additional studies are required to determine if resources are limited in Auke Bay. *Microarthridion* cf. *littorale* was the only species that might have had multivoltine reproduction (several generations per year), with 2 distinct density maxima of ovigerous females (August, and November through March). *M. littorale* is cosmopolitan and exhibits different modes of reproduction in different habitats (Fleeger 1979, Palmer 1980). We observed multivoltine reproduction in laboratory cultures of *M. cf. littorale*, whose females extruded 2 egg clutches 1 mo apart. Interestingly, in South Carolina, *M. littorale* reproduces continuously

subtidally (Coull & Vernberg 1975) but shows discrete reproduction events intertidally (Fleeger 1979). However, interannual variability of copepod reproduction may occur, since Palmer (1980) collected *M. littorale* ovigerous females throughout a different year both intertidally and subtidally from a nearby site in South Carolina.

Temporal separation existed in the peak densities of the copepodites of all 6 species. The majority of harpacticoid copepodites collected in this study belonged to *Microarthridion* cf. *littorale*. Higher survival rates of the juvenile stages of *M. cf. littorale* may be attributed to the absence of interspecific competition created by the almost complete temporal separation of its copepodites (summer) from the copepodites of all other copepod species. In contrast, copepodites of *Stenhelia* (*S.*) *peniculata* occur primarily in winter, and the majority of copepodites of *Halectinosoma* sp., *Amphiascoides dimorphus*, and *Apolethon* sp. occur in the spring but have the highest density in different months. Different rates of development may be a factor controlling temporal separation of the copepodites of the different species; additional factors are likely. At the same Auke Bay intertidal site sampled in the present study, juvenile flatfish (especially starry flounder *Platichthys stellatus*) preyed primarily on harpacticoid copepods (McGregor 1991, McCall 1992), especially on male *M. cf. littorale*. Although McCall (1992) concluded that starry flounder predation did not reduce copepod abundances in this intertidal beach, the contribution of other predators (e.g. juvenile salmon and invertebrates) on the population dynamics of harpacticoids is unknown. Since ovigerous females of the predominant copepods (except *Apolethon* sp.) are present in almost all the samples, species preference of predators (McCall 1992) and/or periodic feeding pressure by different predators on the copepods (Morris & Coull 1992) may explain the differences in abundance of copepodites of different species at particular times of the year.

Temperature may trigger or terminate reproductive activities of copepods (Harris 1972) and determine the development time of copepods. Generally, higher ambient temperatures result in shorter development times for harpacticoid copepods; however, few data are available for development time of harpacticoid copepods in temperatures as cold as the ambient temperatures of Auke Bay. The embryonic, naupliar and juvenile development of copepods occurs from November to April (water temperature varies between 0 and 5°C) whereas in most temperate situations, peak egg production is in the spring and early summer (Hicks & Coull 1983). The lowest temperature recorded for successful culture of a harpacticoid copepod (*Canthocamptus staphylinus*) through a complete life cycle

was 1.7°C (Sarvala 1979). The development time of *C. staphylinus* from egg to copepodite I was 110 d and from egg to adult female about 214 d (Sarvala 1979). The development times at 8°C from egg to copepodite stage I and from egg to ovigerous female of a Washington state, USA, population of *Huntemannia jadensis* (a species present in our samples) were 38 and 95 d, respectively, but development ceased at 4°C (Feller 1980a). Developmental times for *Tachidius discipes*, *Paronychocamptus nanus*, and *Nitocra typica* at 5°C were 83, >105, and >105 d, respectively (Heip & Smol 1976). In our samples, the presence of *Stenhelia* (*S.*) *peniculata* copepodites in December implies a long embryonic and naupliar development time (approximately a year) because peak egg production is 1 mo earlier. This is the longest development time reported for a harpacticoid copepod.

Isocommunity (sensu Por 1964) of harpacticoid assemblages in similar habitats is well established (Soyer 1971, Hicks & Coull 1983, Hall & Bell 1993). Generally, the harpacticoid fauna of our study site were no exception. Epibenthic and burrowing harpacticoids are the usual inhabitants of shallow mud substrates (Hicks & Coull 1983). *Apolethon* sp. and *Stenhelia* (*S.*) *peniculata* can be classified as burrowing copepods (authors' pers. obs.), *Microarthridion* cf. *littorale* is regarded as a surface dweller or epibenthic, and the 3 species of Ectinosomatidae and *Amphiascoides dimorphus* are both burrowing and epibenthic copepods. All 6 numerically predominant copepods (except *Mesochra* sp.) belong to genera of copepods typically encountered in muddy substrates (Hicks & Coull 1983).

Is the reproductive pattern of intertidal harpacticoid copepods in Auke Bay typical of other high latitude sites? The peak egg production of the majority of copepod species in this subarctic situation occurred over the winter and during early spring. *Microarthridion* cf. *littorale* was the only species with ovigerous females in relatively high abundance during the summer months. All other species seemed to 'avoid' reproduction in the summer and were found mostly as non-reproductive adults. In Port Valdez, Alaska, *Harpacticus uniremis* ovigerous females were also collected during December to April (Jewett & Feder 1977). Feller (1980b) studied the life history of *Huntemannia jadensis* in Puget Sound, Washington, where the majority of ovigerous females occurred during approximately the same period of time (December to April). Similar patterns have been observed in high latitude European sites where copepod reproduction occurs in early spring and non-reproductive adults dominate the harpacticoid assemblage during the summer (Barnett 1970, Lasker et al. 1970). This phenomenon may not be representative of other meiofaunal taxa in high latitude

sites. As an example, many nematodes seem to reproduce throughout the year, although some species have ovigerous females mainly during the spring and summer months (Heip et al. 1985). Light limitation governing food resources may be the underlying factor of the spring peak reproduction activity of the harpacticoid copepods in southeast Alaska as well as in the other high latitude sites. During spring, algae in the form of settled phytodetritus or sediment-dwelling flora are plentiful in Auke Bay and may enhance development of copepods. Also, the food requirements of harpacticoid nauplii are probably different than those of adult copepods (Decho & Fleeger 1988). Perhaps the species composition of phytobenthos in Auke Bay shifts from spring to summer to kinds that can be consumed directly only by adult copepods.

Significant intra-annual changes of meiofaunal densities were observed in the present study. Peak densities of copepodites of different species were temporally partitioned, although peak egg production of the harpacticoid copepod species examined was synchronous. Without species-level identification, no apparent life history patterns would have been observed. Meiofauna densities reported in this study are similar to those reported from intertidal muds of the world (Coull 1988). Clear seasonal patterns were not obvious overall, consistent with previous intertidal studies in southeast Alaska. How much of the density variability of meiofauna seen can be attributed to spatial variability? Only a more intensive study, in terms of time and resources, could properly address this question.

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