17. Summer Distribution and Abundance of Macrozooplankton in the Western Gulf of Alaska and Southeastern Bering Sea

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Abstract

The summer distribution and abundance of macrozooplankton collected with a 5 m^2 mouth-opening rigid frame trawl on the continental shelf of the Gulf of Alaska and the Bering Sea were analyzed. A total of 33 species was collected during a single cruise in the Gulf of Alaska during 1991, and 46 species were collected during two cruises in the Bering Sea in 1995 and 1996. Euphausiids dominated both the numeric and wet weight biomass fractions for all cruises, and were a larger fraction of the total biomass in the Gulf of Alaska than in the Bering Sea. Macrozooplankton densities of night samples were significantly higher than those of day samples. This difference is thought to be caused by diel migration of zooplankton, mainly euphausiids, from below the deepest daytime sample depth. Cross-shelf habitat segregation between congeneric species was observed in both regions. *Thysanoessa inermis* and *Themisto pacifica* were found at stations near the continental slope, and *Thysanoessa raschii* and *Themisto libellula* were distributed on the mid-continental shelf.

Introduction

Predation and starvation are considered to be the major causes of larval fish mortality, and macrozooplankton (2-20 mm) are predators, prey, and competitors of larval and juvenile fish. Carnivorous macrozooplankton, (e.g., cnidarians, chaetognaths, euphausiids, mysids and pelagic amphipods) are abundant in the ocean, and are known to consume fish larvae (von Westernhagen and Rosenthal, 1976; Purcell, 1985; Bailey et al., 1992; Alvarez-Cadena, 1993). Predation on eggs and fish larvae is dependent on both spatial and temporal overlap of predators and prey (Bailey and Houde, 1989), therefore research on distribution pattern of macrozooplankton is a requisite to understanding predator-prey interactions. Since many macrozooplankton are also known to consume some of the same foods as fish larvae, competition for food will affect larval survival when food is a limiting resource. Thus, the trophic interrelationship between larval fish and macrozooplankton may affect the mortality of early life stages of fish.

The continental shelf regions of the Bering Sea and Subarctic Pacific Ocean are highly productive (reviewed by Hobson, 1980). Secondary production in these areas is utilized by many species of fish, including walleye pollock (*Theragra chalcogramma*), a dominant fish species in North Pacific. Macrozooplankton are important not only as food for adult pollock, but also serve prey for juvenile pollock in both the Gulf of Alaska and Bering Sea (Brodeur, 1998; Brodeur et al., MS). Although some groups of macro-zooplankton, such as euphausiids, amphipods and jellyfish are known predators of egg and larval stages of walleye pollock (Bailey and Stehr, 1986; Bailey et al., 1992), juvenile pollock are too large to be eaten by most macrozooplankton, and these may be considered as potential competitors of juvenile pollock.

Although some previous studies have examined the abundance and distribution patterns of mesozooplankton (0.2-2.0mm) collected with fine mesh (0.15-0.50mm) plankton nets in the Bering Sea and northern Gulf of Alaska (Motoda and Minoda, 1974; Cooney ,1981, 1986; Cooney and Coyle, 1982; Smith and Vidal, 1986; Coyle et al., 1996; Lee, 1996; Napp et al., 1996; Incze et al., 1997), there are fewer data on areal distribution and abundance of large macrozooplankton, despite their critical importance to the ecosystem. Studies that do exist tend to concentrate on only one or two major taxa (e.g. Nemoto, 1962; Kotori, 1976; Fukuchi, 1977; Smith, 1991) and do not examine the entire macrozooplankton community. A recommendation put forth by a recent U.S. National Research Council study of the Bering Sea was that more studies of the geographic and spatial distributions of macrozooplankton be undertaken to understand their importance to higher trophic levels in the ecosystem (National Research Council, 1996).

As a part of interdisciplinary Fisheries Oceanography Coordinated Investigations (FOCI) program investigating biotic and abiotic influences on the early life history of walleye pollock sampling cruises were conducted for late larval and early juvenile pollock using large plankton/micronekton nets in both western Gulf of Alaska and southeastern Bering Sea. Although the sampling scheme was designed to collect juvenile fishes, many zooplankton taxa were collected during these survey. In this paper, we present data on the summer distribution, abundance, and biomass patterns of the major macrozooplankton groups quantitatively retained by this sampler.

Materials and Methods

Zooplankton sampling was conducted in 1991 at 60 sampling stations in the Gulf of Alaska aboard the NOAA ship *Miller Freeman*, and at 30 (1995) and 24 (1996) stations in the Bering Sea aboard the Hokkaido University research vessel *Oshoro-maru*. Macrozooplankton were collected using 5 m^2 rigid frame trawl (Methot 1986) with a 2x3 mm oval mesh in the body of net and a 1 mm mesh in the codend on the Miller Freeman cruise (23-31 July, 1991). A similar 5 m^2 frame trawl designed by Hokkaido University equipped with the same net was used during the two *Oshoro-maru* cruises (19-24 and 31 July, 1995 and 21-26 July, 1996). All tows were made at an average ship speed of $6km.h^{-1}$ in a oblique pattern from surface to within 10 m of the bottom (maximum 220 m in the Gulf of Alaska, and 114 m in the Bering Sea). Net depth was monitored using an acoustic netsonde. A calibrated flow meters was suspended within the mouth of the net to estimate the filtered volume of water.

Following net retrieval, large jellies were removed from the codend and were not included in this study. The remaining samples were preserved in a 5 % buffered formalin/seawater solution following net recovery. The macrozooplankton (> 2 mm in maximum dimension) were sorted to major taxonomic categories (euphausiids, amphipods, chaetognaths, mysids, and cnidarians) at the Polish Plankton Sorting and Identification Center in Szczecin, Poland, and were later identified to species in the author's laboratory. Siphonophores and ctenophores were also sorted from the samples, but both the number of species and the overall abundance of these groups were low so they were not included our analysis. After identification, subsamples of each taxon were weighed to the nearest milligram to estimate preserved wet weight. All densities and biomasses were expressed as number or grams per 10 m^2 sea surface area.

Results

Western Gulf of Alaska

1. Zooplankton Densities, Biomass and Species Composition

The highest density and biomass number or grams per 10 m^2 sea surface area stations were located near Shumagin and Semidi Islands (Fig. 1). The zooplankton densities and biomass of nighttime collections were significantly higher than those of the surrounding daytime collections (Mann-Whitney test, N= 60, P< 0.01), and consisted almost entirely of euphausiids (Fig. 2).

A total of 32 macrozooplankton taxa occurred in our samples (Table 1), totalling 351607 individuals and 15250.570 g wet weight. Euphausiids made up 93% by number and 92 % of the total macrozooplankton biomass in the Gulf of Alaska collections (Fig. 3). Based on ranked abundance, 4 of the 6 most dominant taxa were euphausiid species (Table 2).

2. Euphausiacea

Thysanoessa inermis was predominant among the 7 euphausiid species collected and it occurred at all stations. The stations with high densities (>10,000 ind./10 m^2) of *T. inermis* were located just west of Shumagin Islands (Fig. 4a). The wet weight of *T. inermis* individuals at each station ranged from 5-88 mg/ind. The average weights were large (> 70 mg) at the stations around Chirikof Island and the Semidi Islands except for one station near Unimak Island. *Euphausia pacifica, T. raschii* and *T. spinifera* were the other abundant euphausiids caught. *Thysanoessa raschii* tended to found be at stations close to the Alaska Peninsula, while *T. spinifera* and *E. pacifica* were comparatively more abundant at the outer shelf stations (Fig. 4). Significant diel differences (nighttime > daytime) were observed in densities of euphausiids (Mann-Whitney test, N= 60, P< 0.01)

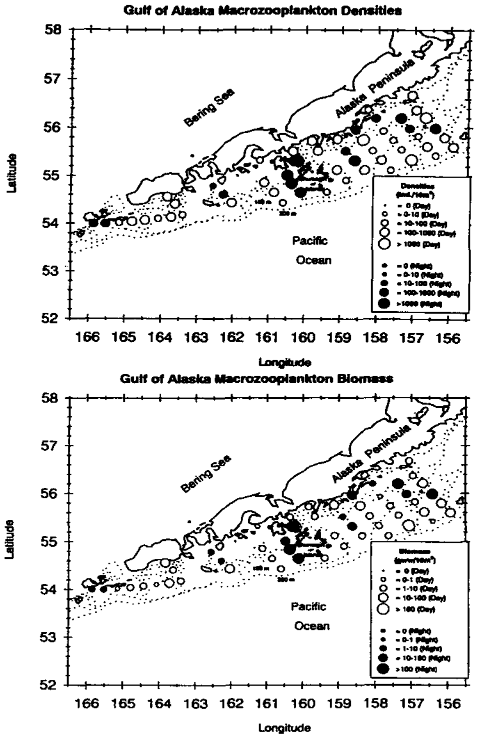

Fig. 1. Densities (top) and biomass (Bottom) of total macrozooplankton collected in July 1991, in the Gulf of Alaska.The size of the circle reflects the relative densities at each station. Open circles indicate day sampling and solid circles indicate nighttime sampling.

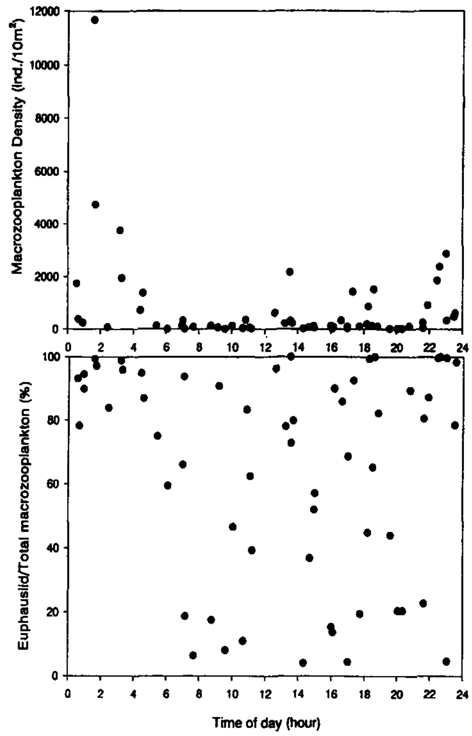

Fig. 2. Diel variation in total macrozoo – plankton density (top) and percentage of the total catch made up of euphausiids (bottom) in the Gulf of Alaska.Time of sunrise was approximately 0630 Alaska Daylight Time (ADT)and sunset was 2230 ADT.

3. *Amphipoda*

Seven hyperiid species were collected. *Hyperia spinigera* were collected at 24 out of 60 stations. *Primno macropa* was also common in the Gulf of Alaska collections. The densities of hyperiid, however, were always less than 10 ind./10 m^2. Although at least 5 taxa of gammarids occurred in our samples, none was among the dominant taxa collected.

4. *Cnidaria*

Among the 9 taxa of small cnidarians collected, *Aglantha digitale* was the most abundant species, and occurred in higher densities at the stations west of 160°W, relative to the stations east of 160°W (Fig. 5a). *Clytia gregaria* and *Aequorea* sp. were also among the 10 most dominant taxa (Table 2).

Table .1. Macrozooplankton taxa collected in Gulf of Alaska and the Bering Sea.

Gulf of Alaska (1991)	**Bering Sea (1995)**	**Bering Sea (1996)**
CNIDARIA		
Hydrozoa		
Aequorea forskalea	*Aequorea forskalea*	*Aequorea forskalea*
Aglantha digitale	*Aglantha digitale*	*Aglantha digitale*
Bougainvillia principis	*Catablema* sp.	*Bougainvillia principis*
Catablema sp.	*Clytia gregaria*	*Eutonia indicans*
Clytia gregaria	*Sarsia* sp.	*Catablema* sp.
Sarsia sp.	*Staurophora mertensii*	*Clytia gregaria*
Staurophora mertensii	*Stomatoca atra*	*Neoturris breviconis*
Stomatoca atra		*Sarsia* sp.
Scyphozoa		
Chrysaora melanaster	*Chrysaora melanaster*	*Chrysaora melanaster*
CHAETOGNATHA		
Sagitta elegans	*Eukrohnia hamata*	*Eukrohnia hamata*
Sagitta scrippsae	*Sagitta elegans*	*Sagitta elegans*
ARTHROPODA		
Mysidacea		
Holmesiella anomala	*Neomysis rayii*	*Neomysis rayii*
Pacificanthomysis nephrophthalma	*Pacificanthomysis nephrophthalma*	*Meterythrops microphthalma*
	Pseudomma truncatum	*Pacificanthomysis nephrophthalma*
	Xenacanthomysis pseudomacropus	
Amphipoda (Gammaridea)		
Anonyx sp.	*Anonyx* sp.	*Anonyx* sp.
Cyphocaris challengeri	*Bathymedon* sp.	*Byblis* sp.
Eusirus cuspidarus	*Byblis* sp.	*Metopa* sp.
Gammarus sp.	*Cleonardo* sp.	
Jassa sp.	*Erichthonius* sp.	
	Metopa sp.	
	Monoculodes sp.	
	Stegocephalus inflatus	
	Pontoporeia femorata	
Amphipoda (Hyperiidea)		
Hyperia medusarum	*Hyperia medusarum*	*Hyperia medusarum*
Hyperia spinigera	*Hyperia spinigera*	*Hyperia spinigera*
Hyperoche medusarum	*Hyperoche medusarum*	*Hyperoche medusarum*
Paraphronima crassipes	*Primno macropa*	*Lanceola sayana*
Primno macropa	*Phronima colletti*	*Paraphronima crassipes*
Themisto libellula	*Themisto libellula*	*Themisto libellula*
Themisto pacifica	*Themisto pacifica*	*Themisto pacifica*
Euphausiacea		
Euphausia pacifica	*Euphausia pacifica*	*Euphausia pacifica*
Tessarabrachion oculatus	*Thysanoessa inermis*	*Thysanoessa inermis*
Thysanoessa inermis	*Thysanoessa longipes*	*Thysanoessa inspinata*
Thysanoessa inspinata	*Thysanoessa raschii*	*Thysanoessa longipes*
Thysanoessa longipes	*Thysanoessa spinifera*	*Thysanoessa raschii*
Thysanoessa raschii		*Thysanoessa spinifera*
Thysanoessa spinifera		

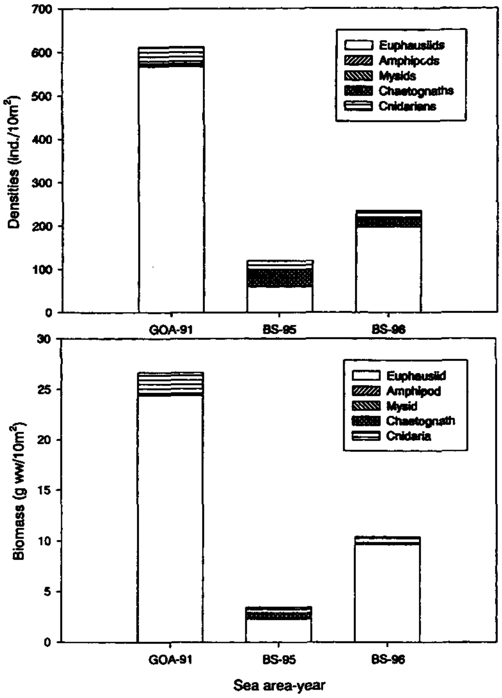

Fig. 3 Composition of macrozooplankton densities (top) and biomass (bottom) by major taxa.

Table. 2. Ranking of the 10 most dominant taxa by mean density(No./10m²)collected in the Gulf of Alaska and Bering Sea for each cruise. Also given are the percent occurrence and percent of total macrozooplankton density.

Gulf of Alaska (1991)

Rank	Species	Percent occurrence	Density (No./10 m²) Mean	Density (No./10 m²) Range	Percent of Total Density
1	*Thysanoessa inermis*	100.00	479.83	0.73-10242.97	78.40
2	*Thysanoessa spinifera*	61.67	28.59	0.07-596.95	4.67
3	*Aglantha digitale*	75.00	19.08	0.21-316.09	3.12
4	*Euphausia pacifica*	38.33	10.51	0.11-337.51	1.72
5	*Sagitta elegans*	50.00	6.09	0.16-144.85	0.99
6	*Clytia gregaria*	51.67	1.79	0.18-18.11	0.29
7	*Aequorea forskalea*	65.00	1.73	0.09-8.17	0.28
8	*Thysanoessa raschii*	30.00	1.41	0.05-67.90	0.23
9	*Primno macropa*	16.67	0.21	0.10-6.70	0.03
10	*Hyperia spinigera*	40.00	0.11	0.04-0.63	0.02

Bering Sea (1995)

Rank	Species	Percent occurrence	Density (No./1000m³) Mean	Density (No./1000m³) Range	Percent of Total Density
1	*Thysanoessa raschii*	73.30	37.07	0.04-400.86	30.98
2	*Sagitta elegans*	96.67	34.99	0.08-246.13	29.24
3	*Aglantha digitale*	83.33	9.62	0.18-109.97	8.04
4	*Thysanoessa inermis*	70.00	8.60	0.04-50.88	7.19
5	*Themisto libellula*	36.67	2.35	0.04-38.20	1.97
6	*Aequorea forskalea*	26.67	0.85	0.23-17.54	0.71
7	*Thysanoessa longipes*	20.00	0.61	0.25-13.16	0.51
8	*Clytia gregaria*	26.67	0.32	0.20-7.32	0.26
9	*Hyperia medusarum*	56.67	0.11	0.05-1.16	0.09
10	*Themisto pacifica*	43.33	0.09	0.04-1.17	0.08

Bering Sea (1996)

Rank	Species	Percent occurrence	Density (No./10 m²) Mean	Density (No./10 m²) Range	Percent of Total Density
1	*Thysanoessa inermis*	87.50	99.08	0.08-1407.44	42.22
2	*Thysanoessa raschii*	70.80	36.34	0.16-377.48	15.49
3	*Thysanoessa longipes*	37.50	17.25	0.08-271.61	7.35
4	*Sagitta elegans*	91.67	14.89	0.09-74.41	6.34
5	*Thysanoessa spinifera*	33.33	8.54	0.16-107.07	3.64
6	*Euphausia pacifica*	25.00	7.03	0.50-139.92	2.99
7	*Aglantha digitale*	83.33	3.86	0.17-27.06	1.64
8	*Sarsia* sp.	70.83	3.47	0.21-26.19	1.48
9	*Clytia gregaria*	41.67	0.93	0.11-10.94	0.40
10	*Themisto libellula*	29.17	0.39	0.08-3.83	0.17

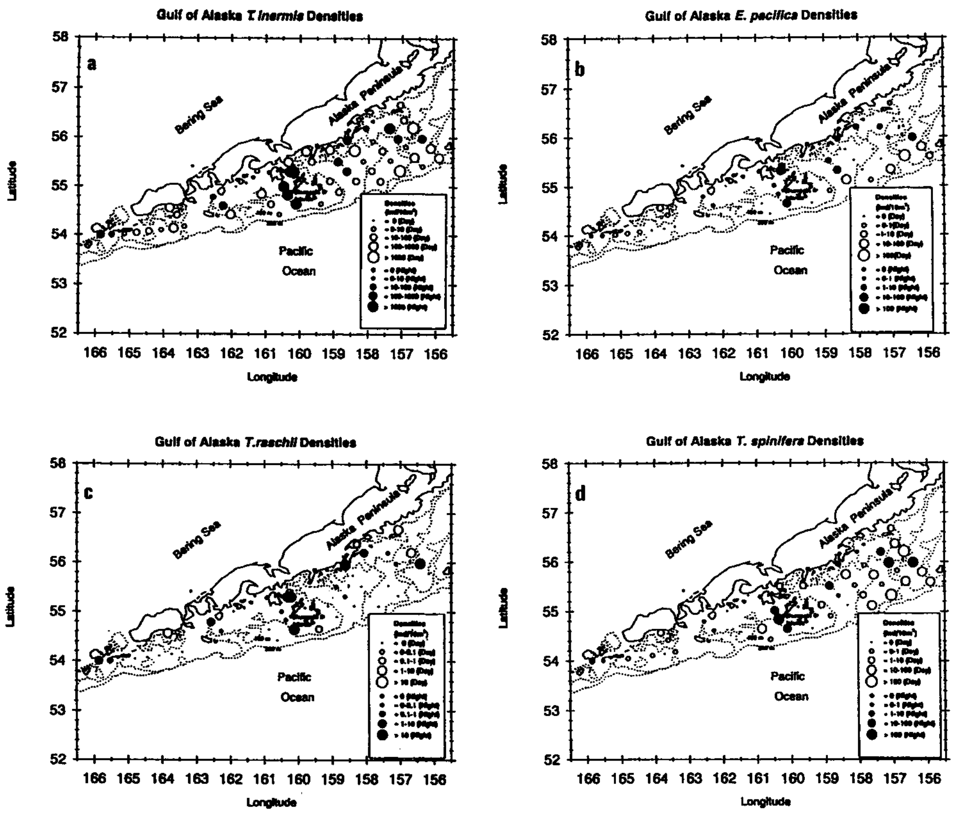

Fig. 4. Densities of Euphausiacea, *Thysanoessa inermis* (a), *Euphausia pacifica* (b), *Thysanoessa raschii* (c), and *Thysanoessa spinifera* (d) collected in July 1991, in the Gulf of Alaska. Symbols are as in Fig. 1.

5. Chaetognatha

The vast majority of chaetognaths collected were *Sagitta elegans,* with only 1 specimen of *S. scrippssae* identified. Most *S. elegans* were found at stations east of 160°W (Fig. 5b).

6. Mysidacea

Only 3 species of Mysids occurred in our Gulf of Alaska samples. They were not a dominant component of the collections and none was among the 10 most dominant species in the Gulf of Alaska.

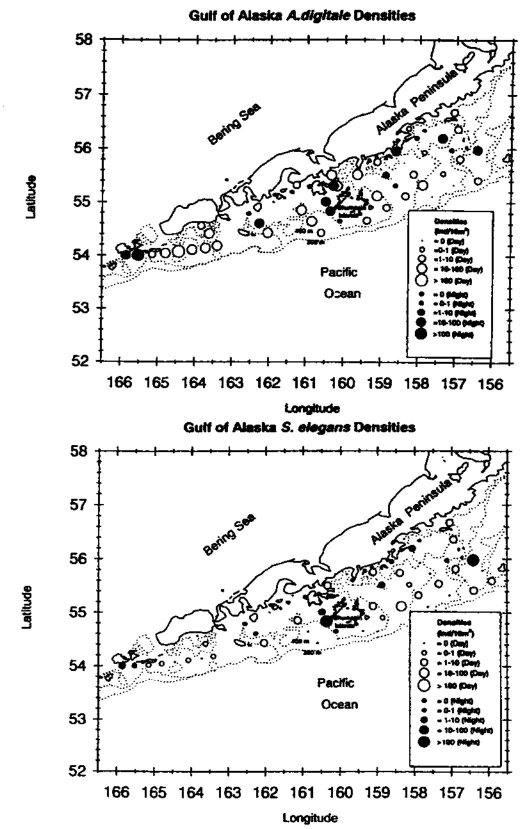

Fig. 5. Densities of geratinous zooplankton, *Aglantha digitale* (top) and *Sagitta elegans* (bottom) collected in July 1991, in the Gulf of Alaska. Symbols are as in Fig. 1.

Southeastern Bering Sea

1. Zooplankton Densities, Biomass and Species Composition

High density (> 500ind./10m^2) of zooplankton were located north of Pribilof Islands and north of Unimak Island in 1995, and were located near Pribilof Islands and eastern stations in 1996. Zooplankton densities and biomass from nighttime collections were significantly higher than those of surrounding daytime sampling stations (Mann-Whitney test, N= 30, P< 0.02 1995; N= 24, P<0.05 1996) and the majority of the catch at night was euphausiids (Figs. 6 and 7). Densities and biomass of macrozooplankton in the Bering Sea were generally less than those in the Gulf of Alaska (Figs. 3 and 8). The density exceeded 1000ind./10m2 at only 1 station (Fig. 8).

A total of 35 and 30 taxa were collected in 1995 and 1996 (Table 1). Compared to

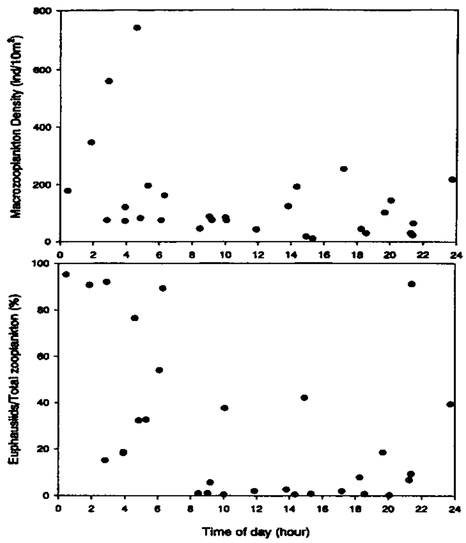

Fig. 6. Diel variation in total macrozooplankton density (top) and percentage of the total catch made up by euphausiids (bottom) in the 1995 Bering Sea samples. Time of sunrise was approximately 0550 ADT and sunset was 2230 ADT.

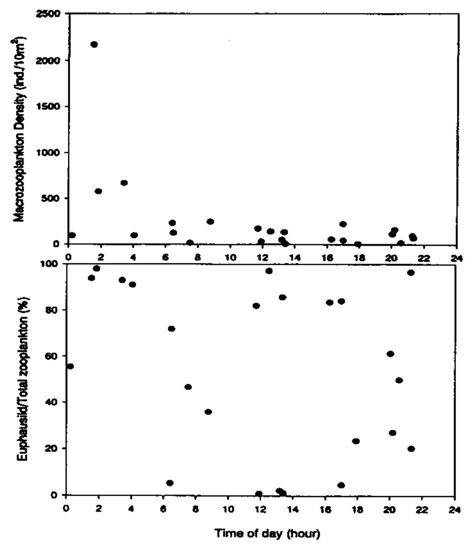

Fig. 7. Diel variation in total macrozooplankton density (top) and percentage of the total catch made up by euphausiids (bottom) in the 1996 Bering Sea samples. Time of sunrise was approximately 0550 ADT and sunset was 2230 ADT.

the Gulf of Alaska, the ratio of biomass of euphausiids to total biomass was low in both years. The densities (45 % in total number) and biomass (64 % in total wet weight) of euphausiids in 1995 were higher than those in 1996 (79.7% in total number and 90.7% in total wet weight; Fig. 3). *Thysanoessa inermis, T. raschii, Sagitta elegans* and *Aglantha digitale* were among the predominant species during both years (Table 2).

2. *Euphausiacea*

Thysanoessa raschii and *T. inermis* were among the dominant species collected (Table 2). *T. raschii* generally occurred at stations shallower than 100m depth, while *T. inermis* were found at deeper stations than *T. raschii,* but not at the deepest offshore stations (Fig. 9). Average wet weight of T. raschii in each stations ranged from 30 to 82 mg/ind. and 30 to 90 mg/ind. in 1995 and 1996, respectively, and those at the shallow stations were (< 100 m) were often > 70 mg/ind. In 1996, *T. spinifera, T. longipes* and *Euphausia pacifica* were also among the 10 most species and their densities exceeded 100 inds/10m^2 at 1 station (Table 2). Significant difference were detected in densities between day and night collections (Mann-Whitney test: 1995, N= 30, P< 0.01; 1996, N=24, P<0.01).

3. *Amphipoda*

Seven hyperiid and 9 species of gammariid taxa were collected in 1995, and 7 hyperiid and 4 gammariid taxa were collected in 1996 (Table 1). Densities of amphipods were not high in either year, although in 1995, *Themisto libellula* was the fifth most dominant

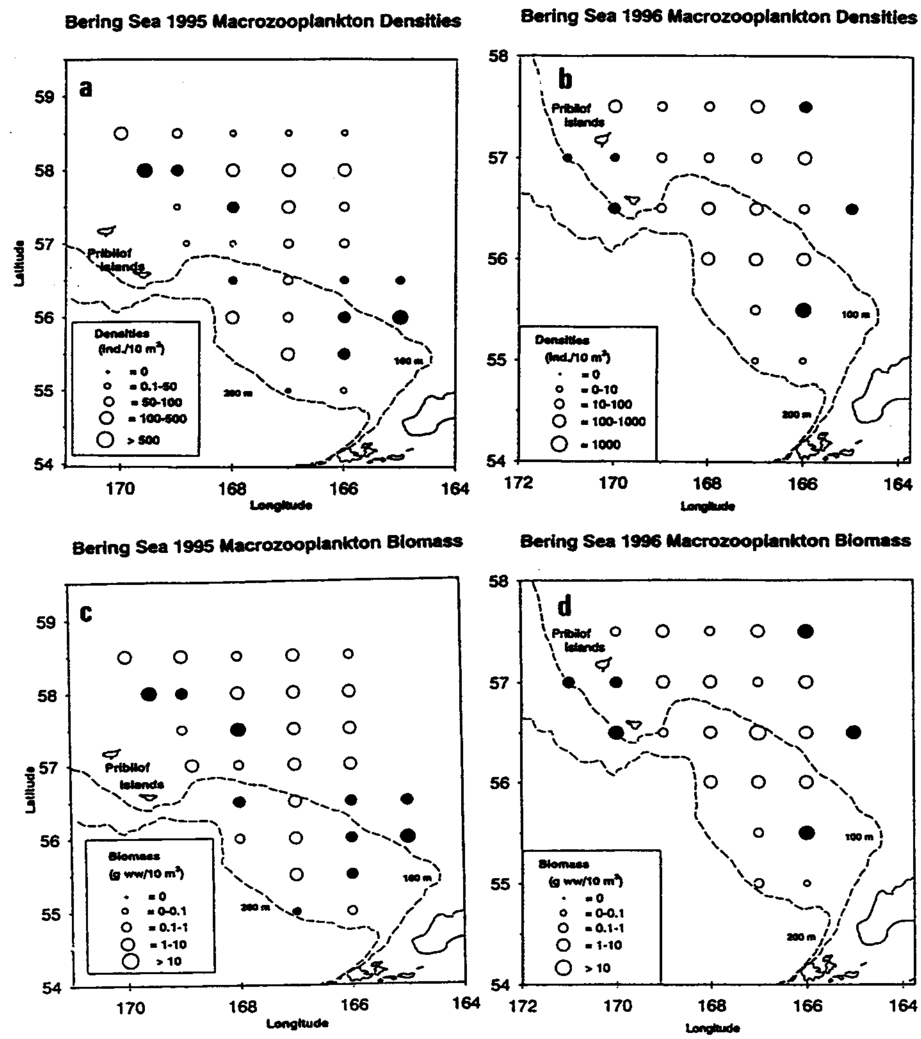

Fig.8. Densities(a,b)and biomass(c,d)of total macrozooplankton collected in July 1995(left) and 1996 (right),in the southeastern Bering Sea. Symbols are in Fig.1.

species collected (Table 2). Densities exceeded 10 ind./10m² at only 2 stations in 1995 and no stations in 1996. The habitat segregation between *T. pacifica* and *T. libellula* was pronounced; *T. pacifica* occurred at more offshore stations than *T. libellula* (Fig. 10) and they were never found to co-occur at the same station.

4. Cnidaria

Among the 8 (1995) and 6 (1996) species of cnidarians collected, *Aglantha digitale* was the most dominant species and occurred in both years in mean densities > 1 ind./10 m² (Table 2). Highest densities were found at the stations less than 100m in water depth (Fig. 11a).

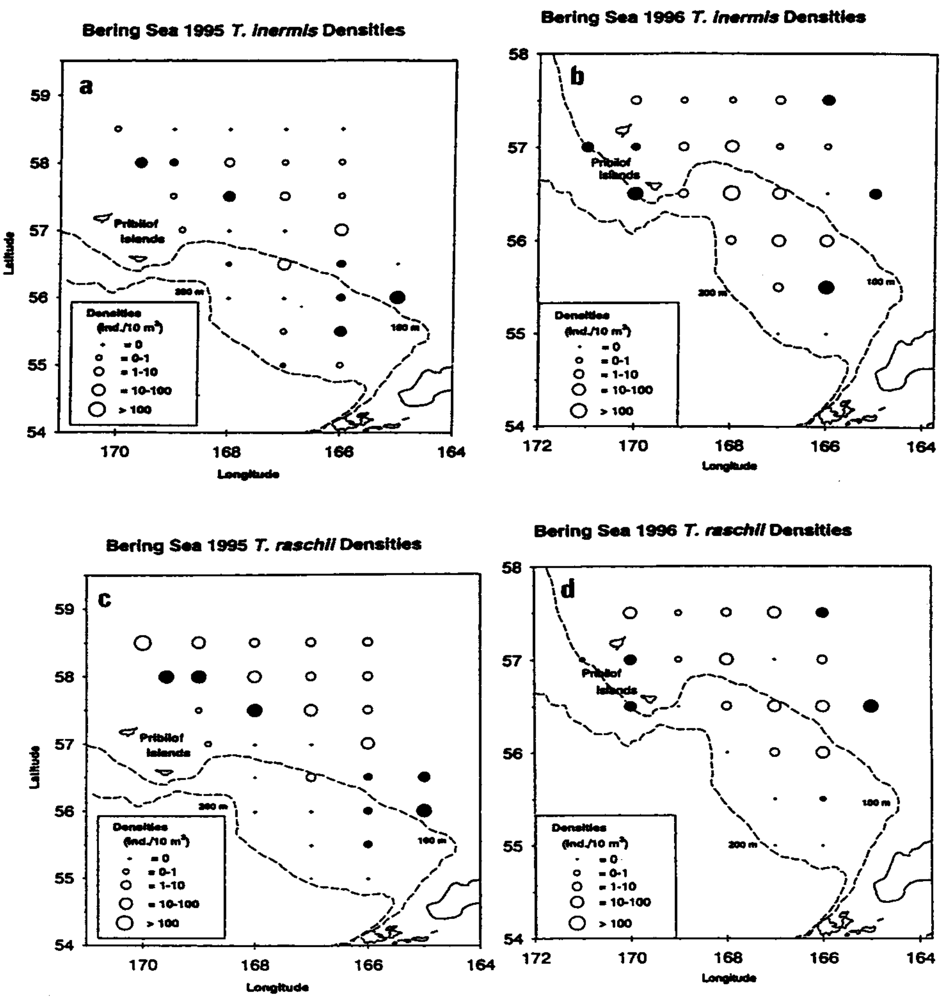

Fig. 9. Densities of *Thysanoessa inermis* (top) and *Thysanoessa raschii* (bottom) collected in July 1995 (left) and 1996 (right), in the southeastern Bering Sea. Symbols are as in Fig. 1.

5. Chaetognatha

Sagitta elegans and *Eukrohnia hamata* were collected in the Bering Sea, although *S. elegans* was by far the predominant chaetognath species collected, ranking second and fourth in total abundance during 1995 and 1996, respectively (Table 2). It also had the highest frequency of occurrence of any zooplankton taxa in both years (Table 2). Highest densities of *S. elegans* were found at the shallowest inner shelf stations in both years (Fig. 11b).

6. Mysidacea

Although 4 and 3 species of mysids were collected in 1995 and 1996, respectively,

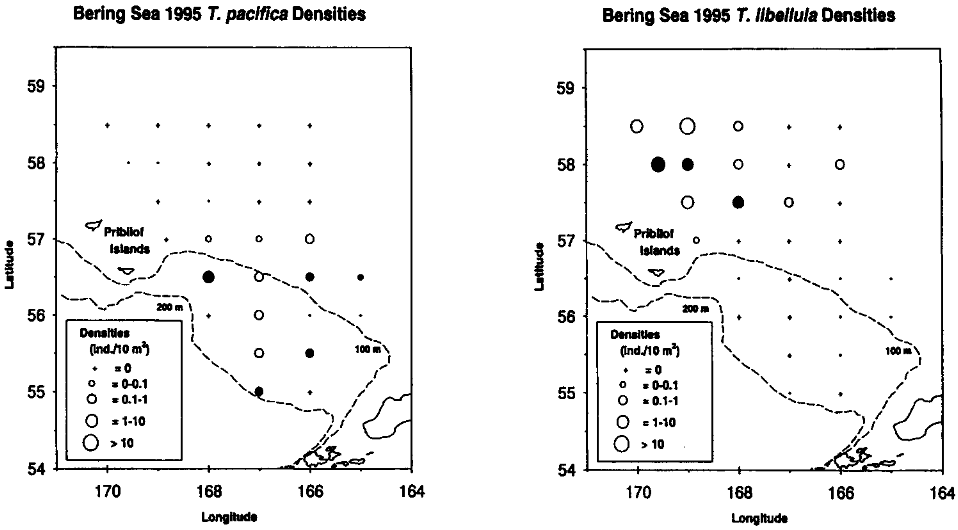

Fig.10. Densities of *Themisto pacifica* (left) and *Themisto libellula* (right) collected in July 1995 , in the southeastern Bering Sea. Symbols are as in Fig. 1.

they were not among the 10 most dominant taxa sampled (Table 2), although *Neomysis rayii* (1995) and *Pacificanthomysis nephrophthalma* (1996) were among the 12 most abundant species.

Discussion

Previous broad-scale regional studies in the Gulf of Alaska and Bering Sea which targeted mesozooplankton have also reported high densities of macrozooplankton. Since all of these studies used small mouthed, fine mesh nets (Omori, 1965; Cooney, 1981, 1986; Cooney and Coyle, 1982; Smith and Vidal, 1984, 1986; Vidal and Smith, 1986; Incze et al., 1997), copepods were usually the dominant taxa collected. Our maximum values of abundance and biomass of euphausiids were higher than the data of previous small mouthed, fine mesh net studies (Table 3), although our median values for the one species that occurred in more than half the samples (*Thysanoessa inermis*) were of similar magnitude in the Gulf of Alaska. Since most plankton nets are designed for collecting mesozooplankton (i.e., copepods), large plankton and micronekton may evade the mouth opening resulting in an underestimate of macrozooplankton biomass. Although most previous sampling strategies were not suitable for collecting euphausiids, they were often the second most abundant group after copepods in the Gulf of Alaska and the Bering Sea (Vidal and Smith, 1986; Incze et al., 1997). Since the trawl used in our study was designed to sample macrozooplankton and micronekton, the biomass estimates of adult euphausiids in this study,

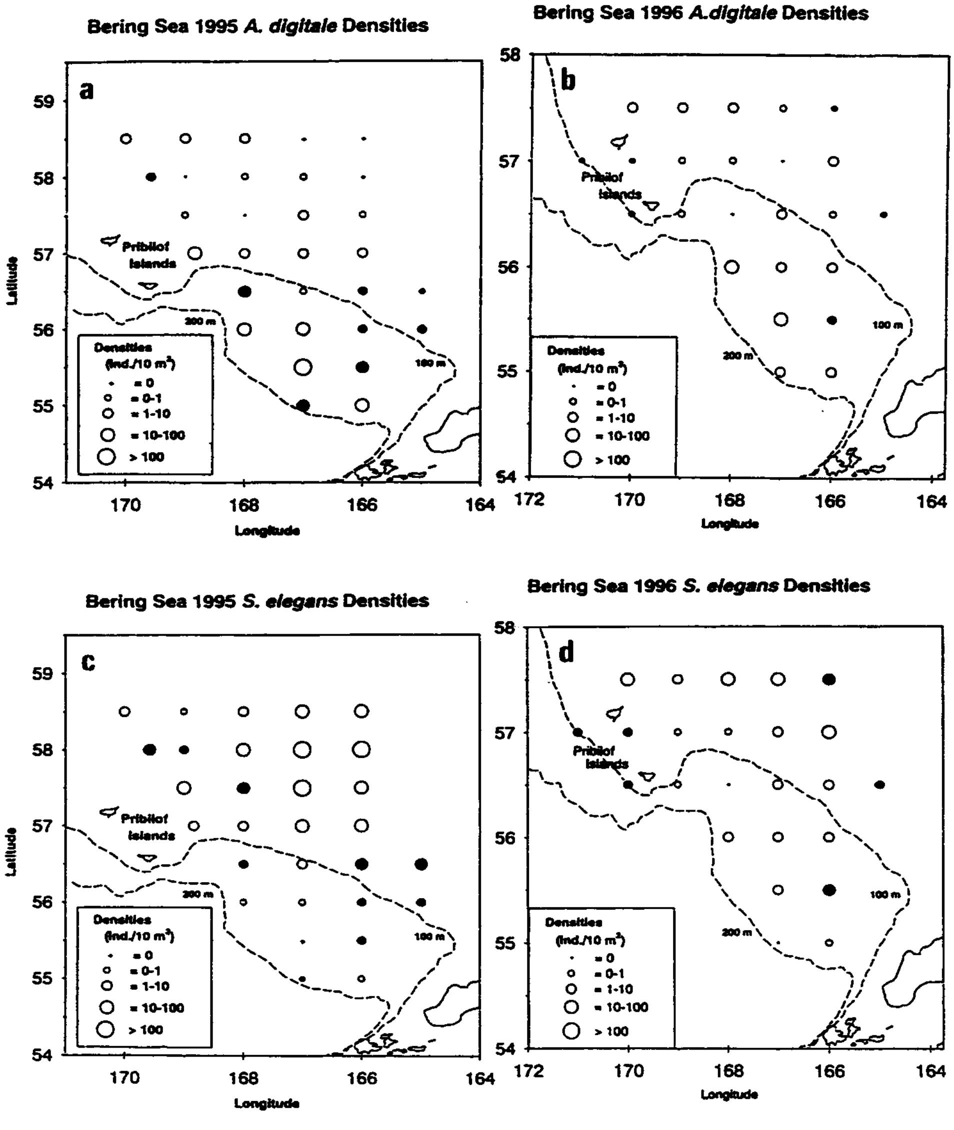

Fig. 11. Densities of *Aglantha digitale* (a, b) and *Sagitta elegans* (c, d) collected in July 1995 (left) and 1996 (right), in the southeastern Bering Sea. Symbols are as in Fig. 1.

especially at night, are thought to be more reliable, although many smaller macroplankton including juvenile euphausiids, amphipods, and chaetognaths may pass through the mesh. For example, Brodeur and Terazaki (MS) found that most juvenile *Sagitta elegans* and almost all specimens of the smaller chaetognath species, *Eukrohnia hamata,* were not retained by the Methot trawl relative to other finer mesh gear used at the same time.

Table.3. Comparison of densities and biomass of euphausiids between this study and previous fine mesh net collections made during summer in the western Gulf of Alaska and Bering Sea.

Northern Gulf of Alaska						
	Density range (ind/10m^2)					
	July 1991 (this study)		July 1985[1]		August 1986[1]	
species	Median	Range	Median	Range	Median	Range
Thysanoessa inermis	80	0-37382	65	0-444	492	26-3694
Thysanoessa spinifera	0.5	0-259	7	0-44	65	0-236
Thysanoessa raschii	0	0-124	0	0-7	0	0-50
Thysanoessa longipes	0	0-1	0	0-49	0	0
Euphausia pacifica	0	0-554	17	0-444	114	50-187
Thysanoessa inspinata	0	0-2	0	0-85	0	0-131
Tessarabrachion occulatus	0	0-1	0	0	0	0-13

Bering Sea					
	Biomass range (gww/10m^2)				
	July 1995 (this study)	July 1996 (this study)	June 1980[2]	June 1981[2]	July 1981[2]
Total euphausiid	0.003-33.951	0.001-90.200	10-17.5	1-12.5	10-25

[1]Incze et al. (1997): sampler were collected with bongo net (60cm mouth opening and 0.333mm mesh)

[2]Smith (1991): samples were collected with an opening/closing MOCNESS (0.149mm mesh)and dry weight data were converted to wet weight using the factor DW/WW = ca.0.2 (Parsons et al., 1984)

Although we found significant differences in the total macrozooplankton densities and euphausiid densities between day and night sampling, no significant differences were detected between day and night densities of other macrozooplankton. No significant diel differences in density or size frequency distribution were found in the early life stage of pollock in the Gulf of Alaska sampling (Brodeur et al., 1995), suggesting that these large fish were not able to avoid the mouth of the oncoming net. This implies that the diel difference in euphausiid catches was probably caused by daytime vertical migration below the depth of our sampling or some other behavioral trait that makes them less susceptible to capture by our gear during the day. Although little near-bottom sampling has occurred in the Bering Sea, underwater video observations made during 1995 have shown that high concentrations of euphausiids are found within 1-2 m of the bottom during daytime (Napp and Brodeur, unpublished).

In this study, habitat segregation between *Thysanoessa raschii* and *T. inermis* was observed. It has been previously shown that *Thysanoessa raschii* are distributed on the middle shelf and *T. inermis* are found over the outer shelf of the eastern Bering Sea (Fukuchi, 1977; Smith, 1991). Similarly, in this study, *Thysanoessa raschii* were distributed at shallow stations in the Gulf of Alaska. In the Bering Sea, *Thysanoessa raschii* tended to be distributed on the middle shelf, while *T. inermis* were distributed more offshore in the middle and outer shelf.

In the Gulf of Alaska, the habitat segregation between *Themisto pacifica* and *T. libellula* was not obvious since only a few *Themisto* were collected. The stations studied, however, were not thought to be within the main habitat of these species. On the other hand, these congeners were clearly segregated by habitat in the Bering Sea. There were no stations at which both species occurred. *Themisto pacifica* is known to be an oceanic species and reside over the basin and outer shelf, while *T. libellula* is known to be a species of middle-shelf and coastal communities in the Bering Sea (Fukuchi, 1977; Cooney, 1981). In plankton collections from the outer shelf region of southeastern Bering Sea near the Aleutian Islands, *Themisto pacifica* strongly dominated the amphipod catch (Sanger, 1974). In our study, *Themisto libellula* was distributed at northern shallow stations and *T. pacifica* occurred at southern stations over the outer shelf, which is in agreement with previous studies (Fukuchi, 1977).

Chaetognaths, primarily *Sagitta elegans*, and cnidarians, primarily *Aglantha digitale*, were very abundant in this study. Only few studies (Hamner, 1983; Incze et al., 1997; Brodeur and Terazaki, MS) have devoted attention to gelatinous zooplankton but these poorly-studied taxa represented a substantial portion of the macrozooplankton biomass in both regions. Although our densities of small cnidarians were similar to those from summer in situ observations (Hamner, 1983), our densities of chaetognaths were much lower than those reported from fine-mesh samplers collected from spring to autumn (Incze et al., 1997; Brodeur and Terazaki, MS). This implies that many chaetognaths passed through the mesh of the trawl used in this study, although some proportion of the population may be found right above bottom and thus are not available to our sampling gear (Brodeur and Terazaki, MS).

Although no single sampling gear can quantitatively sample the full size range of macrozooplankton available, we believe that our density estimates are reliable for most taxa sampled, with the exception of daytime estimates of adult euphausiids, which probably migrate below our maximum sampling depth. In the course of our study, we observed much mesoscale and large-scale variability in the abundance of macrozooplankton in the northern North Pacific, and suggest that this spatial variability may be related to heterogeneities in the physical environment. An analysis of hydrography and physical dynamics of the sampled regions along with a more detailed community analysis will be necessary to elucidate mechanisms of habitat segregation for macrozooplankton. For example, habitat segregation we attribute to depth differences may covary with temperature or some other important environmental variable. In addition, there is a need for more complete information on the vertical distribution and life history of the dominant species for better understanding of the distribution patterns observed.

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