The distribution, community structure and feeding ecology of
micronektonic crustaceans in the subarctic Pacific and the Bering Sea

(太平洋亜寒帯域およびベーリング海における甲殻類マイクロネクトンの
分布、群集構造、および摂餌生態に関する研究)

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This study examined the samples collected during the 1997 trans-Pacific cruise of the RV Hakuho-maru, investigating the chemical and biological processes of the subarctic Pacific and transitional zone. The purpose of this study is to investigate the micronektonic crustacean assemblage and diversity, vertical distribution and feeding patterns, and trophic positioning of micronektonic crustaceans in the subarctic Pacific and Bering Sea.

1. *Micronektonic crustacean assemblages*

The biomass, abundance, diversity and community structure of pelagic crustaceans (decapods, euphausiids and mysids) were examined in the 0-1000 m layer at 19 stations across the subarctic Pacific and Bering Sea with an Isaacs-Kidd Midwater Trawl (IKMT) during July - August 1997. This paper reports the first domain-wide abundance and biomass patterns for mesopelagic mysids. A total of 10 genera and 15 species of decapods, 8 genera and 16 species of euphausiids, and 6 genera and 10 species of mysids were found with no new species or range extensions. Total biomass of micronektonic crustaceans was highest in the western subarctic (WSA) but not significantly different from the eastern subarctic (ESA). Peak biomass for euphausiids and decapods also occurred in the WSA in association with warm temperatures and high chlorophyll *a* concentrations, but peak biomass for mysids was found in the Bering Sea (BS). Species diversity (*H'*) was higher in the eastern subarctic (ESA) than in the WSA for decapods and euphausiids, while mysids had the highest diversity in the WSA. Community structure cluster analysis suggested that there were 3-4 major assemblages of decapods, euphausiids, and mysids. Mysid assemblages showed the highest similarities between stations, followed by decapod and euphausiid assemblages. Higher geographical similarity among pelagic mysid communities may be partly due to their deep habitats and limited vertical migration while lower similarities among euphausiid communities may reflect their migratory behavior upward into the epipelagic zone wherein the constituent species tend to be geographically different. The intermediate vertical movement patterns of the decapods place them between the euphausiids and mysids and decapod community structure reflects their moderate geographical similarity.

2. *Micronektonic crustacean vertical distribution patterns*

Micronektonic crustaceans (euphausiids, decapods and mysids) are considered to be important components of the trophic web between zooplankton and higher trophic animals; however, information regarding biomass/abundance, diversity, vertical distribution, and

community structure of these crustaceans is limited for the subarctic Pacific. The present study examined vertical distribution of pelagic micronektonic crustaceans in the subarctic Pacific and Bering Sea in July - August 1997. At 4 stations, 1 each in the western subarctic Pacific (WSA), the central subarctic Pacific (CSA), the eastern subarctic Pacific (ESA) and the oceanic Bering Sea (BS), 12 contiguous discrete layers were sampled with a Rectangular Midwater Trawl (RMT 1+8 system). A total of 17 species of decapods in 11 genera, 13 species of euphausiids in 7 genera, and 5 species of mysids in 4 genera were found in the study area with no new species or range extensions. Total biomass of micronektonic crustaceans (range = 1.4-4.8 gWW/m^2) was highest in the WSA. Peak euphausiid and decapod biomass was also in the WSA, associated with warm temperatures and high chlorophyll a concentrations, while peak biomass for mysids was in the oceanic BS. There was a clean division between vertical assemblages of epipelagic-mesopelagic MNC and strictly mesopelagic MNC, both day and night. All dominant euphausiid species, *Euphausia Pacifica, Thysanoessa inspinata,* and *T. longipes* underwent extensive diel vertical migrations (DVM), with surface or near-surface biomass peaks at night compared to deeper peaks during the day. Only *Gnathophausia gigas* exhibited limited DVM among the 3 species of dominant mysids (including *Eucopia grimaldii, Boreomysis californica*). *Sergestes similis* was the greatest migratory shrimp, DVM biomass peaks ca. in the epipelagic zone at night compared to day, while *Hymenodora frontalis* tended to rise within the mesopelagic zone at night, with peak biomasses 100 m shallower than daytime peaks. The diversity of species within epipelagic layers (dominated by euphausiids) was more variable than that of species found in mesopelagic layers, which were dominated by mysids and decapods.

3. *Feeding patterns of dominant micronektonic crustacean species*

The feeding patterns of dominant members of the mesopelagic micronektonic crustacean assemblage in the subarctic North Pacific were examined. Numerically dominant shrimp species (*Sergestes similis, Bentheogennema borealis* and *Hymenodora frontalis*) and 1 mysid (*Eucopia grimaldii*) collected by RMT 8 at 4 stations were dissected in a qualitative gut content examination. Specimens collected from up to 12 discrete depth layers, day and night, at each station were examined for evidence of feeding preferences, gut fullness, and degree of digestion to whether feeding patterns differed by depth, time of day or sex. Qualitative data from gut content analysis was compared to depth distributions of prey species concurrently collected by RMT 1 net in order to examine relationships between predators and prey distributions. Except for *Eucopia grimaldii*, results indicate that all species were primarily carnivorous, and that *Sergestes similis* had the most diverse feeding patterns. There were differences between feeding patterns among shrimp species, but these may be related to

feeding methodology rather than actual feeding preference. Within species, there were no differences in feeding patterns between sexes, and there was no significant difference in feeding patterns between regions. This baseline study will be followed by a quantitative examination of prey items (to species level) to better define feeding patterns, especially between regions.

4. *Trophic linkages between micronektonic crustaceans in the subarctic Pacific food web*

The trophic position of micronektonic crustaceans (MNC) in the subarctic Pacific food web is examined. Previous studies of food webs have emphasized the role of some MNC species and taxa (*i.e.* euphausiids and sergestid shrimp) over others. Data from earlier studies of both horizontal and vertical assemblage patterns, qualitative feeding patterns and published predator impacts on the MNC are used in this analysis. This paper attempts to adjust the estimated trophic impact of the MNC using data made available from recent studies. Conclusions regarding the importance of MNC in the overall pelagic food web are also discussed.

5. *Distribution and trophic implications between MNC and zooplankton in the subarctic Pacific: Predation and food web connections*

The distribution patterns of both the MNC and zooplankton are discussed, in light of the findings in the preceding chapters. Comparison and differences between other ocean regions are discussed, as well as areas for future research.

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CHAPTER 1
General Introduction

The subarctic Pacific and Bering Sea (SAP & BS) are one of the world's high nitrate-low chlorophyll (HNLC) regions, much like the subantarctic regions of the Southern Ocean. HNLC areas are regions where phytoplankton do not exhaust surface supplies of nutrients during summer, and protozoans are principal grazers. The protozoans control phytoplankton blooms and recycle nutrients within the upper mixed layer, usually bounded by the halocline at 100 m. Zooplankton within the SAP and BS are dominated by a small number of copepods, all of which primarily feed on protozoans. Zooplankton biomass across the SAP is dominated by a small number of calanoid copepods (*Neocalanus plumchrus, N. flemingeris, N. cristatus* and *Eucalanus bungii*), which due to their large contribution to total zooplankton biomass are a likely important transfer point of food energy from lower trophic levels above through the micronekton to the nekton. These copepods exhibit strong seasonal cycling with subsequent spring increases in biomass in the top 150 m as they rise to exploit spring phytoplankton blooms, followed by summer declines, as they descend below 500 m (Fig. 1-1). Trophically, consumption of primary production follows the same pattern, but two trophic levels away.

The subarctic Pacific (SAP) contains two gyres: the Eastern and Western Subarctic Gyres, the former in the Gulf of Alaska, and the latter to the east of the Kamchatka peninsula; and there is a gyre within the oceanic Bering Sea (BS). Taniguchi (1999) described stocks of phytoplankton and zooplankton were stable across the SAP and BS, while stocks of nitrate and microzooplankton were variable. There is a tendency towards higher total average zooplankton biomass along the northern, western and eastern boundaries of the SAP and the borders of the BS and lower near the centers of the gyres. Mackas and Tsuda (1999) in a review of community structure, seasonal life histories and interannual variability of zooplankton in the western and eastern SAP described how the primary food source for dominant zooplankton in the oceanic gyres switches from phytoplankton to microzooplankton and zooplankton. Brodeur *et al.* (1999) constructed a food web of the North Pacific (Fig. 1-2), showing trophic levels and trophic linkages of major nodes from the western and eastern North Pacific. However, while it includes euphausiids, only one group of shrimps (Sergestiids) is shown as a link, but no mysids. These are primarily mesopelagic species, some of which occur in relatively high abundances and biomasses (Aizawa, 1974; Krygier, 1981; Iwasaki, 1987), but whose contributions to the pelagic food web are still poorly quantified.

There was a large ENSO event in during the 1997 sampling period. The influence of ENSO events has been described, especially in coastal environments, in the ESA (e.g. Peterson, 2002), where the influx of warmer surface layers introduces species with subtropical affinities and drives
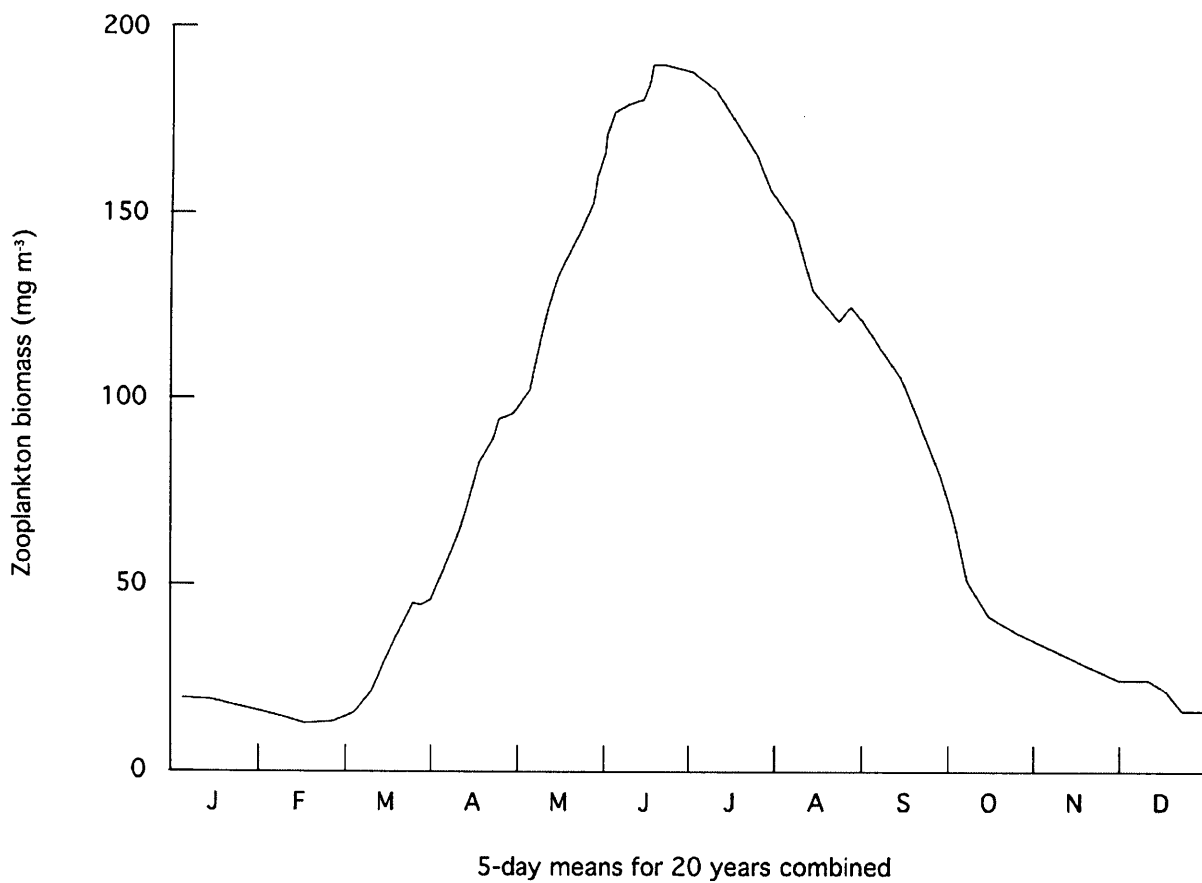
Fig. 1-1. Annual cycle of zooplankton biomass in the upper 150 m in the oceanic subarctic Pacific. The build-up in spring is from growth, mostly of large copepods. Decline in early summer is from descent of these copepods to depths below 500 m for diapause. (In Miller 2004, after Fulton 1983.)

Subarctic Food Web
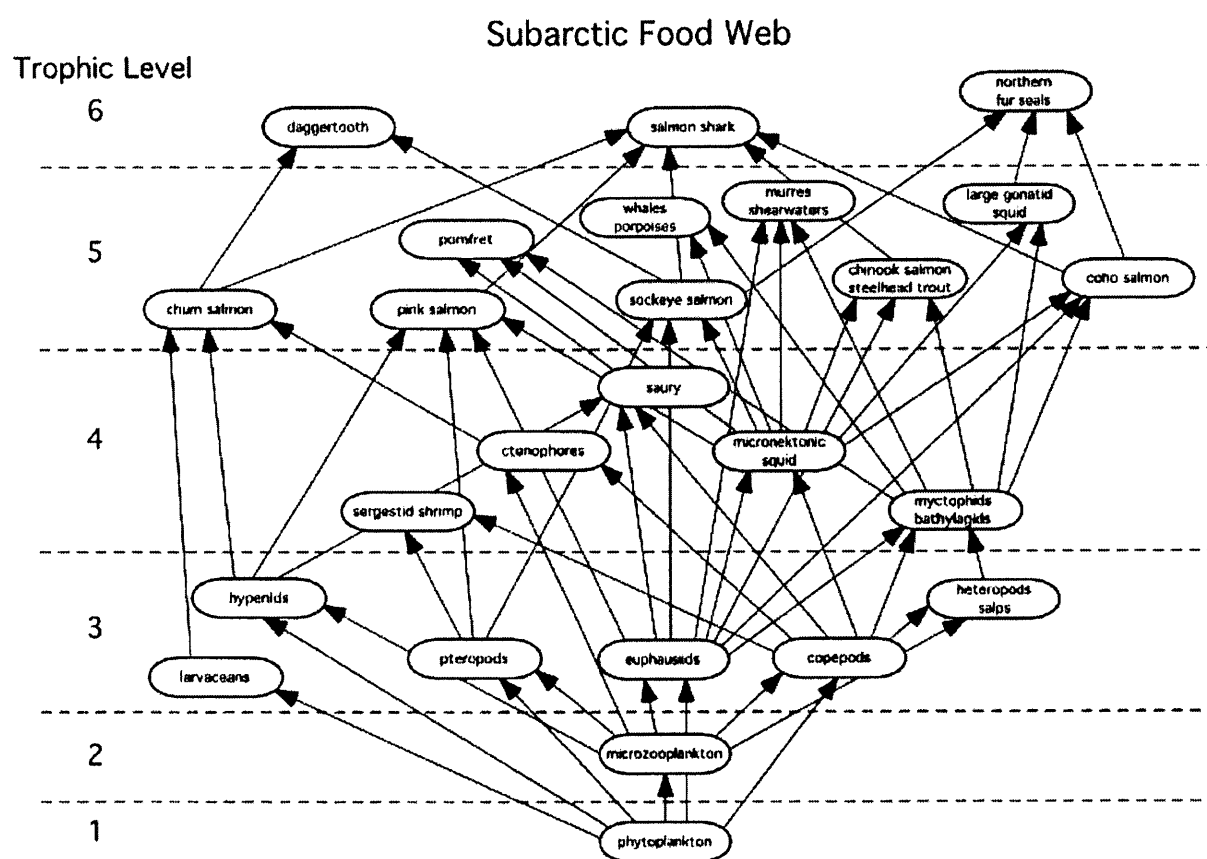
Fig. 1-2. Food web for the Transition Region showing major trophic linkages. The web is arranged by increasing trophic level from bottom to top. An attempt was also made to show eastern (left side) and western (right side) Transition Region differences when possible. (Adapted from Brodeur *et al*, 1999).

out the usual boreal species. How much of an effect ENSO events have on MNC is not well known, and neither are the effects on their vertical distribution patterns.

Micronektonic crustaceans (MNC, euphausiids, decapods, and mysids) are important components of the subarctic North Pacific and Bering Sea. They occupy the ecological space between the smaller and more abundant mesoplankton (e.g. copepods and chaetognaths) and the larger nekton (e.g. squids and fishes). They also share certain similarities in horizontal and vertical distribution with some important differences. The majority of euphausiid species are epipelagic in distribution, although some species inhabit mesopelagic and bathypelagic depths. Decapods on the other hand, are primarily mesopelagic, with some species found in the upper epipelagic waters and the lower bathypelagic zones. Many species within both of these taxa exhibit diel vertical migration, or the movement from deeper waters to shallower waters and back again over the course of a 24-hour period. This behavior is particularly significant in epipelagic species and to a lesser extent in mesopelagic ones. Pelagic mysids have not been shown to exhibit diel migration, but neretic species do. These differing migration patterns, combined with preferred habitation zones, may be very important in the transfer of energy from the food-rich epipelagic zone down through the meso- and bathypelagic zones in a step-like progression, as has been reported by many workers (e.g. Vinogradov, 1968; Omori, 1974; Hopkins, 1998; Mincks, 2000).

Mesopelagic MNC typically have short lifespans (mainly less than 3 years), high reproduction rates (up to twice a year), and are dominant members of the North Pacific ecosystem. These crustaceans feed not only on microzooplankton and zooplankton (e.g. diatoms, chaetognaths and copepods), on each other, and also on juveniles of nektonic species. Epipelagic euphausiids tend to be herbivorous, feeding primarily upon phytoplankton and microzooplankton (particularly formaniferans, ciliates, and diatoms) (Ponomareva, 1963), while mesopelagic euphausiids tend to be carnivorous, feeding upon copepods, other euphausiids (Nemoto, 1966). Decapods and mysids primarily feed upon copepods, euphausiids, chaetognaths and juvenile fishes (Aizawa 1974; Nishida, 1988; Cartes, 1998). Therefore, the high abundances and biomasses of MNC can potentially have a large impact on zooplanktonic and nektonic prey species via feeding. While data concerning vertical distribution and feeding patterns of MNC exists, the predominant portion of this data concerns euphausiids, and then the decapods, while this information regarding pelagic mysids is totally lacking.

There are 85 species of euphausiids in the worlds' oceans, but only about 20 are found in the subarctic north Pacific, and they have been the subjects of intensive research effort, with a massive literature regarding them. Euphausiid investigations in the north Pacific date from the 1900's (Holmes 1900; Hansen 1913; and Esterly 1914a; 1914b) when euphausiid (classified with mysids as

Schizopoda) species and genera off California were first described. Banner in the late 1940's and early 1950's extended knowledge regarding the geographical ranges and taxonomy of both mysids and euphausiids in the eastern subarctic Pacific and Bering Sea (Banner, 1948a; 1950; 1954). Boden *et al,* (1955) further expanded and updated the role of euphausiids while Brinton (1962) presented quantitative aspects of both horizontal and vertical distributions of 4 subarctic euphausiid species in relation to the water masses they inhabit. Mauchline and Fisher (1969) and Mauchline (1980), reviewed current knowledge regarding the life history, behavior, breeding, feeding and biochemistry of krill in the world ocean. Nemoto (1963) described a new species of euphausiid in the north Pacific, *Thysanoessa inspinata*, which was split from the co-generic *T. longipes*, on the basis of morphological differences in male copulatory organs and spination. Ponomareva (1963) reported a quantitative analysis of the dietary composition and seasonality of euphausiid feeding from the Bering Sea, Sea of Japan and Sea of Ohkhotsk. Euphausiid feeding in other regions of the north Pacific MNC has also been well documented (Mauchline, 1980; Ohman, 1984).

There are 39 species of pelagic penaeid and caridean decapods that have been reported from the subarctic Pacific and Bering Sea. Pelagic decapods were first collected in the western North Pacific by the Challenger Expedition (Bate, 1888; Hansen 1903; Kemp 1909) and during cruises from the Albatross (Rathburn, 1904; Faxton 1895; Schmitt 1921). Pearcy and Forss (1966) described the depth distributions of 16 species of pelagic decapods off the Oregon shelf and also identified groups of shrimps on the basis of their vertical migration patterns. In the western subarctic Pacific, Omori (1974) and Kikuchi and Omori (1985, 1986), described ontogenetic vertical migration patterns of pelagic shrimps off Japan, and concluding that there was no apparent association between diel migration and ontogenetic migration patterns. Aizawa (1974) described the vertical distribution patterns of a limited number of species in the WSA, while Krygier and Pearcy (1981) did the same for a larger group of pelagic shrimps in the ESA. Horizontal distribution patterns (Wasmer, 1972; Iwasaki, 1987) and zoogeography (Krygier, 1988) of pelagic shrimps across the subarctic Pacific have been described, defining fauna groups for the important water masses in the North Pacific. Nevertheless, the decapod assemblage within the SAP and BS has not yet been analyzed in depth. Feeding studies of pelagic shrimp has focused on gut content examination of a small number of species in the western (Tchindonova 1959; Omori, 1969; Aizawa, 1974) central (Walters, 1976) and eastern (Renfro, 1966; Nishida, 1988) North Pacific. However, feeding data is lacking for many species, especially in terms of the SAP basin.

There are about 29 species of mysids that have been reported from the pelagic subarctic Pacific and Bering Sea. Recently there has been a taxonomic split dividing the Mysidacea into 2 orders: Mysida and Lophogastrida, both of which are important components of the mysid

assemblage in the North Pacific. There have been very few studies of pelagic or mesopelagic species beyond taxonomic descriptions or general distribution within the North Pacific. There are few reports of pelagic mysid zoogeographical and vertical distribution, regarding a limited number of species (e.g. *Gnathophausia gigas*), in the western (Murano, 1975, 1976, 1977) and eastern subarctic Pacific (Pequegnat, 1965; Krygier, 1988; Murano, 1985). Respiration of the mysids in the genus *Gnathophausia* and *Boreomysis* have been described (Childress, 1968, 1971b, 1975; Hilleradams, 1983), but little else is known of the biology and ecology of other pelagic mysid species in the North Pacific.

There are no studies of MNC encompassing the entire subarctic region. Little is known of the MNC species assemblages in the SAP and BS, and how these assemblages differ among the western, central and eastern sections of the SAP, and whether the SAP differs from the BS. The distributional and feeding relationships within and between MNC taxa are not well known and need clarification. In addition, it is not known whether these patterns change according to region, day or night, sex and depth.

Therefore, in order to better understand the role that MNC play in the subarctic Pacific, this thesis proposes to examine the assemblage structure, abundance, biomass and species diversity of MNC within the SAP and BS, and what factors influence these assemblages. Then I will examine the vertical distribution patterns of the MNC, and how these patterns occur across the study area, along with any influences from physical/chemical parameters on DVM. The thesis will then examine the diets and feeding patterns of dominant decapod and mysid species, estimated daily ration of production consumed and their estimated contributions to vertical flux, and changes by region and/or time of day. Finally, the trophic positioning of micronektonic crustaceans (MNC) in combination with the diel vertical distribution patterns of zooplankton will be discussed.

CHAPTER 2
Assemblage Structure and diversity of micronektonic crustaceans in the subarctic Pacific and Bering Sea in summer, 1997.

INTRODUCTION

Recently, there has been increased interest in productivity and biomass differences of lower trophic levels between the western subarctic (WSA), the eastern subarctic (ESA) and the Bering Sea (BS) (Beamish, *et al.*, 1999; Nishikawa, *et al.*, 2001). Taniguchi (1999) discussed structural differences within lower trophic levels throughout the subarctic Pacific and Bering Sea, finding clear differences in average values of stock size between regions, especially between the western and eastern SAP. The zooplankton community in the subarctic Pacific is relatively simple, consisting of similar sets of major species throughout the deep waters of the subarctic Pacific. Mackas and Tsuda (1999) summarized present knowledge regarding ecology, temporal and spatial variability of mesozooplankton in the subarctic Pacific and compared productivity and population dynamics between the eastern and western sides of the basin. They found that on average, the subarctic gyre centers have lower biomass and productivity than along their margins. They also reported that there is some evidence that the WSA gyre is more productive than the ESA gyre, but whether or not this east–west gradient is permanent is unclear.

There are many reports on biomass/abundance, diversity, and community structure of micronektonic crustaceans (MNC) in other oceans around the world (*i.e.* the North Atlantic, Roe, 1984; Roe *et al.*, 1984; South Atlantic, Pillar *et al.*, 1992; Mediterranean, Cartes and Sorbe, 1998; and Southern Ocean, Iwasaki and Nemoto, 1987a, 1987d; Hosie, *et al.*, 2000). Abundance and/or biomass distributions of euphausiids in the subarctic Pacific and Bering Sea (*e.g.* Johnson and Brinton, 1963; Ponomareva, 1963; Sugisaki, *et al.*, 1998; Taki, 2002) have been well described, especially in the WSA and ESA, but less so for the central subarctic Pacific (CSA) and oceanic BS.

However, there have been far fewer studies within the SAP and BS regarding the biogeography and community structure of pelagic decapods (*e.g.* Krygier and Wasmer, 1988) and mysids (*e.g.* Krygier and Murano, 1988). Particularly, the abundance and biomass of decapods in the oceanic WSA has been very well described (Aizawa, 1974; Iwasaki and Nemoto, 1987b, 1987c) but not in the oceanic ESA (Pearcy, 1969; Coyle and Pinchuk, 2005). In addition, previous zoogeographic studies were largely based on the presence-absence of species (Wasmer, 1972; Krygier and Wasmer, 1988) within one taxon, thus necessitating an examination of the entire community structure taking into account the relative abundance/biomass of species.

Information about the respiration, reproduction, life cycle, vertical distribution, and community structure of pelagic mysids remains limited. Geographic and vertical distributions, and ranges in the subarctic Pacific and Bering Sea has been reported by Ii (1964), Pequegnat (1965), Mauchline and Murano (1977), Murano and Krygier (1985), and Krygier and Murano (1988);

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however, except for a limited number of genera (*e.g. Boreomysis, Eucopia,* and *Gnathophausia*) much remains unknown.

The objectives of this study are to examine pelagic MNC abundance and biomass patterns as well as their community structure within and between taxa in the subarctic Pacific and Bering Sea. This would identify any changes in species dominance patterns regarding abundance and biomass as well as differences in these patterns between and among the WSA, ESA and BS. If present, changes in community structure among the three regions will tell us about the relative continuity of communities across the SAP and BS, and what factors, either biological or physical, may affect the composition of these communities.

METHOD

Sampling

All sampling was carried out during the KH 97-2 cruise of the RV Hakuho Maru, Ocean Research Institute, University of Tokyo, in the subarctic Pacific and Bering Sea from 18 July to 12 August 1997. Oblique tows to examine abundance, biomass, and community structure were made at 19 stations (Fig. 2-1) with a 3 m Isaacs-Kidd Midwater Trawl (7.3 m^2 mouth area and 1mm mesh) (IKMT; Isaacs and Kidd, 1951). Each tow was made at a ship speed of about 2 knots with 3000 m of wire out and reached maximum depths of 721 - 1061 m. Sampling depths were recorded with a depth time recorder (RMD Depth Meter, Rigosya Co. Ltd.) and the volume of water filtered during each tow was estimated using a flow meter (Rigosya Co. Ltd.) and the average volume of water filtered was 50,700 m^3 (range 41,224–73,287 m^3). All tows were made at night, except for at 2 stations (Stns 10 in the BS, and 15 in the ESA), where tows finished at dawn.

Half of the samples were immediately fixed and preserved in a 10% formalin/seawater solution (buffered with sodium tetraborate) and the other 1/2 of each sample was frozen. Mysid, euphausiid and decapod juveniles and adults were sorted in the laboratory, identified by species; individual numbers counted, and wet weight measured (Mettler AE 100 top-loading electronic scale).

Hydrographic data was collected at each station via CTD carousel casts, for the water column from 0 – 3000 m. Dissolved oxygen (DO), chlorophyll (Chl-*a*), salinity (PSU) and water temperature for each cast is available from the 1997 cruise report (CTD data, Ocean Research Institute, University of Tokyo 1997).

Species dominance was determined in terms of both proportional abundance and biomass (> 60%, respectively), some species of rare, large-bodied shrimp (*e.g. Notostomus japonicus*) were not included as dominant species. Two difficulties were encountered in identifying some
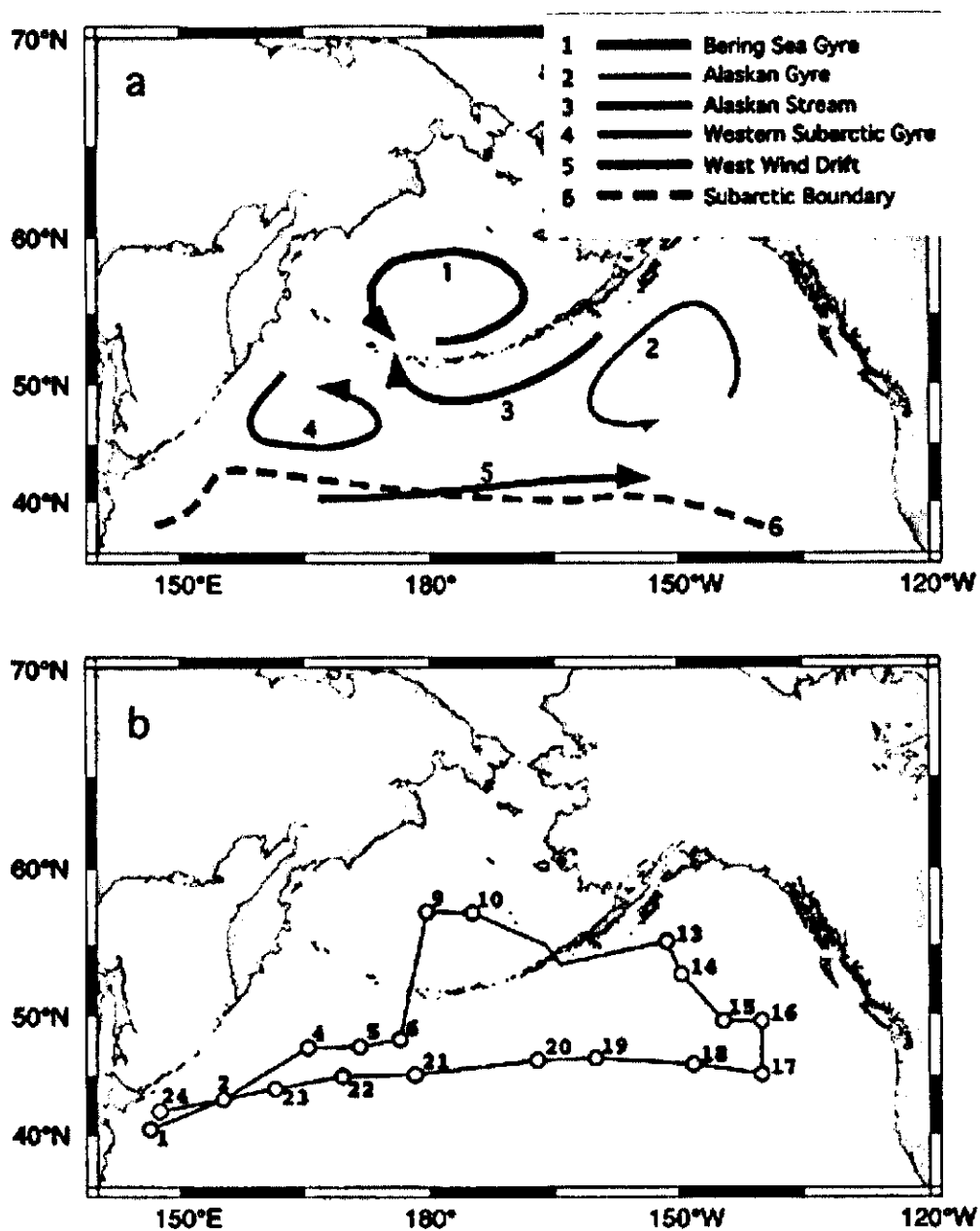
Fig. 2-1. Study area showing: (a) Major ocean current and gyre systems (see current legend) (Currents after Dodimead et al. (1963) and Tadokoro (1996)), and (b) map of stations (n=19).

specimens of the genera *Boreomysis* and *Eucopia*; some were so damaged that only genus-level identification was possible, and secondly, the taxonomy of the genus *Eucopia* is in dispute. Of the five *Eucopia* species identified in the literature, only two have been accepted as valid by morphological (Nouvel, 1942; Tattersall, 1951; Roe, 1984b) or genetic (Casanova *et al.*, 1998) characteristics. Therefore, *Eucopia* specimens were identified as *E. grimaldii* based on the genetic evidence in literature cited above.

Fixed decapod and mysid samples were counted in their entirety, but large numbers of euphausiids required an aliquot (1/4 to 1/32) of each sample to be split with a Folsom plankton splitter and examined. Both biomass and abundance of each species were expressed in values per 1000 m^3. The assemblages of pelagic crustaceans at the 19 IKMT stations were compared using cluster analysis using the Morisita-Horn similarity index (C_λ, Horn, 1966). The Morisita-Horn index was selected for the cluster analysis to avoid the complexities involved when samples have different abundances and diversities (Wolda, 1981). Because the Morisita-Horn index is very sensitive to the presence of abundant species, the catch data were log transformed, and the transformed data were then used to calculate similarity (C_λ) between stations. Station assemblages were grouped by their similarity to each other (Morisita-Horn similarity index and UPGMA), and then the diversity (Shannon diversity index *H'*, Shannon and Weaver, 1949) of each station was charted, to compare the species diversity of stations within and between taxonomic groups. Species evenness (Pileou's Evenness index, *J'*) was used to measure the distribution of individuals in the communities within the SAP and BS. The Kruskal-Wallis test was used to examine differences between abundance and biomass among the three main taxa of MNC in the SAP & BS. The Mann-Whitney *U*-test was used to examine differences in mean abundance and biomass within taxa among stations within the WSA, ESA and BS.

RESULTS

Hydrography

The study area was divided into 3 regions: the Bering Sea (BS), the western subarctic Pacific (WSA), and the eastern subarctic Pacific (ESA). The division between the WSA and ESA was made at 180° longitude between the western subarctic gyre and the Alaskan gyre, while the Aleutian Islands separated the BS from the subarctic Pacific (Fig. 2-1). The western subarctic domain was included with the WSG into the WSA, while the central subarctic domain and Alaskan Stream were linked to the Gulf of Alaska (GoA) in the ESA. This enables the WSA and ESA to be compared to determine if there are any differences in abundance or biomass patterns between the western and eastern portions of the subarctic Pacific.

A large El Nino event in 1997 (Huyer *et al*, 2002) resulted in warmer than average (2 – 5 °C) sea surface temperature (SST) in the ESA and BS and cooler than average (1 – 4 °C) SST in the WSA (satellite data NOAA, 1997) (Fig. 2-2). CTD data also showed the effects of the El Nino as a pool of warm (>14 °C) water in the upper 50 m of the ESA and warm water (>10 °C) in the top 125 m (CTD data, Ocean Research Institute, University of Tokyo 1997) (Fig. 2-3). Although warmer (>10 °C) water also reached depths of 125 m in the WSA, the pool of warm water in the ESA was more extensive and consistent throughout the top 200 m. Dissolved oxygen (DO) patterns were similar to temperature: 4 ml/L in the upper 125 m of both the WSA and ESA. However, the highest concentrations of DO (>6 ml/L) were in the WSA, associated with high (>4 μg/L) chlorophyll concentrations. The Cold Intermediate Water (CIW) (Dodimead 1963; Vinogradov 1997), a region of low zooplankton biomass, was recognized at depths of 100 - 125 m in the WSA. Salinity was highest (>33.5) in the upper 100 m of the northern part of the study area (BS and northern gulf of Alaska).

Species composition

A total of 8 genera and 16 species of euphausiids, 10 genera and 15 species of decapods, and 6 genera and 11 species of mysids were collected with no new species reported. Within the euphausiids and decapods, some typically transitional zone or subtropical zone species were recovered (Table 2-I). Decapods reported from the WSA and ESA were also found in central waters, "filling in" the space between previously reported ranges. The WSA had the most species (35 species) while the BS had the fewest (13 species). Common species were largely the same for all 3 taxa throughout the study area.

Abundance

Total abundance for MNC in the WSA and ESA were similar (279.6 vs. 236.5 ind/1000 m^3) (Table 2-II) but higher than that of the BS (82.9 ind/1000 m^3) showed no significant differences between regions (Table 2-VI; Kruskal-Wallis, $P<0.01$) or within any of the three groups of MNC among regions (Mann-Whitney U-test, $P>0.05$). Euphausiids accounted for over 80% of the total abundance at all stations except in the BS (Stn 9) where their proportional abundance was 50% of the total and the proportional abundance of mysids was 30% (Fig. 2-4). At all other stations decapods and mysids together accounted for less than 20% of the total abundance.

Euphausiid mean abundance was higher in the WSA and ESA (264.8 vs. 226.5 ind/1000 m^3, respectively) and lowest in the BS (57.3 ind/1000 m^3). Dominant species in terms of proportional
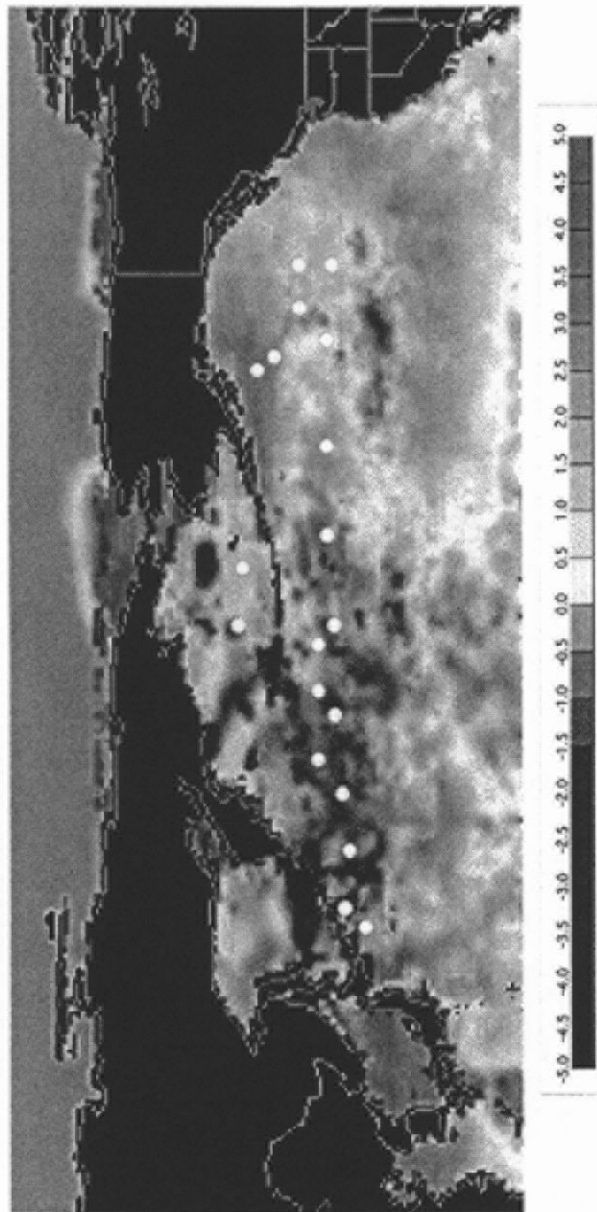
Fig. 2-2. Sea surface temperatures (SST) for 25 July 1997, by satellite. SST (°C) anomalies in the North Pacific, with higher than average temperatures shown in yellows and reds, and lower than average temperatures shown in blues and violets (NOAA Office of Satellite Data Processing and Distribution OSDPS – original data smoothed). Stations are shown in white, overlaid across the study area.
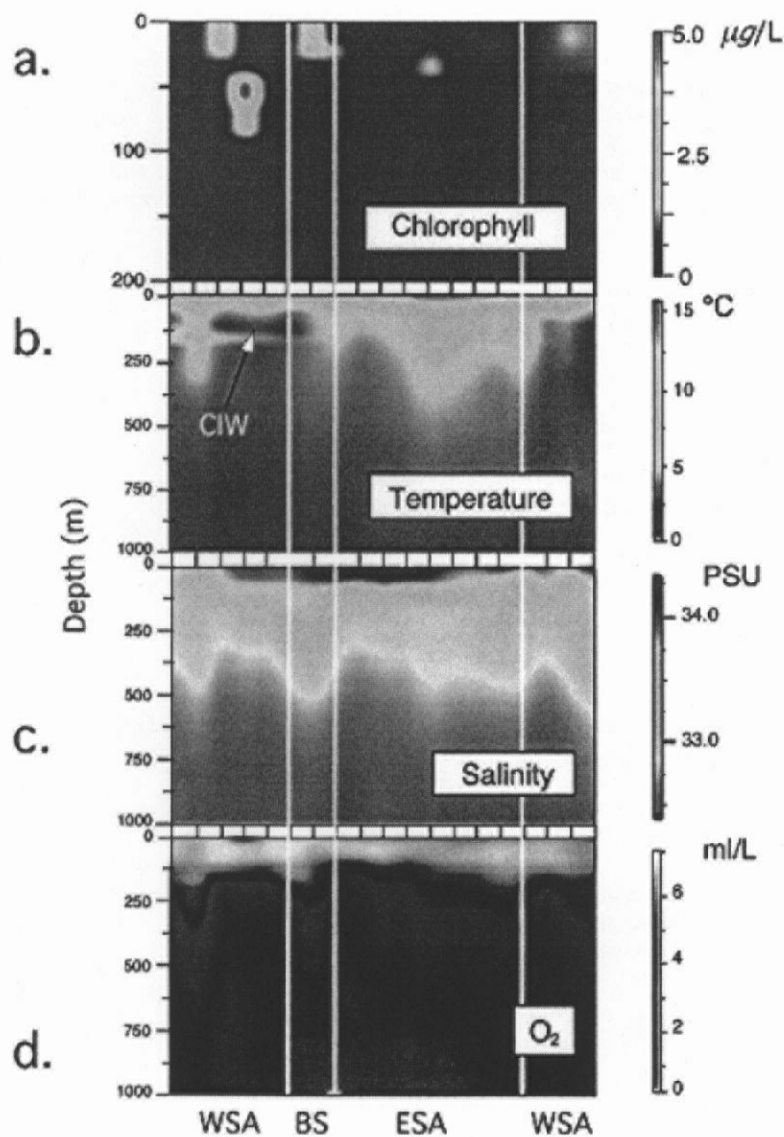
Fig. 2-3. Hydrographic profile of the study area: (a) Chlorophyll (μg/L), (b) temperature (°C), (c) salinity (PSU), and (d) dissolved oxygn (ml/L). Depth shown in meters. Note that Chl-a data extends to 200 m. The arrow indicates the cold intermediate water (CIW). WSA, ESA and BS regional abbreviations are as in text.

Table 2-I. Species groups of MNC (euphausiids, decapods, and mysids) for the WSA, ESA and BS are shown in decreasing order of abundance, by taxa. Number of stations for each region are indicated below each region. WSA, Western Subarctic; ESA, Eastern Subarctic; BS, Bering Sea. Total number of species for each region are listed along the bottom in bold type. Underlined species are typical transition zone or subtropical zone species.

WSA	ESA	BS
9 Stations	**8 Stations**	**2 Stations**
Euphausiacea		
Euphausia pacifica	*Thysanoessa inspinata*	*Thysanoessa longipes*
Thysanoessa inspinata	*Euphausia pacifica*	*Thysanoessa inspinata*
Tessarabrachion oculatum	*Tessarabrachion oculatum*	*Thysanoessa inermis*
Thysanopoda acutifrons	*Nematoscelis difficilis*	*Bentheuphausia ambylops*
Bentheuphausia ambylops	*Thysanoessa longipes*	*Euphausia pacifica*
Thysanoessa longipes	*Thysanopoda acutifrons*	
Stylocheiron maximum	*Stylocheiron maximum*	
Thysanopoda monocantha	*Thysanoessa spinifera*	
Nematoscelis gracilis	*Bentheuphausia ambylops*	
Nematobrachion flexipes	*Nematobrachion boopis*	
Thysanoessa inermis	*Nematoscelis spp.*	
	Stylocheiron elongatum	
Decapoda		
Hymenodora frontalis	*Hymenodora frontalis*	*Hymenodora frontalis*
Sergestes similis	*Sergestes similis*	*Sergestes similis*
Bentheogennema borealis	*Hymenodora gracilis*	*Bentheogennema borealis*
Hymenodora gracilis	*Bentheogennema borealis*	*Systellaspis braueri*
Sergia japonica	*Notostomus japonicus*	*Sergia tenuiremis*
Systellaspis braueri	*Sergia japonica*	
Pasiphaea japonica	*Systellaspis braueri*	
Notostomus japonicus	*Pasiphaea japonica*	
Sergia gardineri	*Parapasiphae sulcatifrons*	
Parapasiphae sulcatifrons	*Sergia laminata*	
Pasiphaea tarda		
Acanthephyra armata		
Physetocaris micropthalma		
Mysidacea		
Eucopia grimaldii	*Eucopia grimaldii*	*Eucopia grimaldii*
Boreomysis californica	*Boreomysis californica*	*Boreomysis californica*
Eucopia sp.	*Gnathophausia gigas*	*Gnathophausia gigas*
Gnathophausia gigas	*Eucopia sp.*	
Boreomysis sp.	*Boreomysis sp.*	
Meterythrops micropthalma	*Boreomysis microps*	
Dactylambylops iii		
Pleurerythrops secunda		
Boreomysis microps		
Meterythrops sp.		
Boreomysis intermedia		
35	**28**	**13**

Table 2-II. Mean (and Standard Deviation in italics) of abundance (inds/1000 m³) and biomass (gWW/1000 m³) for euphausiids, decapods, and mysids, by species for each region. Number of stations and region abbreviation as in Table 2-I.

	WSA (9 Stations)				ESA (8 Stations)				BS (2 Stations)			
	Abundance		Biomass		Abundance		Biomass		Abundance		Biomass	
	average	+/- SD	average	+/- SD	average	+/- SD	average	+/- SD	average	+/- SD	average	+/- SD
Euphausiacea	**264.8**	*145.8*	**5.4**	*4.6*	**226.5**	*149.1*	**3.3**	*1.2*	**53.7**	*44.2*	**1.1**	*0.3*
Euphausia pacifica	135.26	*127.43*	3.60	*4.37*	89.26	*74.28*	1.21	*0.89*	0.27	*0.38*	<0.01	*0.01*
Thysanoessa inspinata	103.38	*58.91*	1.17	*0.66*	103.19	*104.89*	0.87	*0.69*	1.87	*2.65*	0.03	*0.04*
Thysanoessa longipes	0.64	*1.33*	0.03	*0.06*	3.23	*6.60*	0.10	*0.21*	47.29	*44.17*	1.04	*0.22*
Tessarabrachion oculatum	4.20	*5.12*	0.12	*0.15*	6.18	*3.04*	0.15	*0.07*	-	-	-	-
Bentheuphausia amblyops	0.79	*0.80*	0.02	*0.02*	1.16	*0.86*	0.05	*0.04*	0.57	*0.71*	-	-
Thysanoessa inermis	0.01	*0.03*	-	-	-	-	-	-	0.60	*0.66*	0.03	*0.04*
Thysanopoda acutifrons	1.06	*1.70*	0.27	*0.47*	2.18	*3.44*	0.51	*0.73*	-	-	-	-
Nematoscelis difficilis	-	-	-	-	3.52	*9.95*	0.16	*0.46*	-	-	-	-
Stylocheiron maximum	0.37	*0.56*	0.04	*0.07*	1.82	*1.90*	0.12	*0.12*	-	-	-	-
Thysanoessa spinifera	-	-	-	-	1.41	*4.00*	0.03	*0.08*	-	-	-	-
Nematobrachion boopis	-	*0.01*	-	-	0.12	*0.23*	0.02	*0.04*	-	-	-	-
Nematobrachion flexipes	0.02	*0.08*	-	-	-	-	-	-	-	-	-	-
Nematoscelis spp.	-	-	-	-	0.09	*0.26*	<0.01	-	-	-	-	-
Thysanopoda monocantha	0.07	*0.22*	0.01	*0.02*	-	-	-	-	-	-	-	-
Nematoscelis gracilis	0.07	*0.22*	-	-	-	-	-	-	-	-	-	-
Stylocheiron elongatum	-	-	-	-	0.05	*0.13*	-	-	-	-	-	-
Decapoda	**6.8**	*3.9*	**2.1**	*1.2*	**4.3**	*1.0*	**1.8**	*0.9*	**10.9**	*0.9*	**1.5**	*0.4*
Hymenodora frontalis	2.83	*0.92*	0.61	*0.27*	2.07	*0.68*	0.79	*0.24*	9.38	*1.17*	1.46	*0.38*
Sergestes similis	2.23	*3.54*	0.48	*0.89*	0.88	*0.57*	0.24	*0.15*	0.02	*0.02*	0.01	*0.02*
Bentheogennema borealis	0.76	*0.53*	0.64	*0.80*	0.17	*0.18*	0.18	*0.23*	0.02	*0.02*	0.04	*0.06*
Hymenodora gracilis	0.52	*0.52*	0.01	*0.01*	0.73	*0.63*	0.01	*0.01*	-	-	-	-
Sergia japonica	0.07	*0.09*	0.04	*0.05*	0.05	*0.05*	0.01	*0.02*	0.02	*0.02*	-	-
Systellaspis braueri	0.03	*0.07*	-	-	0.05	*0.05*	0.01	*0.01*	-	-	-	-
Pasiphaea japonica	0.03	*0.04*	-	-	0.01	*0.02*	0.01	*0.02*	-	-	-	-
Sergia gardineri	0.01	*0.03*	-	-	-	-	-	-	-	-	-	-
Notostomus japonica	0.02	*0.04*	0.24	*0.39*	0.10	*0.13*	0.58	*0.83*	-	-	-	-
Pasiphaea tarda	<0.01	-	-	-	-	-	-	-	-	-	-	-
Parapasiphae sulcatifrons	0.01	*0.02*	0.01	*0.05*	0.01	*0.02*	0.01	*0.02*	-	-	-	-
Sergia laminata	-	-	-	-	0.01	*0.01*	<0.01	-	-	-	-	-
Sergia tenuiremis	-	-	-	-	-	-	-	-	0.02	*0.02*	0.01	*0.02*
Acanthephyra armata	<0.01	-	<0.01	-	-	-	-	-	-	-	-	-
Physetocaris microphthalma	<0.01	-	-	-	-	-	-	-	-	-	-	-
Mysidacea	**7.9**	*2.8*	**0.7**	*0.2*	**5.7**	*2.1*	**0.7**	*0.2*	**18.3**	*1.4*	**1.2**	*0.2*
Eucopia grimaldii	6.02	*1.76*	0.57	*0.17*	5.15	*1.70*	0.54	*0.20*	13.24	*1.18*	1.03	*0.12*
Boreomysis californica	1.09	*0.97*	0.02	*0.02*	0.29	*0.49*	0.01	*0.01*	4.68	*<0.01*	0.07	*0.005*
Gnathophausia gigas	0.23	*0.20*	0.09	*0.08*	0.21	*0.13*	0.18	*0.08*	0.20	*0.05*	0.09	*0.10*
Eucopia sp.	0.25	*0.29*	0.02	*0.02*	0.03	*0.04*	0.00	*0.00*	-	-	-	-
Boreomysis microps	0.01	*0.03*	-	-	0.01	*0.03*	<0.01	-	-	-	-	-
Boreomysis intermedia	<0.01	-	<0.01	-	-	-	-	-	-	-	-	-
Boreomysis sp.	0.14	*0.23*	<0.01	-	0.02	*0.03*	<0.01	-	-	-	-	-
Dactylamblyops iii	0.03	*0.06*	<0.01	-	-	-	-	-	-	-	-	-
Meterythrops microphthalma	0.09	*0.18*	-	-	-	-	-	-	-	-	-	-
Pleurerythrops secunda	0.02	*0.06*	-	-	-	-	-	-	-	-	-	-
Meterythrops sp.	0.01	*0.01*	-	-	-	-	-	-	-	-	-	-
Totals	**279.6**	*152.5*	**8.1**	*6.0*	**236.5**	*152.2*	**5.9**	*2.3*	**82.9**	*46.5*	**3.9**	*0.9*
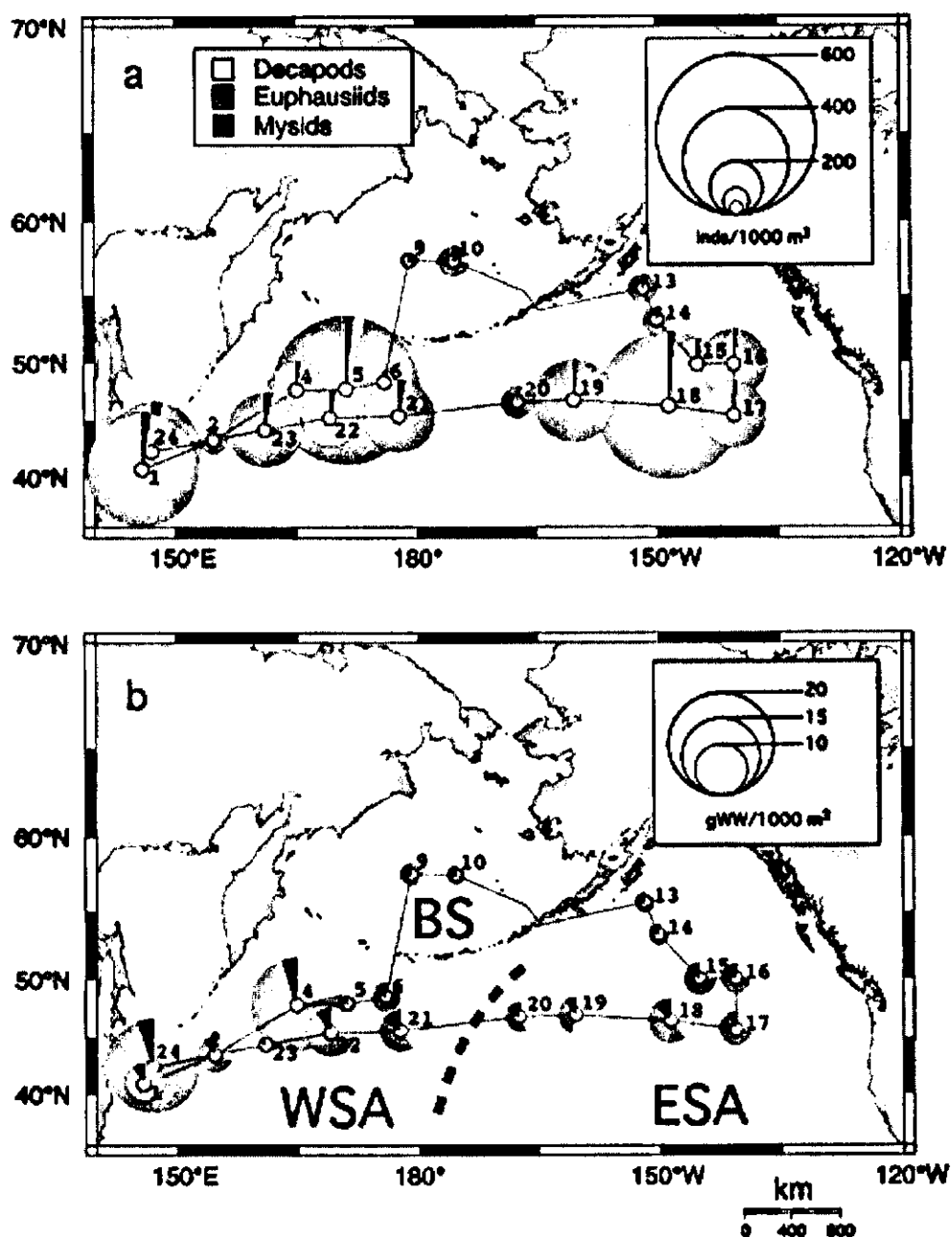
Fig. 2-4. Total (a) abundance (inds/1000 m³), and (b) biomass (gWW/1000 m³). Breakdown by taxa by station (see legends). Although median abundance and biomass were both higher in the WSA compared to the ESA and BS, there was no significant difference ($t_{abundance}$ = 0.708; $t_{biomass}$ = 0.708; p>0.05) between areas. The broken line marks the division between WSA and ESA in this study. Station and cruise track as shown.

abundance were the same in the WSA and ESA: *Euphausia pacifica*, *Thysanoessa inspinata* and *Tessarabrachion oculatum*. However, the dominant species in the BS (Stns 9 and 10) was *Thysanoessa longipes* (70 - 90% total abundance), while species common to the WSA and ESA were rare.

Among decapods, mean abundance was highest in the BS (10.9 ind/1000 m^3) but lower in the WSA and ESA (6.9 vs. 4.2 ind/1000 m^3, respectively). The dominant species in the BS (9 ind/1000 m^3) in terms of abundance was *Hymenodora frontalis*. Other common species in the WSA were *Sergestes similis* and *Bentheogennema borealis*, and *Sergestes similis* and *H. gracilis* in the ESA.

Mysids mean abundance was also highest in the BS (18.3 ind/1000 m^3). The most common mysid was *Eucopia grimaldii*, and was most abundant in the BS (13.2 ind/1000 m^3). Only 2 other species were common in our samples, *Gnathophausia gigas* and *Boreomysis californica*, in that order.

Biomass

Total MNC biomass was highest in the WSA (8.0 gWW/1000 m^3) and lowest in the BS (3.9 gWW/1000 m^3) (Table 2-II), but showed no significant differences between regions (Table 2-VI; Kruskal-Wallis, P<0.01) or within any of the three groups of MNC among regions (Mann-Whitney U-test, P>0.05). Euphausiids accounted for more than 50% of the total biomass at 12 stations within the WSA and ESA and less than 50% in the BS stations (Fig. 2-4). Decapods composed more than 25% of total biomass at most (n=13) WSA and ESA stations and in the BS. Mysids comprised less than 12% of the total biomass in the WSA and ESA stations but more than 25% in the BS stations.

Dominant euphausiid species in terms of biomass in the WSA and ESA were *Euphausia pacifica* (55 and 38% in the WSA and ESA), *Thysanoessa inspinata* (31 and 26% in the WSA and ESA), and *Thysanopoda acutifrons* (5% in the WSA, but 12% in the ESA). However, euphausiid biomass in the BS was dominated by *Thysanoessa longipes* (94%).

Dominant decapod species in the WSA were *Sergestes similis, Bentheogennema borealis* and *Hymenodora frontalis* (22, 26 and 38 % of total biomass, respectively). Dominant species in the ESA included *Notostomus japonicus* but not *B. borealis* (22 and 4% of total biomass, respectively). *Hymenodora frontalis* completely dominated biomass in the BS (94%).

Dominant mysid species in the WSA were *Eucopia grimaldii* (78%), *Boreomysis californica* (13%) and *Gnathophausia gigas* (3%). In the ESA, *E. grimaldii* was by far the most abundant

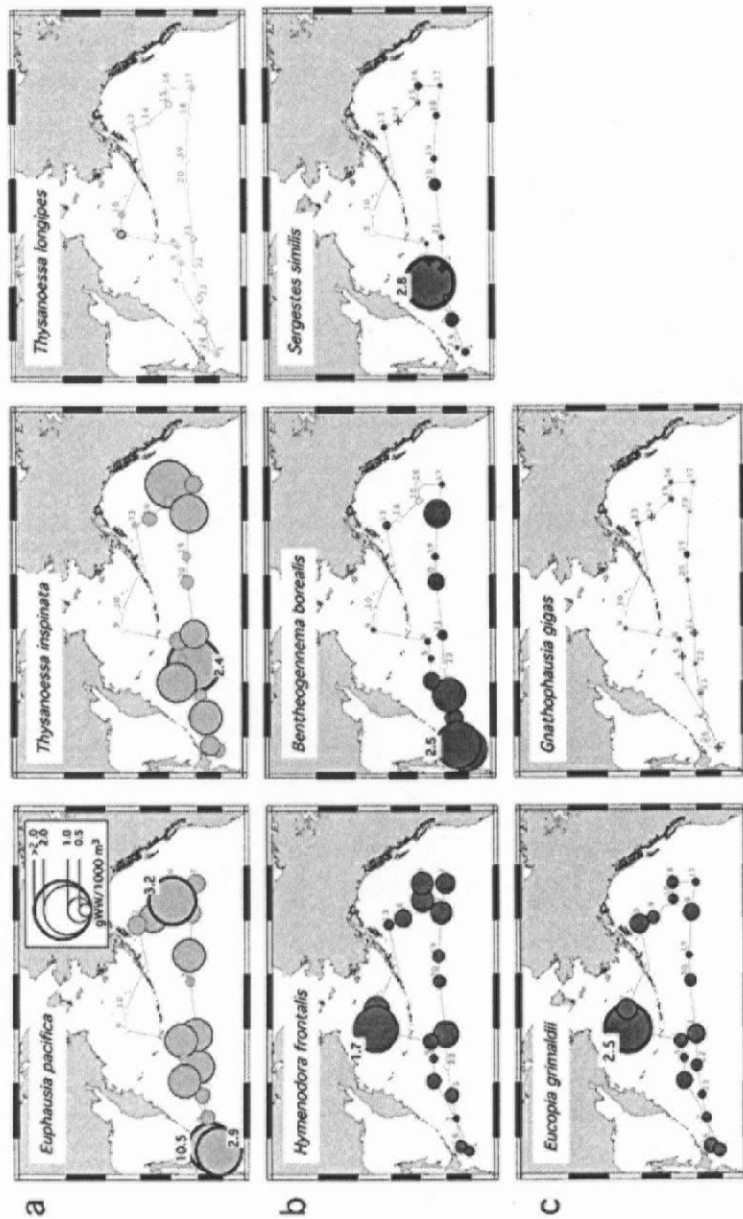**Fig. 2-5.** Horizontal distribution by biomass (gWW/1000 m^3) (legend top left) of the 3 most common species of: (a) euphausiids, and (b) decapods. The 2 most common mysid species are shown in the bottom row. Numbers refer to biomass exceeding the legend, crosses signify biomass below 0.1 gWW/1000 m^3.

Table 2-III. Number of species, numerically dominant species, percent dominance, diversity index (H'), and eveness (J') for total MNC, euphausiids, decapods, and mysids in the WSA, ESA and BS. The asterix (*) indicates stations where 2 species co-dominated.

Total MNC / Euphausiids

Stn	Species Number	Dominant Species	Percentage Dominance	H'	J'
		Total MNC			
		WSA			
1	25	Euphausia pacifica	60.1	1.14	0.35
2	19	Thysanoessa inspinata	67.5	1.25	0.43
4	13	E. pacifica	60.2	0.97	0.38
5	20	T. inspinata	54.4	1.28	0.43
6	13	T. inspinata	46.0	1.16	0.45
21	21	T. inspinata	47.3	1.19	0.39
22	20	T. inspinata	64.3	1.09	0.36
23	23	T. inspinata	54.4	1.51	0.48
24	22	E. pacifica	76.5	0.92	0.30
		ESA			
13	18	Euphausia pacifica	33.4	2.00	0.69
14	17	E. pacifica	40.5	1.65	0.58
15	14	E. pacifica	62.9	1.01	0.38
16	17	Thysanoessa inspinata	82.0	0.79	0.28
17	22	E. pacifica	34.8	1.67	0.54
18	23	T. inspinata	57.3	1.17	0.37
19	19	E. pacifica	72.6	0.95	0.32
20	19	T. inspinata	50.1	1.54	0.52
		BS			
9	11	Thysanoessa longipes	32.1	1.70	0.71
10	13	T. longipes	67.8	1.14	0.44
		Euphausiids			
		WSA			
1	10	Euphausia pacifica	63.2	0.90	0.39
2	8	Thysanoessa inspinata	72.6	0.96	0.46
4	3	E. pacifica	63.1	0.76	0.69
5	8	T. inspinata	58.1	1.00	0.48
6	5	T. inspinata	48.9	0.92	0.57
21	7	T. inspinata	50.7	0.88	0.45
22	6	T. inspinata	69.2	0.76	0.43
23	6	T. inspinata	60.5	1.08	0.60
24	6	E. pacifica	80.0	0.69	0.38
		ESA			
13	10	Euphausia pacifica	38.5	1.64	0.71
14	7	E. pacifica	45.2	1.31	0.67
15	6	E. pacifica	65.5	0.84	0.47
16	7	Thysanoessa inspinata	85.7	0.58	0.30
17	10	E. pacifica	37.8	1.38	0.60
18	8	T. inspinata	59.3	1.00	0.48
19	7	E. pacifica	74.6	0.80	0.41
20	6	T. inspinata	54.2	1.24	0.69
		BS			
9	5	Thysanoessa longipes	71.4	0.92	0.57
10	4	T. longipes	92.5	0.28	0.20

Decapods / Mysids

Stn	Species number	Dominant species	Percent Dominance	H'	J'
		Decapods			
		WSA			
1	8	Hymenodora frontalis	50.8	1.48	0.71
2	7	Sergestes similis	60.0	1.05	0.54
4	7	S. similis	66.9	0.88	0.45
5	6	H. frontalis	75.4	0.69	0.39
6	4	H. frontalis	80.5	0.69	0.50
21	9	H. frontalis	46.0	1.47	0.67
22	8	H. frontalis	51.9	1.23	0.59
23	11	H.frontalis and S.similis *	30.7	1.81	0.75
24	7	H. frontalis	44.4	1.49	0.77
		ESA			
13	5	Hymenodora gracilis	40.4	1.35	0.84
14	7	Hymenodora frontalis	54.0	1.24	0.63
15	5	H. frontalis	80.2	0.73	0.45
16	7	H. frontalis	54.2	1.15	0.59
17	9	H. frontalis	50.7	1.32	0.60
18	10	H. frontalis	46.5	1.57	0.68
19	7	H. frontalis	46.5	1.47	0.75
20	8	Sergestes similis	45.5	1.33	0.64
		BS			
9	3	Hymenodora frontalis	99.3	0.04	0.04
10	5	H. frontalis	74.1	0.62	0.39
		Mysids			
		WSA			
1	7	Eucopia grimaldii	67.8	0.96	0.49
2	4	E. grimaldii	86.0	0.48	0.35
4	3	E. grimaldii	72.4	0.65	0.59
5	5	E. grimaldii	86.7	0.52	0.32
6	4	E. grimaldii	89.6	0.38	0.27
21	5	E. grimaldii	85.2	0.58	0.36
22	6	E. grimaldii	79.6	0.78	0.44
23	6	E. grimaldii	71.7	1.00	0.56
24	9	E. grimaldii	62.3	1.31	0.60
		ESA			
13	3	Eucopia grimaldii	80.5	0.60	0.54
14	3	E. grimaldii	94.8	0.23	0.21
15	3	E. grimaldii	94.4	0.24	0.22
16	3	E. grimaldii	91.6	0.34	0.31
17	3	E. grimaldii	96.7	0.17	0.15
18	5	E. grimaldii	94.7	0.28	0.17
19	5	E. grimaldii	83.3	0.63	0.39
20	5	E. grimaldii	89.5	0.44	0.27
		BS			
9	3	Eucopia grimaldii	71.6	0.65	0.59
10	4	E. grimaldii	72.9	0.69	0.50

* co-dominant species

Table 2-IV. Previous records of abundance and biomass (expressed in values per 1000 m³) of MNC by taxa within the subarctic Pacific and Bering Sea, by region (WSA, ESA, BS – see text).

WSA Biomass (gWW)	WSA Abundance (inds)	ESA Biomass (gWW)	ESA Abundance (inds)	BS Biomass (gWW)	BS Abundance (inds)	References	Gear used	Mesh size (mm)
Decapods								
-	-	2.0 - 3.2	0.7 - 19.0	-	-	Krygier & Pearcy (1981)	IKMT, 50 m²	0.57
0.7	0.1 - 14.6	-	-	-	-	Kikuchi & Omori (1985)	KOC, KMT	5.6
11.4	-	-	-	-	-	Omori (1974)	ORI, IKMT	0.33/1
3.2	-	1.0	-	1.0	-	Iwasaki & Nemoto (1987)	IKMT	5
8.5	-	-	-	-	-	Aizawa (1968)	ORI	2, 1, 0.33
0.44 - 1.24	-	-	-	-	-	Aizawa (1974)	ORI	2 & 0.33
1.9	7.1	2.0	2.0	1.6	10.9	**This study**	IKMT	1
Euphausiids								
0.5 - 1.0	500 - 1000	0.5 - 1.0	100 - >1000	3	100 - >1000	Ponomareva (1963)	Juday/Nansen	no. 140 silk
-	50 - 500	-	50 - 500	-	-	Brinton (1962c)	various	0.65/(n/a)
-	-	-	-	240	-	Sugisaki, et al. (1998)	Methot trawl	2x3/1
5.5	267.1	3.4	229.8	1.1	53.7	**This study**	IKMT	1
Mysids								
-	-	-	-	0.05 - 3.0	-	Vinogradov (1970a)	n/a	n/a
0.06 - 0.07	0.3 - 0.5	-	-	-	-	Murano, et al (1976)	ORI	0.33
0.7	7.9	0.8	5.9	1.2	18.3	**This study**	IKMT	1

(90%). The 2 dominant species in the BS were *E. grimaldii* and *B. californica* (72 and 26% of total biomass, respectively).

MNC assemblages and diversity

Dominant species and species diversity are shown in Table 2-III. There were no significant differences in diversity among the euphausiids or decapods across the SAP and BS, but mysid diversity did significantly differ (Kruskal-Wallis test, $p>0.01$). Euphausiids (especially *Euphausia pacifica* and *Thysanoessa inspinata* in the SAP and *T. longipes* in the BS) were the dominant MNC within the SAP and BS. Dominant species were few (n=3) and these species typically comprised >50% of abundance and biomass, except in the central regions of the SAP (Stns 6 and 21) and the northern stations in the ESA (Stns 13 and 14). The community at Stn 13 was the most diverse ($H'=2.00$) and the relative composition of species was the most even within the SAP ($J'=0.69$). Although *Euphausia pacifica* was the dominant species at this station, it only comprised about 33% of either relative abundance or biomass, the lowest in the SAP. Station 16, also in the ESA was where the lowest diversity and evenness were found ($H'=0.79$, $J'=0.28$); *Thysanoessa inspinata* was overwhelmingly dominant biomass and abundance (82%). The dominant species in the BS, *Thysanoessa longipes*, was different from the SAP.

Within the euphausiids, diversity and evenness were highest ($H'=1.64$, $J'=0.71$) in the ESA (Stn 13) where the dominant species, *Euphausia pacifica*, composed 38% of abundance (Table 2-III). Diversity and evenness were lowest ($H'=0.28$, $J'=0.20$) among the euphausiids in the BS (Stn 10), where *Thysanoessa longipes* dominated abundance at over 90%. There was no significant difference in euphausiid diversity (H') between the WSA and ESA.

Decapod diversity was more even than that within euphausiids in the SAP, but not in the BS, where the lowest diversity of all taxa was at Stn 9, where *Hymenodora frontalis* completely dominated decapod diversity at 99% of abundance.

The mysids were dominated by *Eucopia grimaldii* (>60% dominance of abundance) throughout the entire study area.

Dendrograms

MNC assemblage dendrograms are shown in Fig. 2-6a. At about 77% similarity, the total MNC species assemblages were clustered into 3 groups. Group I consisted of the 2 BS stations. Group II was comprised of all but 5 of the stations in the subarctic Pacific (SAP), which subsequently made up the composition of Group III. Group III consisted of 3 stations in the WSA (Stns 1, 24 and 4) and 2 in the ESA (Stns 16 and 19).
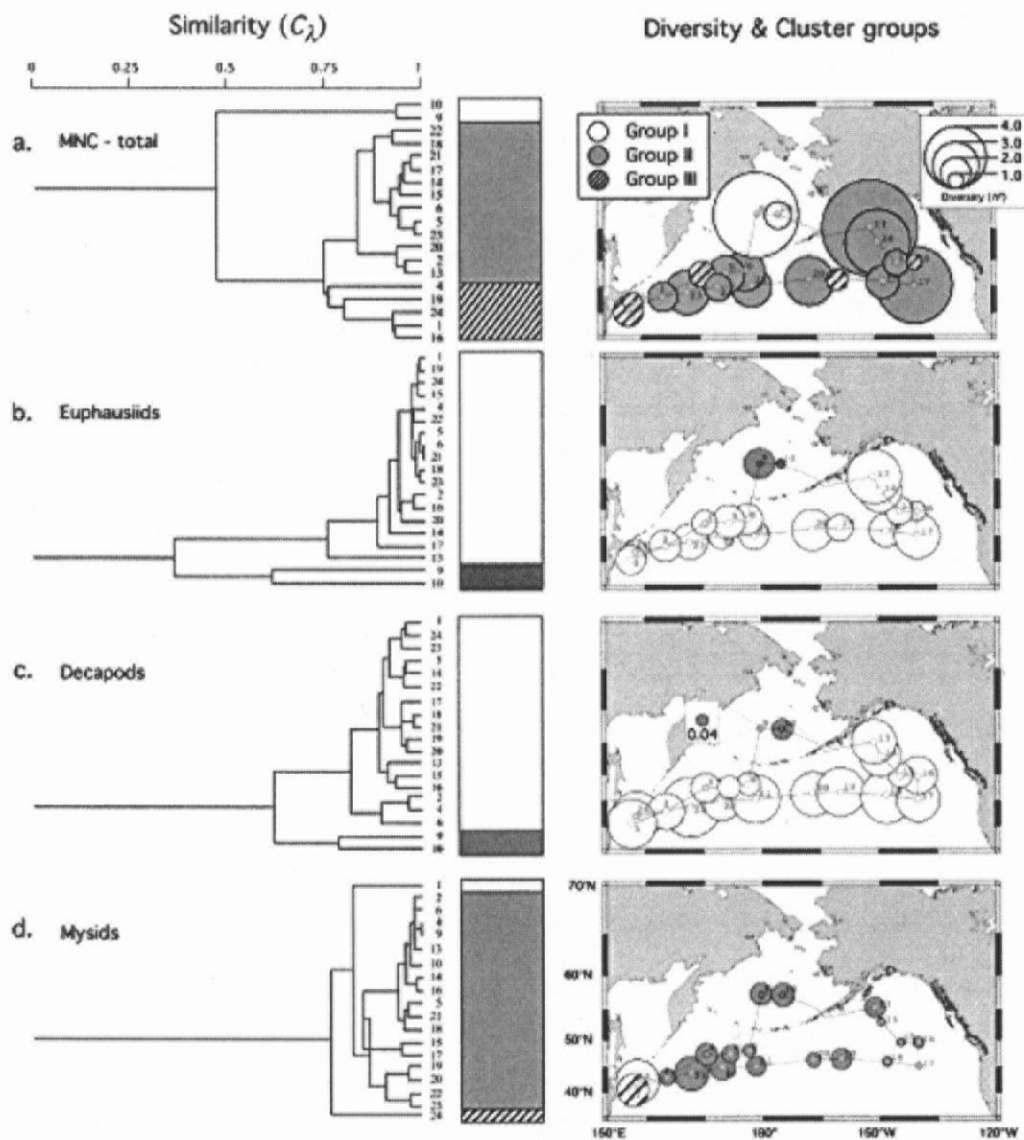
23

Fig. 2-6. Community structure and diversity of: (a) total MNC, (b) euphausiids, (c) decapods, and (d) mysids. Similarity dendrograms of communities and resulting group clustering (left column) and map (right column) are shown. Similarity (C_λ) and diversity (H') as described in text.

Euphausiid assemblages were clustered at a similarity level of 62% into 2 groups (Fig. 2-6b). Group I was composed of all the SAP stations. *Thysanoessa longipes* dominated total abundance (70%) in the BS euphausiid assemblage of Group II (Stn 9 and Stn 10; >92%).

Decapod assemblages were clustered at a similarity level of 70% into 2 groups (Fig. 2-6c). Group I was comprised of all the WSA and ESA stations. Group II consisted of the 2 BS stations, where *H. frontalis* dominated the shrimp assemblage (74 vs. 99%; Stn 9 and 10, respectively).

Mysid assemblages were clustered at a similarity level of 80% into 3 groups (Fig. 2-6d). Group I and III each comprised a single station (Stn 1 and 24, respectively). Group II consisted of all but 2 station in the WSA (Stn 24 and 1). Group III (Stn 24) was the most diverse, and had the greatest species evenness (H'=1.31, J'=0.60).

DISCUSSION

This study is the first to examine the euphausiids, decapods and mysids simultaneously with a uniform sampling regimen within the whole of the SAP and BS. There is a distinct latitudinal boundary in the North Pacific separating the SAP from the central North Pacific water masses (McGowan and Williams, 1973), and these water masses have distinct faunal compositions associated with a number of habitat variables, including climate effects (Brodeur and Ware, 1992). A distinct subarctic Pacific and Transitional zone euphausiid and decapod fauna has been described (Brinton, 1962a; Krygier and Wasmer, 1988), but not for pelagic mysids. Wasmer (1972) reported that the gyres in the WSA and ESA did more to concentrate and isolate species of shrimp from the "poorer central waters" and the distributions of pelagic shrimps associate with physico-chemically defined water masses and are not limited solely by temperature and salinity.

There were few differences in the composition of fauna among regions across the SAP. Although the results discussed here are from one cruise using one particular net, compared to previously reported records of MNC species in the SAP and BS, there were fewer species collected by the IKMT net in this Chapter. Of the 23 species of euphausiids reported from the SAP (Table 2-Va), 16 were collected in IKMT hauls. These included such meso- bathypelagic species as *Bentheuphausia ambylops, Thysanopoda acutifrons, T. monocantha, Nematobrachion boopis, N. flexipes, Stylocheiron elongatum,* and *S. maximum.* Of these, *S. elongatum, T. monocantha* and *N. boopis* are considered subtropical or transitional species within the North Pacific (Brinton 1962), so their presence in the SAP may be a result of the transport of warmer waters from lower latitudes during the 1997 ENSO. Species collected within the BS (n=5) included *T. spinifera,* a neretic species typically restricted to coastal regions of the BS and ESA (Sugisaki *et al*, 1998) mostly along the Alaskan and Canadian Pacific coasts (Brinton, 1962; Mackas and Tsuda, 1999). Therefore,

Table 2-Va. Pacific MNC. List of euphausiids reported in the SAP, with references. Species and distributions marked in parentheses and in bold type are records from this study. Numbers refer to reference list at the bottom of the table.

	Bering Sea	Subarctic-Transitional transpacific	ESA	WSA	Transitional	Central-Transitional	Reference
Euphausiids							
Bentheuphausia ambylops	(x)	x (x)	x (x)	x (x)	x	x	1, 2
Euphausia brevis					x	x	1, 2
Euphausia gibboides					x	x	1, 2
Euphausia hemigibba			x		x	x	1, 2
Euphausia mutica		x	x		x	x	1, 2
Euphausia pacifica	(x)	x (x)	x (x)	x (x)			1, 2
Euphausia pseudogibba					x		1, 2
Euphausia recurva			x		x	x	1, 2
Euphausia tenera				x	x	x	1, 2
Nematobrachion boopis			x (x)		x	x	1, 2
Nematobrachion flexipes			x	(x)	x	x	1, 2
Nematoscelis atlantica					x	x	1, 2
Nematoscelis difficilis		x	x (x)	x	x		1, 2
Nematoscelis gracilis				x (x)	x	x	1, 2
Nematoscelis microps					x	x	1, 2
Nematoscelis tenella					x	x	1, 2
Stylocheiron abbreviatum				x	x	x	1, 2
Stylocheiron affine (central form)					x	x	1, 2
Stylocheiron carinatum					x	x	1, 2
Stylocheiron elongatum			(x)		x	x	1, 2
Stylocheiron longicorne			x		x	x	1, 2
Stylocheiron maximum		x (x)	x (x)	x (x)	x	x	1, 2
Stylocheiron microphthalma					x	x	1, 2
Stylocheiron robustum					x	x	1, 2
Stylocheiron suhmii					x	x	1, 2
Tessarabrachion oculatum		x (x)	x (x)	x (x)			1, 2
Thysanoessa gregaria					x	x	1, 2
Thysanoessa inermis	(x)	x	x	x (x)			1, 2
Thysanoessa inspinata	(x)	x (x)	x (x)	x (x)			1, 2
Thysanoessa longipes	(x)	x	x (x)	x (x)			1, 2
Thysanoessa parva					x		1, 2
Thysanoessa rashii	x		x	x			1, 2
Thysanoessa spinifera	x		x (x)				1, 2
Thysanopoda acutifrons		x	x (x)	x (x)	x		1, 2
Thysanopoda aequalis					x	x	1, 2
Thysanopoda cornuta			x				1, 2
Thysanopoda egregia						x	1, 2
Thysanopoda monocantha			x	(x)	x	x	1, 2
Thysanopoda obtusifrons						x	1, 2
Thysanopoda orientalis					x	x	1, 2
Thysanopoda pectinata					x		1, 2
Thysanopoda subaequalis						x	1, 2
Thysanopoda tricuspidata					x		1, 2
total 43	7	10	20	15	32	29	

1. Mauchline & Fisher 1969
2. Brinton 1962
3. Krygier&Wasmer 1988
4. Aizawa 1974
5. Iwasaki 1989
6. Krygier&Pearcy 1981
7. Iwasaki & Nemoto 1987
8. Kikuchi & Nemoto 1986
9. Hayashi 1988
10. Krygier&Murano 1988
11. Mauchline&Murano 1977
12. Murano 1981
13. Ii 1964
14. Pequegnat 1965

collection in the pelagic ESA showed that this euphausiid was being transported much further off shore than usual. The dominant euphausiids described within the SAP are the same as those identified by Brinton (1962) and Mackas and Tsuda (1999) as dominant, therefore showing that even under conditions such as the 1997 ENSO, the core of the euphausiid community remains the same. During the same event, Peterson *et al.* (2002) found that the zooplankton community of the Oregon coast was strongly affected by the 1997 ENSO, such that usually dominant boreal copepods were replaced by subtropical species. This was not the case in this Chapter, where the presence and low abundance (< 0.1 ind/1000 m^3) of central/transitional euphausiid species in the WSA and ESA did not apparently affect the SAP community structure.

There are 65 species of pelagic shrimps reported from the North Pacific (Table 2-Vb). However, only 15 of these species were collected by IKMT. There are fewer records of pelagic shrimp from the BS (n=6) (Iwasaki and Nemoto, 1985), of which 5 were collected. The dominant species in the SAP & BS collected via IKMT were the same as previous records with three exceptions in BS hauls from this Chapter: the absence of *Notostomus japonicus* and *Pasiphaea tarda*, and the presence of *Sergia tenuiremis,* not previously reported from the BS. These were all rare or uncommon species, and their presence and absence are most likely reflections of their rarity. Most of the MNC species discussed in this Chapter were widely distributed across the entire region. The transitional or subtropical species recovered in the SAP (Table 2-I) included *Pasiphaea japonica* in both the ESA and WSA, *Sergia gardineri* and *Physetocaris micropthalma* in the WSA. With the exception of *Pasiphaea japonica*, the presence of these tropical-transitional species, especially given their low abundances (< 0.01 ind/1000 m^3), may be attributed to chance transport into the study area. This transport may be more common for epipelagic compared to mesopelagic species, as shown by the presence of *P. japonica*, described by Krygier and Wasmer (1988) as part of the western Pacific Tropical-Transitional group. Abundances of this species were higher (> 0.01 ind/1000 m^3) and more widely distributed (stations: ESA n=3, WSA=5).

Only 8 of the 36 species of pelagic mysids reported from the North Pacific, and only 4 species out of 32 species of pelagic mysids described as typical of the ESA off the Oregon coast (Krygier and Murano, 1988) were collected in this Chapter (Table 2-Vc). These comprised primarily mesopelagic and bathypelagic species, with biomass centers usually below 1000 m (Mauchline and Murano, 1977; Krygier and Pearcy, 1981; Kikuchi and Omori, 1985). Overall, the stability of mysids across the study region is a phenomenon not previously reported in the SAP and BS.

The stability of the mysid community is presumably a reflection of the stable mesopelagic environment in which they predominate. The only portion of the SAP&BS where there was any

Table 2-Vb. Pacific MNC. List of pelagic decapods reported in the SAP, with references. Species and distributions marked in parentheses and in bold type are records from this study. Numbers refer to reference list at the bottom of the table.

	Bering Sea	Subarctic-Transitional			Transitional	Central-Transitional	Reference
		transpacific	ESA	WSA			
Decapods							
Bentheogennema borealis	x (x)	x (x)	x (x)	x (x)	x		3, 4, 5, 6, 7, 8
Bentheogennema burkenroadi			x	x	x		3, 4, 6
Bentheogennema intermedia				x			3, 5, 8
Gennadas incertus			x	x		x	3, 4, 5, 6, 8
Gennadas propinquus			x	x		x	3, 4, 5, 6, 8
Gennadas tinayraei			x	x		x	3, 4, 5, 6, 8
Gennadas bouveri				x			3, 4, 5, 8
Gennadas capensis				x			3, 5
Gennadas parvus				x			3, 4, 5, 8
Gennadas scutatus				x			4, 5, 8
Sergestes similis	x (x)	x (x)	x (x)	x (x)	x		3, 4, 5, 6, 7, 8
Sergestes vigilax			x			x	3, 5
Sergestes armatus				x			8
Sergestes pectinatus				x			8
Sergestes sargassi				x			8
Sergestes seminudus				x			8
Sergia creber			x	x			3, 5, 8
Sergia prehensilis				x			3, 5, 8
Sergia japonica			(x)	x (x)	x		3, 5, 6, 8
Sergia tenuiremis	(x)		x				6
Sergia kroyeri					x		3
Sergia gardineri				x (x)			3, 5
Sergia laminata			(x)	x			3, 5, 8
Petalidium suspiriosum			x	x	x		5, 6, 8
Hymenodora frontalis	x (x)	x (x)	x (x)	x (x)	x		3, 4, 5, 6, 7, 8
Hymenodora glacialis		x	x	x			3, 5, 6, 8
Hymenodora gracilis	x (x)		(x)	x (x)			3, 5, 6, 8
Hymenodora acanthitelsonis			x	x	x		3
Pasiphaea affinis			x				3
Pasiphaea corteziana			x				3
Pasiphaea emarginata			x				3
Pasiphaea japonica		x (x)	x (x)	x (x)			3, 5
Pasiphaea tarda		x (x)					3, 6
Pasiphaea chacei			x		x		3, 6
Pasiphaea magna			x		x		3, 6
Pasiphaea pacifica			x		x		3, 6
Pasiphaea sivado				x			4
Parapasiphae sulcatifrons		(x)	x (x)	x (x)	x		3, 5, 6, 8
Parapasiphae cristata			x		x		3, 6
Panalopsis ampla					x		3
Parapandalus zurstrasseni				x			4
Acanthephyra armata				(x)			8
Acanthephyra acutifrons				x			3, 4, 5, 8
Acanthephyra eximia			x	x			3, 4, 5
Acanthephyra smithi				x			3, 4, 5
Acanthephyra chacei			x				3
Acanthephyra cucullata				x			8
Acanthephyra curtirostris		x	x	x	x	x	3, 4, 5, 6, 8
Acanthephyra gracilipes				x			8
Acanthephyra quadrispinosa			x	x		x	3, 4, 5, 6, 8
Acanthephyra microphthalma				x			4
Notostomus japonicus	x	x (x)	x (x)	x (x)		x	3, 4, 5, 6, 7, 8
Meningodora mollis			x	x	x	x	3, 5, 6, 8
Meningodora vesca				x			8
Systellaspis braueri	x (x)	x (x)	x (x)	(x)			3, 5, 6, 7, 8
Systellaspis cristata		x	x	x	x		3, 5, 6, 8
Systellaspis debilis			x	x			3, 4, 5, 6, 8
Oplophorus gracilirostris				x	x		3, 4, 5
Oplophorus spinosus				x			3, 4, 5, 8
Oplophorus spinicauda				x			4, 5
Aristaeomorpha foliacea			x	x		x	3, 5
Benthesicymus carinatus				x			8
Crangon abyssorum			x				6
Ephyrina benedicti				x			3, 5
Hymenopenaeus laevis				x			8
Heterogenys microphtalma					x		3
Nematocarcinus exilis			x	x			6, 8
Physetocaris microphthalma				x (x)			3, 4, 5, 8
total	**68**	**6**	**11**	**38**	**53**	**19**	**9**

1. Mauchline & Fisher 1969
2. Brinton 1962
3. Krygier&Wasmer 1988
4. Aizawa 1974

5. Iwasaki 1989
6. Krygier&Pearcy 1981
7. Iwasaki & Nemoto 1987
8. Kikuchi & Nemoto 1986

9. Hayashi 1988
10. Krygier&Murano 1988
11. Mauchline&Murano 1977
12. Murano 1981

13. Ii 1964
14. Pequegnat 1965

Table 2-Vb. Pacific MNC. List of pelagic mysids reported in the SAP, with references. Species and distributions marked in parentheses and in bold type are records from this study. Numbers refer to reference list at the bottom of the table.

	Bering Sea	Subarctic-Transitional			Transitional	Central-Transitional	Reference
		transpacific	ESA	WSA			
Mysids							
Acanthomysis stelleri		x					10, 11
Archaomysis grebnitzkii		x					10
Acanthomysis borealis			x				10, 11
Acanthomysis brunnea			x				10
Acanthomysis californica			x				10
Acanthomysis columbiae			x				10, 11
Alienacanthomysis macropsis			x				10, 11
Amathimysis trigibba			x				10
Boreomysis californica	(x)	x (x)	x (x)	x (x)	x	x	10
Boreomysis inermis		x	x	x	x	x	10
Boreomysis pearcyi			x				10
Boreomysis microps	(x)	x (x)		(x)			12
Boreomysis intermedia				(x)			13
Bacescomysis pacifica			x				10
Ceratomysis spinosa		x	x	x	x	x	10
Caesaromysis hispida		x	x	x	x	x	10
Columbiaemysis ignota			x				10
Dactylerythrops latisquamosa			x				10
Dactylambylops iii				(x)			12
Disacanthomysis dybowskii		x					10
Meterythrops micropthalma				(x)			13
Euchaetomera tenuis		x	x	x	x	x	10
Euchaetomeropsis pacifica			x				10
Exacanthomysis alaskensis			x				10
Eucopia australis		x	x	x	x	x	10
Eucopia grimaldii	(x)	x (x)	x (x)	x (x)	x	x	10
Eucopia sculpticauda		x	x	x	x	x	10
Gibbambylops longisquamosa			x				10
Gnathophausia gigas	(x)	x (x)	x (x)	x (x)	x	x	10, 14
Gnathophausia ingens		x	x	x	x	x	10
Inusitatomysis insolita		x					10
Holmesiella anomala		x					10
Petalophthalmus armiger		x	x	x	x	x	10
Pleurerythrops secunda				(x)			11
Pseudomma berkeleyi			x				10
Teraterythrops robusta		x					10
total	**36**	**18**	**26**	**16**	**11**	**11**	

1. Mauchline & Fisher 1969
2. Brinton 1962
3. Krygier&Wasmer 1988
4. Aizawa 1974

5. Iwasaki 1989
6. Krygier&Pearcy 1981
7. Iwasaki & Nemoto 1987
8. Kikuchi & Nemoto 1986

9. Hayashi 1988
10. Krygier&Murano 1988
11. Mauchline&Murano 1977
12. Murano 1981

13. Ii 1964
14. Pequegnat 1965

difference in either community structure or composition was in the westernmost WSA stations. These stations were heavily influenced by the influx of species from the offshore regions of eastern Japanese coast, which have not been reported east of 150° E. These included *Pleurerythrops secunda*, a shallow (ca. 80m) neretic epipelagic mysid (Murano, 1970), of which only one individual was collected from the western-most station in the WSA (Stn 1), and *Dactylambylops iii*, previously only described from lower latitude waters off Japan: i.e. the Honshu coast (Ii, 1964; Nouvel and Lagadere, 1976; Mauchline and Murano, 1977; Murano, 1981) may be additional evidence of increased transport into the oceanic regions as a result of the 1997 ENSO. An exception was *Meterythrops micropthalma* previously described from collections of the USFC RV *Albatross* in the northwestern SAP from meso- bathypelagic depths (350 – 1829 m) (Tattersall, 1951).

Abundance and Biomass

There was a modest relationship between euphausiid and decapod biomass, but only a very weak relationship between abundance (Fig. 2-7). Conversely, there was a modest relationship between decapod and mysid abundance, and only a very weak one between biomass. There was a very weak negative relationship between mysid and euphausiid abundance and only a weak relationship between biomass. The modest relationships between euphausiid and decapod biomass may be a reflection of large concentrations of euphausiid biomass compared to the smaller biomasses of predatory decapods. Decapods like *Sergestes similis* are known to feed upon euphausiids (Omori, 1979), and are the only dominant decapods in the SAP and BS to vertically migrate into the epipelagic zone where the bulk of euphausiid biomass is known to congregate. The weak relationships between mysid and euphausiid abundance and biomass most likely a reflection of the different vertical partitioning patterns between the epipelagic euphausiids and the mesopelagic mysids. The modest relationship between decapod and mysid abundance likely reflects their similar mesopelagic distribution, since there is little information regarding the feeding of decapods on mysids. The coefficient of variation (Table 6) supports this, since in terms of abundance and biomass mysids were the lowest, suggesting moderate regional differences, and euphausiids the highest, suggesting greater variability in this epipelagic group.

The biomass and abundance patterns between the Sap and BS differed as well as community structure patterns. The simplest explanation for this is the limited number of sampled sites in the BS compared to the SAP. Vertical distribution sampling with the RMT 8+1 net (discussed in Chapter 3) indicate that biomass and abundance do not differ across the study area, and although variability is high, means are comparable across regions. Previous large-scale regional studies of

Table 2-VI. Kruskal-Wallis test of abundance and biomass, by regions, for MNC taxa.

Group		Ind/1000 m³	
	d.f.	X^2	P
Euphausiids	2	6.3558	0.0417
Decapods	2	6.8294	0.0329
Mysids	2	5.1435	0.0764
		gWW/1000 m³	
Euphausiids	2	8.1281	0.0172
Decapods	2	7.4487	0.0241
Mysids	2	4.2536	0.1192

Table 2-VII. Coefficient of variation (CV) for the 0 – 1000 m water column abundance and biomass for MNC taxa based on oblique hauls at all stations.

Group	CV	
	Abundance	Biomass
Euphausiids	65.8	85.2
Decapods	54.7	52.2
Mysids	54.5	34.2

macrozooplankton and euphausiids in the BS and ESA have all reported high abundances, particularly along the margins of the SAP and BS and their associated gyre systems (e.g. Sugisaki *et al* 1998). More biomass than abundance data is available (Table 4), there are large variations in gear and mesh sizes used, and data are often summarized from samples collected via multiple cruises, conducted over several years (*e.g.* Brinton, 1962a, 1962c; Ponomareva, 1963; Krygier and Pearcy, 1981; Krygier and Wasmer, 1988). Even so, the abundance found in this study was often within the range of previous studies, while biomass values reported here tended to be higher in the ESA and WSA. Only biomass in the BS reported by Sugisaki, *et al.* (1998) was much higher than reported here, presumably due to gear variations (e.g. the Methot trawl used by Sugisaki, *et al.*).

The large abundances of younger, or smaller (< 12 mm) euphausiids at Stn 5 in the WSA may be related to the exploitation of primary production, since Chl-*a* at this station was the highest recorded (> 4.5 μg/L) of all stations in this cruise. However, this was concentrated at 50 m, which is within the normal nighttime vertical range of the dominant species (*Thysanoessa inspinata*) at this station. Since younger euphausiids tend to be found higher in the water column than older individuals, this may reflect younger euphausiids schooling to exploit the Chl-*a*-rich resource found during the daytime at this station. Honda (2003) in describing the biological pump in the WSA gyre reported higher annual average primary production in the ESA (OSP; 384 mg m^{-2} day^{-1}) compared to the WSA (KNOT; 220 - 384 mg m^{-2} day^{-1}). Although Honda mentioned that these averages may be skewed due to the inclusion of earlier data sets that were derived from primarily coastal stations, he concluded that the springtime blooms in the WSA must be higher than the global average (Honda, 2003). Summer increases in zooplankton biomass could be utilized by the MNC since higher trophic levels, such as chum and sockeye salmon, were more abundant in the Bering Sea in 1977–1984 and 1991–2000 when SST was relatively high in the Gulf of Alaska (Ishida, *et al.* 2002). However, since a vertical distribution profile of *T. inspinata* is unavailable for this station, the connection between the large abundance of *T. inspinata* individuals and the high Chl-*a* concentration cannot be clearly discerned. There were only very weak correlations between physical or chemical parameters within the SAP and BS.

Stations with the highest abundance and biomass in the WSA (Stns 24, 1 and 4) were characterized by higher chlorophyll-*a* concentrations (2, 1.3 and 5 μg/L, respectively) than at other stations. The coincident abundance and biomass peaks may represent intense swarming of dominant euphausiid species, feeding on rich food resources associated with the blooms at these stations. In the BS, there was a chlorophyll-*a* maximum at Stn 10 (2.5 μg/L), which may explain why abundance was higher compared to Stn 9. However, there were only very weak correlations

between Chl-*a* and abundance or biomass across the study area for any of the three MNC taxa ($R^2<0.07$).

There were very weak negative correlations between dissolved oxygen and abundance and biomass of euphausiids, and virtually no correlation between DO and either decapod and mysid abundance or biomass ($R^2<0.008$). In addition, there was a modest negative relationship between the concentrations of DO and Chl-*a*. There were very weak relationships between salinity (psu) and abundance and biomass for all MNC taxa, although in the case of euphausiids, there was a very weak negative relationship between psu and abundance ($R^2=0.032$). Similarly, there were only very weak relationships between water temperature and either abundance or biomass of the MNC in the SAP and BS ($R^2<0.19$). That the abundance and biomass patterns of the MNC are relatively stable and their weak relationships to the relatively homogenous physical and chemical parameters (Fig. 2-3) are supported by the relatively uniform assemblage clustering among the MNC shown above (Fig. 2-6). This would seem to suggest that the communities of MNC are not greatly influenced by the relatively small changes in the vertical structure of the SAP and BS across the region, and that there are other factors besides the physical and chemical parameters of the water column that are responsible for the variations in abundance and biomass reported here. These factors may be related to vertical distribution or feeding patterns, which will be examined in the following chapters.

CHAPTER 3

Diel vertical distribution of micronektonic crustaceans

in the subarctic Pacific and Bering Sea in summer, 1997.

INTRODUCTION

Vertical migration in pelagic animals is a well-described phenomenon and has been observed in all oceans (Donaldson, 1975; Krygier and Pearcy, 1980; Cartes, 1993; Hopkins, *et al.* 1994). Diel vertical migration (DVM) is the movement of biomass or abundance peaks up in the water column at night and down during the day, and has been described in many pelagic animals such as copepods, chaetognaths, micronektonic crustaceans, and fishes.

Vinogradov (1968) identified this constant movement up and down in the water column as an "elevator" that transports energy (in the form of food, feces, detritus, etc.) from surface layers down through the water column. When combined with the DVM patterns of species whose vertical ranges slightly overlap, this creates a stepped ladder from the top of the water column into the depths. While DVM in the MNC has been intensively studied in the north Pacific (Brinton, 1962; Brinton, 1962; Pearcy and Forss, 1966; Aizawa, 1974; Maynard, *et al.* 1975; Walters, 1976; Krygier and Pearcy, 1981; Iwasaki and Nemoto, 1987; Brodeur, *et al.* 1999), and Bering Sea (Iwasaki and Nemoto, 1987; Smith, 1991), these studies have mainly focused on the vertical distribution patterns, diel vertical migration and ecological aspects of a limited number of species. There are few reports regarding the abundance, biomass and vertical distribution patterns of pelagic mysids, particularly for the subarctic north Pacific (SAP) and Bering Sea (BS).

Much effort has been put into describing the food web of the subarctic Pacific, and defining the relationships and trophic pathways between and within trophic levels (Brodeur, *et al.* 1999; Taniguchi 1999; McFarlane, *et al.* 2000; etc.). The roles of top predators, such as whales and fishes has been described (e.g. Nemoto and Kawamura 1977; Brodeur 1988; Beamish, *et al.* 1999; Tamura and Fujise 2002), as well as the production and importance of primary and secondary producers (e.g. Parsons and Anderson 1970; Silver and Gowing 1991; Mackas and Tsuda 1999; Imai, *et al.* 2002; etc.); however, the role of MNC in the subarctic Pacific is still not clearly understood. Studies of MNC in the north Atlantic (Angel and Pugh 2000), the Gulf of Mexico (Hopkins, *et al.* 1994), the southern Ocean (Pakhomov, *et al.* 1999) and the Mediterranean (Maynou and Cartes 1998) have shown that the predatory impact of MNC can be as important as midwater fishes, such as myctophids (Moku and Hidaka 2002).

In order to better understand the role of MNC in the SAP and BS pelagic food web, first their DVM patterns across the region must be clarified. This will identify, by depth distribution, important species in terms of abundance and biomass and then allow examination of their trophic roles in more detail. Therefore, because available data regarding pelagic MNC species and their horizontal and vertical distribution patterns in the SAP (Pearcy and Forss 1966; Wasmer 1972;

Aizawa 1974; Kikuchi and Omori 1985; Krygier and Murano 1988; Krygier and Wasmer 1988; Sugisaki, et al. 1998) have mainly come from stations confined to limited geographical extent, this chapter presents a detailed description of the vertical profile within each of the 3 major regions of the subarctic Pacific: western subarctic (WSA), central subarctic (CSA), eastern subarctic (ESA), and the Bering Sea, (BS). Differences between these 4 regions, influences on vertical structure from physical/chemical parameters, and the resulting implications for trophic partitioning are discussed. Understanding the similarities and differences in the vertical community structure of these four regions will help clarify the relative importance of species within certain vertical depth ranges, and provide a foundation for further detailed examination of feeding and trophic importance of the MNC in the SAP and BS.

METHODS

The MNC examined in this chapter were collected in the subarctic Pacific and Bering Sea during the period 18 July- 12 August 1997 (Fig. 3-1) during the cruise of the RV Hakuho Maru (KH 97-2, see Chapter 2).

Samples were collected with an opening/closing rectangular midwater trawl (RMT 1+8) system, (Baker *et al.*, 1973), which consists of 3 pairs of nets (1-m^2 and 8-m^2 nets) and can sample 3 discrete layers in a single tow; on this cruise the nets were opened and closed by a release gear connected to an electric net monitor. Samples were collected at 4 stations (Fig. 3-1) with the 8-m^2 nets (mesh size: 4.5 mm) from 12 depth layers from 0 to 1000 m both day and night (Table 3-I). Each station was chosen as representative of each major water mass: the western subarctic gyre (WSA), the central subarctic (CSA), the eastern subarctic gyre (ESA), and the oceanic Bering Sea (BS). The depths of each sampling layer above 300 m at each station were decided according to vertical thermal water column structure obtained from CTD casts (Ocean Research Institute, University of Tokyo, 1998). The nets were towed at ca. 2 knots, and the average volume of water filtered by the net in a single layer was ca. 12,300 m^3 (range ca. 2000 - 33,200 m^3). Due to complications with net equipment at the BS and ESA stations, night sampling for deeper layers was not completed, resulting in a nighttime sampling of the water column from 0 - 500 m in the BS and 0 - 700 m in the ESA. After collection, the samples were immediately fixed and preserved in a 10% formalin/seawater solution buffered with sodium tetraborate. Euphausiids, decapods and mysids were sorted out in the laboratory, identified to species, individual numbers counted, and then wet weight determined with a Mettler AE 100 top-loading electronic scale. Decapod and mysid samples were counted in their entirety; however, due to the high numbers of euphausiids, an aliquot
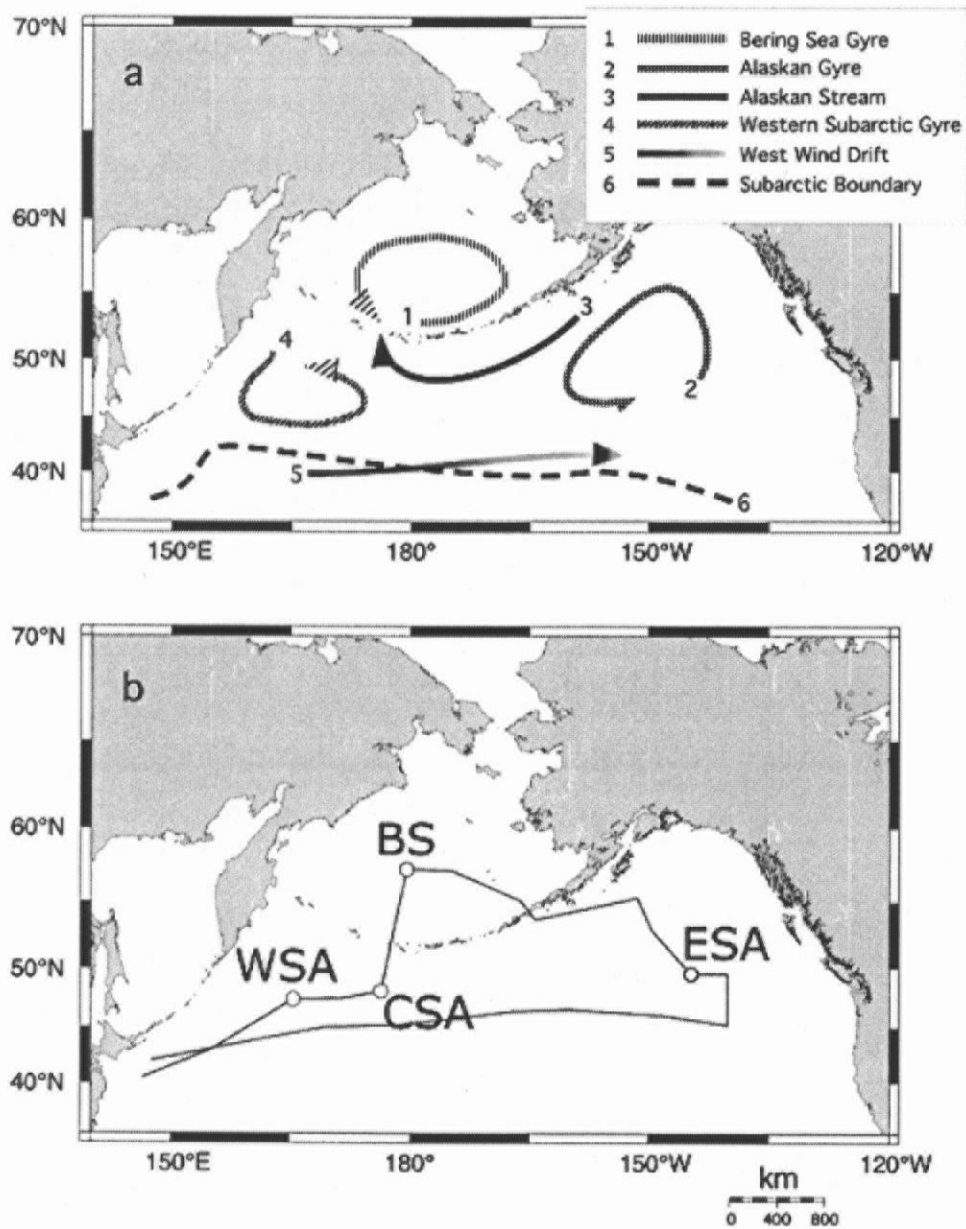
Fig. 3-1. Current systems in the subarctic Pacific and Bering Sea (a), and RMT stations examined in Chapter 3 (b). Station labels are as in text. The solid black line represents the cruise track.

Table 3-I. RMT 8+1 sampling data from the SAP and BS. Local time indicates sampling times per associated depth layers. (After Nishikawa et al., 2001).

Region (Day/Night)	Date	Sampling Depth (m)	Local Time (h)
WSA (N)	18 July 1997	1000 - 700	2112 - 2222
WSA (N)	18 July 1997	150 - 0	2324 - 2400
WSA (N)	19 July 1997	400 - 150	0057 - 0138
WSA (D)	19 July 1997	1000 - 700	0527 - 0616
WSA (D)	19 July 1997	700 - 400	0805 - 0856
WSA (D)	19 July 1997	400 - 150	1025 - 1126
WSA (D)	19 July 1997	150 - 0	1234 - 1308
WSA (N)	19 July 1997	700 - 400	2034 - 2124
CSA (D)	22 July 1997	1000 - 700	0633 - 0741
CSA (D)	22 July 1997	400 - 150	0951 - 1040
CSA (D)	22 July 1997	150 - 0	1139 - 1229
CSA (N)	22 July 1997	1000 - 700	2158 - 2237
CSA (N)	22 July 1997	400 - 150	2349 - 0139
CSA (N)	22 July 1997	150 - 0	0209 - 0317
CSA (D)	23 July 1997	700 - 400	1021 - 1112
CSA (N)	23 July 1997	700 - 400	2139 - 2328
BS (D)	25 July 1997	180 - 0	1358 - 1542
BS (D)	25 July 1997	500 - 180	1636 - 1903
BS (N)	25 July 1997	180 - 0	2355 - 0002
BS (N)	26 July 1997	500 - 180	0152 - 0336
BS (D)	27 July 1997	1000 - 700	0944 - 1130
BS (D)	27 July 1997	700 - 400	1312 - 1414
ESA (N)	10 August 1997	120 - 0	2355 - 0016
ESA (N)	11 August 1997	400 - 120	0152 - 0443
ESA (D)	11 August 1997	700 - 400	0641 - 0941
ESA (D)	11 August 1997	400 - 120	1051 - 1344
ESA (D)	11 August 1997	120 - 0	1436 - 1506
ESA (N)	11 August 1997	700 - 400	2358 - 0248
ESA (D)	12 August 1997	1000 - 700	1251 - 1550

(1/4 to 1/32) of each sample was taken with a Folsom plankton splitter and then examined. The number of individuals and wet weight in the water column of 0 - 1000 m were calculated on the basis of stratified sampling data. Remarks detailing previous records for each dominant species, when available, follow vertical distribution results.·

RESULTS

Hydrography

Hydrographic conditions of the study area are described in Chapter 2.

Vertical distribution - dominant species

MNC abundance considered here (Table 3-II) averaged about 160.7 vs. 244.8 ind./m^2 (day vs. night, respectively) while biomass averaged 14.4 vs. 14.0 gWW/m^2 (day vs. night, respectively) in the upper 1000 m across the study area. These 35 species constitute all but 48% of the total number of pelagic decapod and mysid species previously reported from the subarctic Pacific but 100% of the total euphausiid species in this depth zone. 27,715 animals were examined in this study (14,622 euphausiids, 4,699 decapods, and 8,394 mysids).

There were 4 numerically dominant euphausiids: *Euphausia pacifica*, *Thysanoessa inspinata*, *T. longipes*, and *Tessarabrachion oculatum* (Fig. 3-2), all of which exhibited typical DVM patterns. These epipelagic species were concentrated in the top 400 m of the water column, day or night, at all 4 stations.

Except for the large daytime biomass peak shown by *E. pacifica* in the ESA, nighttime peaks (0 - 100 m) greatly exceeded those in the daytime (200 - 300 m). Large *E. pacifica* biomass was usually found in the 20 to 100 m layer at night in the WSA and CSA, while in the ESA this layer had much lower nighttime biomasses. [Remarks: Reported nighttime abundances or biomasses for *E. pacifica* are typically larger than in the daytime (Brinton 1962; Brinton 1967; Alton and Blackburn 1974). Brinton (1962c) reported that from 0 to 1000 m in the eastern subarctic, nighttime abundances can reach 2000 inds/1000 m^3 in the top 140 m, while daytime abundances in the same layers were less than 750 inds/1000 m^3.]

Nighttime biomass peaks of *Thysanoessa inspinata* were in the 0 - 150 m layers. Except for the relatively large daytime biomass in the 150 - 200 m layer in the CSA, daytime biomasses were almost non-existent. [Remarks: in the subarctic Pacific, Brinton (1962) reported the maximum density for *T. longipes*, unspined form (= *T. inspinata*) in the 0 - 280 m layer both day and night. According to Nemoto (1963), this species differs ecologically from the congener *T. longipes* by

Table 3-II. Abundance (this page) and biomass (following page) of all euphausiids, decapods, and mysids collected via RMT+8 net, KH 97-2. Extrapolated night values are presented in italic text, drawn from daytime values for stations with missing data (ESA and BS nighttime).

Abundance

	WSA Day 0-1000m inds/m²	WSA Night 0-1000m inds/m²	CSA Day 0-1000m inds/m²	CSA Night 0-1000m inds/m²	ESA Day 0-1000m inds/m²	ESA Night 0-700m inds/m²	ESA Night* 0-1000m inds/m²	BS Day 0-1000m inds/m²	BS Night 0-500m inds/m²	BS Night* 0-1000m inds/m²	Day-total 0-1000m inds/m²	Night-total 0-1000m inds/m²
Euphausiids												
Euphausia pacifica	26.51	25.09	11.61	70.68	46.68	1.51	*1.53*	0.11	0.19	*0.20*	84.91	97.48
Thysanoessa longipes	2.59	40.64	0.19	1.26		7.89	*7.90*	3.97	4.58	*4.71*	6.75	46.48
Thysanoessa inspinata	0.43	30.95	0.68	4.05	0.13			0.03	0.42	*0.42*	1.26	43.31
Thysanoessa inermis	0.01	0.01						0.50	0.30	*0.31*	0.51	0.31
Unknown (damaged) sp.	0.53	5.43		0.114	0.85	1.03	*1.04*	0.06	0.07	*0.07*	1.44	6.64
Euphausiids (damaged) sp.	0.03										0.03	0
Bentheuphausia amblyops	7.78	5.44	0.09	0.07	0.28	0.30	*0.33*	0.01	0.02	*0.03*	8.17	5.82
Tessarabrachion oculatum	0.02	0.00	0.16	0.04	0.97	1.77	*1.79*	0.04	0.02	*0.02*	1.20	1.83
Stylocheiron abbreviatum				0.01							0	0.01
Stylocheiron elongatum											0	0.01
Stylocheiron maximum					0.21	0.59	*0.59*		0.01	*0.01*	0.21	0.59
Stylocheiron sp.					0.004		*0.004*				0.004	0
Nematobrachion flexipes						0.02	*0.02*				0	0.02
Nematobrachion boopis					0.004						0.004	0
Thysanopoda acutifrons					0.004	0.01	*0.01*				0.004	0.01
Total	37.9	107.6	12.7	76.2	49.1	13.1	*13.2*	4.7	5.6	*5.8*	104.5	202.5
Decapods												
Hymenodora sp.	0.03	0.01									0.03	0.01
Hymenodora frontalis	4.33	4.59	3.82	3.63	1.66	1.25	*2.16*	7.79	1.21	*6.44*	17.60	10.68
Hymenodora acanthielsonis							*0.04*	0.01	0.04	*0.04*	0.01	0.04
Sergestes similis	0.19	0.47	0.79	0.07	0.36	0.36	*0.36*	0.005	0.01	*0.01*	1.34	0.91
Bentheogennema borealis	0.76	1.69	1.13	1.22	0.20	0.24	*0.28*	0.04			2.13	3.16
larvae	0.17			0.008							0.19	0.01
Sergia japonica	0.03	0.01	0.06		0.06	0.06		0.02	0.02		0.09	0.01
Sergia tenuiremis	0.01				0.02	0.06	*0.10*				0.01	0
Systellaspis braueri	0.03			0.05			*0.06*				0.08	0.06
Pasiphaea japonica		0.02	0.02	0.005				0.01	0.01	*0.02*	0.06	0.14
Pasiphaea sinensis					0.003						0.003	0.01
Pasiphaea tarda				0.005							0.01	0
Parapasiphaea sulcatifrons			0.01					0.01			0.01	0.01
Funchalia sagamiensis			0.02					0.02			0.02	0
Meningodora marptocheles			0.01		0.02	0.04	*0.05*		0.02	*0.02*	0.03	0.04
Notostomus japonicus				0.01							0.02	0
damaged (unknown)								0.01	0.01	*0.01*	0.01	0.01
Pandalus sp. (?)								0.01		*0.02*	0.01	0.02
Unknown sp. (Caridean)				0.01	0.003						0.01	0
Total	5.5	6.8	5.9	5.0	2.3	2.0	*3.0*	7.9	1.3	*6.6*	21.6	15.1
Mysids												
Boreomysis californica	1.99	1.98	0.38	0.73	0.06	0.03	*0.06*	2.01	0.21	*1.68*	4.44	2.95
Eucopia grimaldii	8.01	8.96	6.66	7.99	4.93	4.89	*6.61*	9.42	0.89	*6.36*	29.02	22.72
Eucopia sculpticauda					0.003						0.00	0
Gnathophausia gigas	0.09	0.07	0.22	0.74	0.28	0.29	*0.35*	0.53	0.42	*0.47*	1.12	1.52
Mysida (sp.)					0.01			0.01			0.01	0
Unknown sp.								0.01			0.01	0
Total	10.1	11.0	7.3	9.5	5.3	5.2	*7.0*	12.0	1.5	*8.5*	34.6	27.2
Total	53.5	125.3	25.8	90.7	56.7	20.3	*23.2*	24.6	8.4	*20.9*	160.7	244.8

Table 3-II. (Continued) biomass of all euphausiids, decapods, and mysids collected via RMT+8 net, KH 97-2.

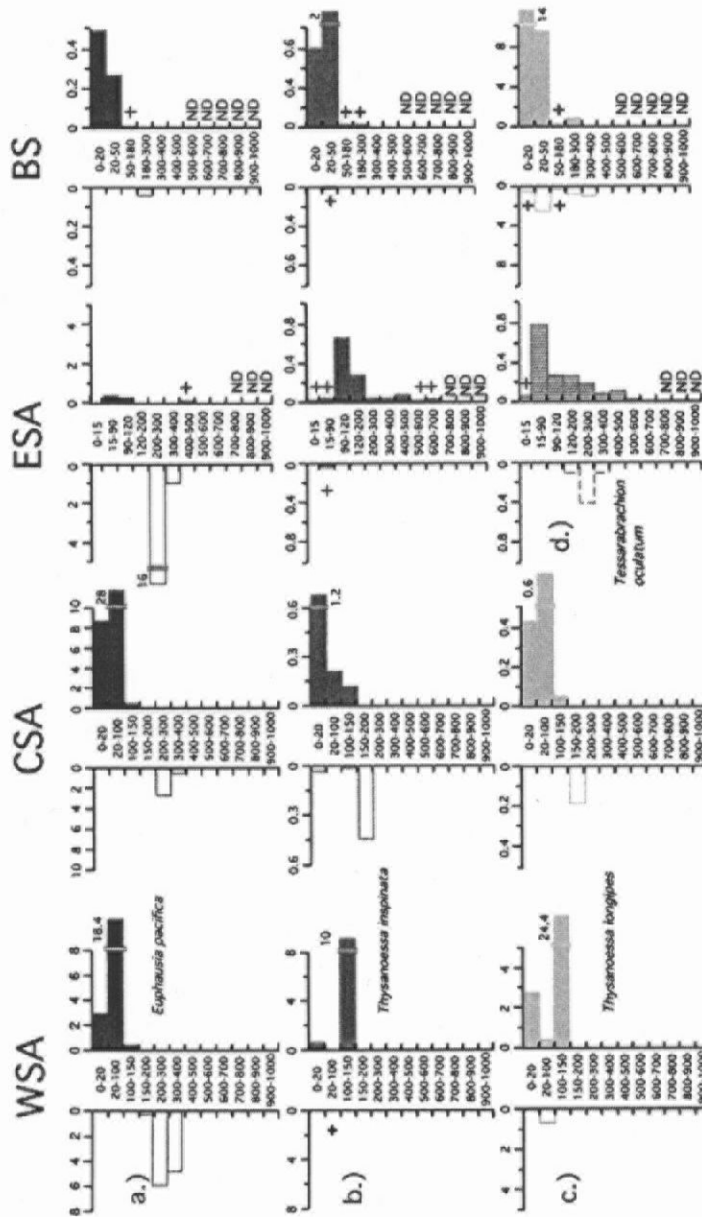|	Biomass											
	WSA		CSA		ESA			BS			Total	
	Day 0-1000m g/m^2	Night 0-1000m g/m^2	Day 0-1000m g/m^2	Night 0-1000m g/m^2	Day 0-1000m g/m^2	Night 0-700m g/m^2	Night* 0-1000m g/m^2	Day 0-1000m g/m^2	Night 0-500m g/m^2	Night* 0-1000m g/m^2	Day-total 0-1000m g/m^2	Night-total 0-1000m g/m^2
Euphausiids												
Euphausia pacifica	1.105	1.075	0.335	2.443	1.682	0.050	0.050	0.004	0.006	0.006	3.127	3.574
Thysanoessa longipes	0.072	0.919	0.009	0.057		0.064	0.064	0.279	0.266	0.278	0.360	1.242
Thysanoessa inspinata	0.006	0.382	0.023	0.047	0.002			0.001	0.016	0.016	0.032	0.508
Thysanoessa inermis	0.0004	0.0002				0.009	0.009	0.030	0.017	0.017	0.030	0.017
Unknown (damaged) sp.	0.012	0.051		0.001	0.022			0.001	0.001	0.001	0.036	0.062
Euphausiids (damaged) sp.	0.001										0.001	0
Bentheuphausia amblyops	0.006	0.002	0.017	0.008	0.024	0.042	0.045	0.001	0.002	0.004	0.048	0.054
Tessarabrachion oculatum	0.001	0.0002	0.004	0.002	0.066	0.108	0.109	0.002	0.001	0.001	0.072	0.111
Stylocheiron abbreviatum				0.001							0	0.001
Stylocheiron elongatum											0	0.001
Stylocheiron maximum					0.023	0.067	0.067		0.001	0.001	0.023	0.067
Stylocheiron sp.					0.0002	0.002	0.0002				0.0002	0
Nematobrachion flexipes					0.001						0	0
Nematobrachion boopis					0.001		0.002				0.001	0.002
Thysanopoda acutifrons						0.005	0.005				0.001	0.005
Total	1.20	2.43	0.39	2.56	1.82	0.35	0.35	0.32	0.31	0.32	3.73	5.64
Decapods												
Hymenodora sp.	0.0009	6.09257E-05									0.001	0.0001
Hymenodora frontalis	0.92	0.99	1.17	0.94	0.59	0.24	0.68	1.88	0.16	1.88	4.55	2.31
Hymenodora acanthitelsonis								0.0002	0.0004	0.001	0.0002	0.0004
Sergestes similis	0.04	0.12	0.21	0.02	0.15	0.16	0.16	0.002	0.005	0.005	0.41	0.30
Bentheogennema borealis	0.46	1.27	0.51	0.76	0.18	0.16	0.20	0.06	0.01	0.06	1.20	2.20
larvae	0.01		0.05	0.0002				0.0002			0.01	0.0002
Sergia japonica	0.04	0.007			0.07	0.003	0.07				0.09	0.01
Sergia tenuiremis	0.004				0.07	0.01	0.01				0.004	0.004
Systellaspis braueri	0.14										0.21	0.003
Pasiphaea japonica		0.02	0.013	0.010				0.001	0.001	0.002	0.08	0.05
Pasiphaea sinensis				0.094							0	0.09
Pasiphaea tarda											0.02	0
Parapasiphaea sulcatifrons				0.017	0.02						0.001	0.02
Funchalia sagamiensis			0.001								0.001	0
Meningodora marptocheles			0.001					0.002		0.002	0.003	0
Notostomus japonicus			0.001	0.001	0.30	0.57	0.63				0.30	0.57
damaged (unknown)								0.0003	0.0004	0.0003	0.0003	0.001
Pandalus sp. (?)								0.0002		0.0004	0.0002	0.0004
Unknown sp. (Caridean)					0.0001			0.0006			0.001	0
Total	1.61	2.40	1.95	1.84	1.37	1.15	1.76	1.95	0.17	1.96	6.87	5.56
Mysids												
Boreomysis californica	0.054	0.043	0.010	0.019	0.002	0.0005	0.002	0.031	0.004	0.024	0.097	0.067
Eucopia grimaldii	0.975	0.824	0.689	0.915	0.451	0.299	0.563	0.759	0.045	0.610	2.874	2.083
Eucopia sculpticauda					0.0004						0.000	0
Gnathophausia gigas	0.133	0.273	0.226	0.227	0.210	0.079	0.142	0.222	0.093	0.195	0.791	0.673
Mysida (sp.)					0.0002			0.0003			0.000	0
Unknown sp.											0.000	0
Total	1.163	1.140	0.926	1.161	0.662	0.379	0.706	1.013	0.142	0.829	3.764	2.822
Total	4.0	6.0	3.3	5.6	3.9	1.9	2.8	3.3	0.6	3.1	14.4	14.0

Fig. 3-2. Diel vertical distribution patterns (biomass, gWW/1000 m³) of the 4 dominant euphausiids (a) *Euphausia pacifica*, (b) *Thysanoessa inspinata*, (c) *Thysanoessa longipes*, and (d) *Tessarabrachion oculatum*, collected by RMT-8. White bars signify daytime biomass, filled bars represent nighttime. Crosses (+) indicate biomass less than 0.01 gWW/1000 m³. Layers where no data was collected are marked "ND".

having a range extending farther to the south, and deeper in the water column.]

T. longipes was distributed in the top 200 m both day and night at all but the ESA, where it was poorly represented. Populations in the daytime BS extended to 300 m. [Remarks: Brinton (1962) found *T. longipes* (spined form) concentrated in the 0 - 280 m layer, both day and night, with the nighttime peaks mainly from 0 to 140 m.]

At night, *Tessarabrachion oculatum* had peaks in the 15 - 90 m layer, and in the daytime, in the 200 - 300 m layer. The range of the biomass distribution was between 0 - 600 m, the deepest of the 4 species. (Ponomareva 1963; Youngbluth 1976).

There were 3 dominant decapod species, defined here as species with more than 10% of the relative abundance and recorded at all stations: *Hymenodora frontalis*, *Bentheogennema borealis*, and *Sergestes similis* (Fig. 3-3). The decapods exhibited 2 vertical distribution patterns: 1) mainly mesopelagic distributions below 400 m day or night: 2) daytime mesopelagic populations that rose into epipelagic layers at night. There was no evidence of net avoidance in terms of day-night differences in sizes of catches for any species.

Biomass peaks of *Hymenodora frontalis* were below 500 m, both day and night. While there was little difference between the depths of the major portion of the biomass, there was a tendency for the nighttime populations to extend their range into shallower waters. [Remarks: previous workers (e.g. Aizawa, 1974; Pearcy et al., 1977; Krygier and Pearcy, 1981; Kikuchi and Omori, 1985, 1986; Iwasaki, 1988) reported *H. frontalis* as a non-migrator. Off Oregon, Krygier and Pearcy (1981) reported ranges from 100 to 2400 m, with the population maximum between 600 and 1250 m. Kikuchi and Omori (1985) also recorded the bulk of the population off Japan between 600 and 1500 m.]

Peak daytime biomasses of *Bentheogennema borealis* were found in the 500 - 600 depth layers in the WSA and CSA. Only in the CSA was there a very clear DVM from a daytime biomass peak in the 500 – 600 m depth layer, to the nighttime 20 – 300 m depth layer. In the ESA, like the WSA, daytime and nighttime biomass peaks were in the same depth layers. Biomass in the BS was very low, day or night. [Remarks: *B. borealis* has been described as a slight or non-migrator, with the species occurring in the 200 - 1000 m layer off Oregon (Pearcy and Forss, 1966) and the 140 - 4500 m layer off Japan (Kikuchi and Omori, 1985). Aizawa (1974) reported that the center of distribution was in the 500 - 300 m layer.]

Sergestes similis was the only decapod to exhibit marked diel vertical migration (DVM). Daytime peak biomass was generally found below 300 m for all regions. Nighttime biomass peaks
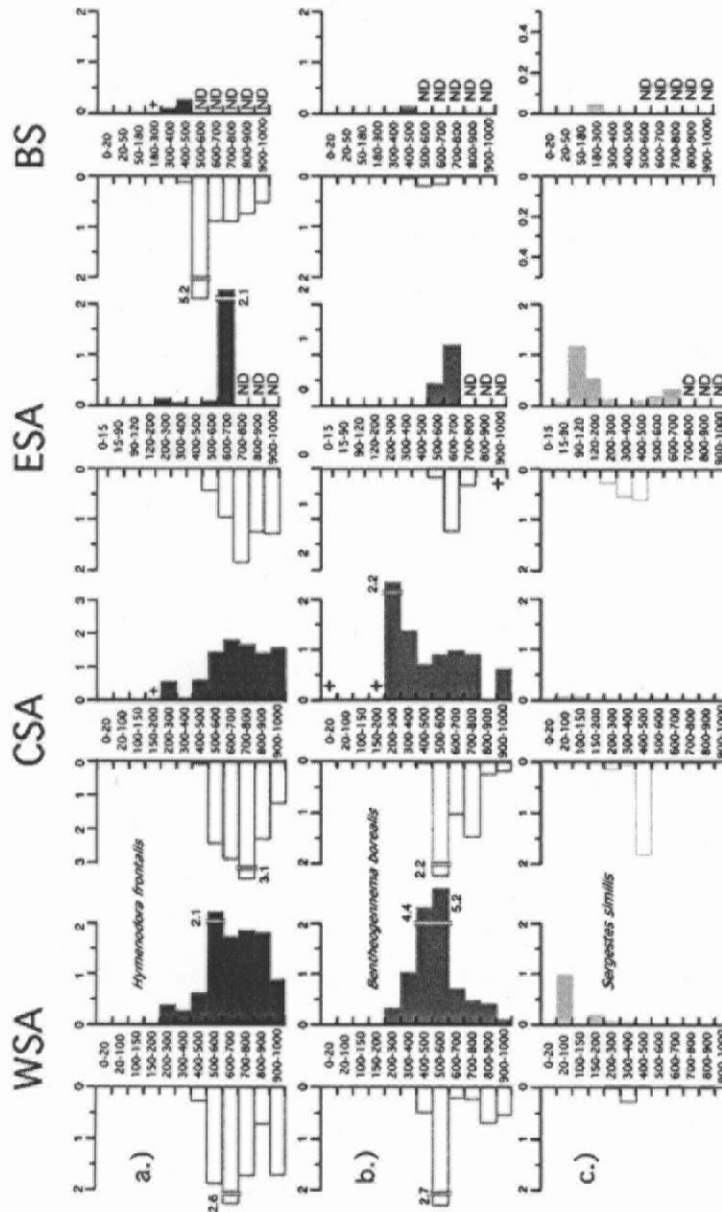
Fig. 3-3. Diel vertical distribution patterns (biomass, gWW/1000 m³) of the 3 dominant decapods (a) *Hymenodora frontalis*, (b) *Bentheogennema borealis*, and (c) *Sergestes similis*, collected by RMT-8. White bars signify daytime biomass, filled bars represent nighttime. Crosses (+) indicate biomass less than 0.01 gWW/1000 m³. Layers where no data was collected are marked "ND".

were typically higher in the water column, usually within the 20 – 150 m depth layers. Only in the BS was nighttime peak biomass below 180 m. [Remarks: *S. similis* has been reported as exhibiting strong DVM with populations in the western and eastern subarctic occurring between 200 to 400 m in the daytime, and in the upper 100 m at night (Pearcy and Forss, 1966; Aizawa, 1974; Pearcy et al., 1977; Krygier and Pearcy, 1981; Kikuchi and Omori, 1985).]

There were 3 mysid species, dominant in terms of both biomass and abundance: *Boreomysis californica, Eucopia grimaldii* and *Gnathophausia gigas* (Fig. 3-4).

    B. californica was found in 400 - 1000 m layer during the day. The nighttime distribution was similar, but with minor portions of the population extending to the 200-300 m layer in the WSA and CSA, and in the 180 – 300 m layer in the BS. [Remarks: in pelagic mysids, only *B. californica* and *E. grimaldii* have been found to exhibit any DVM, but apparently, only on a seasonal basis (Pearcy, et al., 1977). Off Oregon, they observed a limited DVM in winter, but not in summer, for *B. californica*. In the same area, Krygier and Murano (1988) reported no diel differences in depth distribution, with 75 % of the population between 600 and 1500 m. Pearcy, et al. (1977) also concluded that *B. californica* is under sampled due to its small size.]

    E. grimaldii was found as shallow as 0 – 20 m at night in the WSA, however, the major portion of biomass was restricted between 400 and 1000 m both day and night. Biomass peaks were in the 500 - 600 m layer day and night, however ca. 80 % of the biomass was concentrated in deeper layers. [Pearcy et al (1977), reported that in *Eucopia unguiculata* off Oregon, small fractions of biomass were found in the upper 200 m in winter. However, the greater fraction of biomass was located below 500 m.]

    Gnathophausia gigas was found to have a bimodal distribution. Biomass peaks were typically separated by 200 m, day or night. The daytime CSA and nighttime BS were the only regions where biomass distribution was not bimodal. There was evidence of DVM as nighttime biomass tended to peak higher in the water column when compared to daytime distributions. [Remarks: this species ranged in the water column from 600 to 4400 m, day and night (Pequegnat 1965) in the ESA. Banner (1947) reported specimens from 400 to 1200 m off Canada and 300 to 900 m off Alaska. In the ESA Krygier and Murano (1988) also found 75 % of the population abundance between 600 to 1000 m, with no difference between day and night distributions.]

Vertical distribution - non dominant species

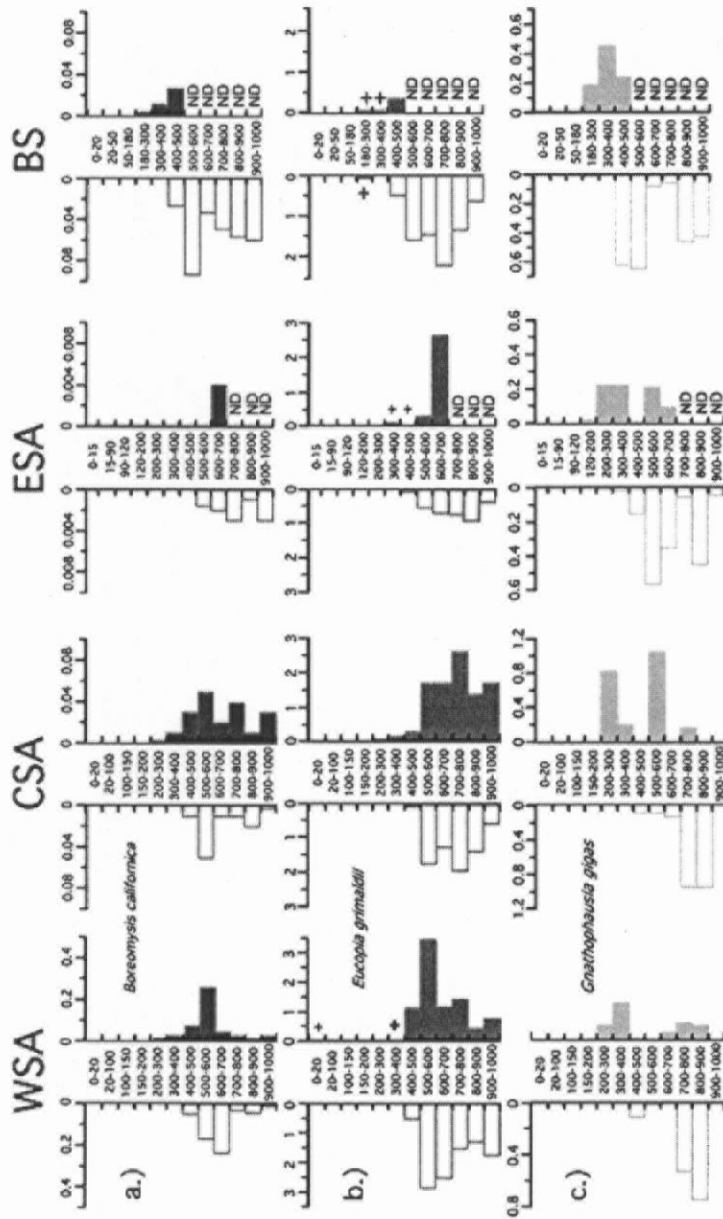There were 9 species of euphausiids, 13 species of decapods and 3 minor species of mysid that

Fig. 3-4. Diel vertical distribution patterns (biomass, gWW/1000 m³) of the 3 dominant mysids (a) *Boreomysis californica*, (b) *Eucopia grimaldii*, (c) *Gnathophausia gigas*, collected by RMT-8. White bars signify daytime biomass, filled bars represent nighttime. Crosses (+) indicate biomass less than 0.01 gWW/1000 m³. Layers where no data was collected are marked "ND".
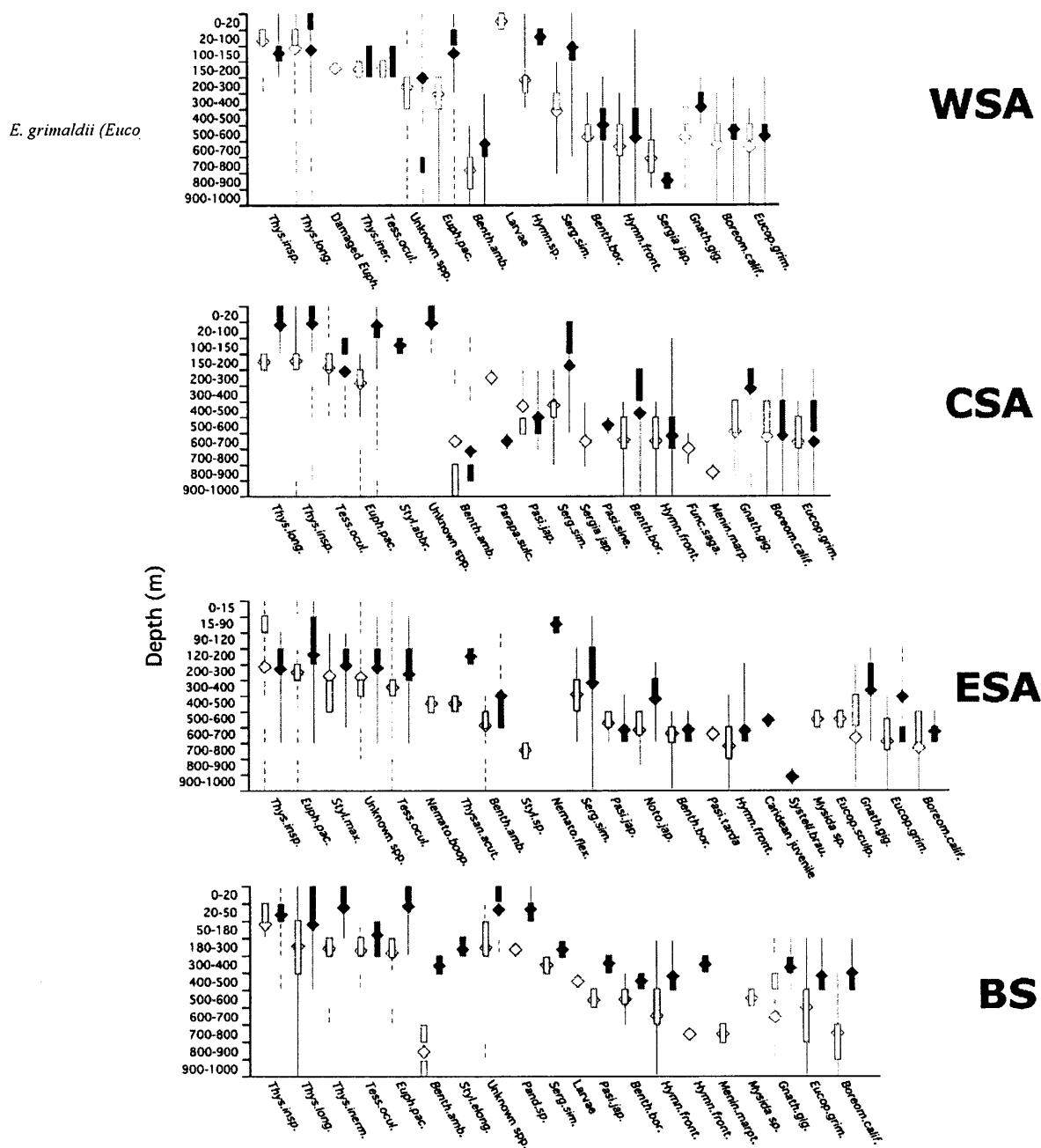
Fig. 3-5. Depth range, depth of >50% abundance and weighted mean depth of all MNC collected in this study. Euphausiids (left) are in red, decapods (center) are in blue, and mysids (right) are in orange. Vertical lines represent occurrence range, broken lines indicate disjunct ranges, boxes represent >50% abundance, and diamonds the weighted mean depth. White and black fill indicate day and night, respectively. Abbreviations as below.

Euphausia pacifica (Euph. pac.)	*Thysanoessa longipes (Thys. long.)*	*Thysanoessa inspinata (Thys. insp.)*
Thysanoessa inermis (Thys. iner.)	*Bentheuphausia amblyops (Benth. amb.)*	*Stylocheiron. abbreviatum (Styl. abbr.)*
S. elongatum (Styl. elong.)	*S. maximum (Styl. max.)*	*S. sp. (Styl. sp.)*
Nematobrachion boopis (Nemato. boop.)	*N. flexipes (Nemato. flex.)*	*Thysanopoda acutifrons (Thysan. acut.)*
Tessarabrachion oculatum (Tess. ocul.)		
Sergia japonica (Sergia jap.)	*Bentheogennema borealis (Benth. bor.)*	*Hymenodora frontalis (Hymn. front.)*
S. tenuiremis (Sergia tenu.)	*Sergestes similis (Serg. sim.)*	*Hymenodora acanthitelsonis (Hymn. acan.)*
P. tarda (Pasi. tarda)	*Pasiphaea japonica (Pasi. jap.)*	*H. sp. (Hymn. sp.)*
Parapasiphaea sulcatifrons (Parapa. sulc.)	*P. sinensis (Pasi. sine.)*	*Notostomus japonicus (Noto. jap.)*
Pandalus sp. (Pand. sp.)	*Funchalia sagamiensis (Func. saga.)*	*Systellaspis braueri (Systell. brau.)*
Meningodora marptocheles (Menin. marp.)		
Boreomysis californica (Boreom. calif.)	*Gnathophausia gigas (Gnath. gig.)*	*Eucopia sculpticauda (Eucop. sculpt.)*

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comprised the remainder of the MNC examined in this Chapter (Fig. 3-5). These are all listed within Fig. 3-6.

Tessarabrachion oculatum was only a dominant species in the ESA, and a minor constituent species in all other regions. The minor species all exhibited diel vertical migration and occurred in much lower abundances than dominant species, less than 140 ind/m^2 for any region. The ESA not only had the most euphausiid species of any region (n = 11) but was also where these minor species were most abundant (Table 3-II). Of these species, *Tessarabrachion oculatum, Bentheuphausia ambylops, Thysanoessa inermis* and *Stylocheiron maximum* contributed most to biomass (in that order).

Non-dominant decapod species occurred in much lower abundances than dominant species (< 24 ind/m^2). The CSA had the most decapod species of any region, day or night (n = 11) and the ESA the least (n=8). The minor species did not engage in the same level of diel vertical migration as the dominant species and their distribution patterns differed by region.

The few minor species of mysid all occurred in low abundances with vertical distributions patterns coincident with that of the dominant species.

Vertical diversity patterns

Diversity (*H'*) tended to be highly variable in the upper layers (above 500 m) at all regions except the ESA day or night (Fig. 3-6). Euphausiids tended to dominate the community in the top 400 – 500 m during the day, while the community below 500 m tended to be dominated by the pelagic mysid, *Eucopia grimaldii*. Decapod species were usually dominant at depths between the epipelagic euphausiids and the mesopelagic mysids, and there was a tendency towards a greater vertical range of dominant decapod species at night compared to daytime.

In the WSA, *Thysanoessa longipes* dominated (>73%) the 0 – 100 m depth layers while *Euphausia pacifica* dominated the 150 – 400 m by day (>78%). At night however, species dominance was not as clear, since *T. longipes* and *E. pacifica* were not only dominant in alternate layers within the 0 – 150 m depth layer, but also had lower percent dominance as well (>46%). There were no dominant decapods in any depth layers by day, but *Sergestes similis* and *Hymenodora frontalis* were dominant in nighttime midlevels (150 – 400 m layers; > 23%) with *H. frontalis* also dominant in the 800 – 900 m layer. In general, abundance below 300 m in the day and 400 m at night was dominated by the mesopelagic mysid *Eucopia grimaldii* (> 31%). The 100 – 150 m layer was remarkable in that it was the only depth layer in the entire study from which no MNC were recovered.
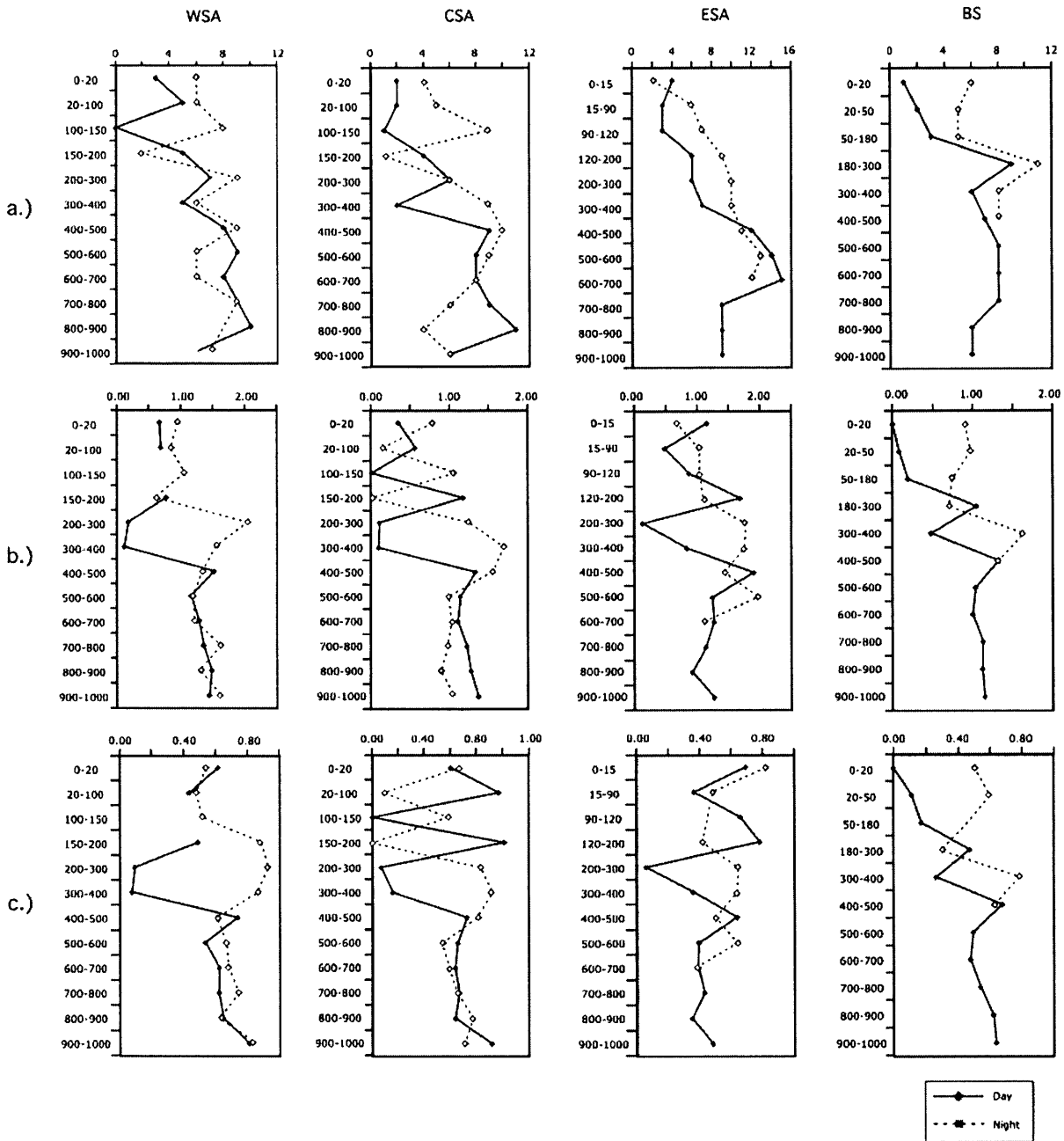
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Fig. 3-6. Species number (a), diversity (*H'*) (b), and eveness (*J'*) (c), for the WSA, CSA, ESA and BS. Day values indicated by the solid line, night values by the dashed line. Depth layers indicated to the left of each figure.

Table 3-III. Dominant species, percent dominant, and depth layers for each region. Daytime data shown in the left column, nighttime in the right. Regions (WSA, CSA, ESA, BS) as in text.

WSA

Day			Night		
Depth Layer (m)	Dominant Species	Percent Dominant	Depth Layer (m)	Dominant Species	Percent Dominant
0-20	*Thysanoessa longipes*	73.5	0-20	*Thysanoessa longipes*	60.5
20-100	*Thysanoessa longipes*	79.1	20-100	*Euphausia pacifica*	73.2
100-150			100-150	*Thysanoessa longipes*	46.2
150-200	*Euphausia pacifica*	78.8	150-200	*Sergestes similis*	70.0
200-300	*Euphausia pacifica*	96.7	200-300	*Hymenodora frontalis*	23.1
300-400	*Euphausia pacifica*	98.0	300-400	*Sergestes similis*	36.7
400-500	*Eucopia grimaldii*	40.9	400-500	*Eucopia grimaldii*	57.3
500-600	*Eucopia grimaldii*	57.3	500-600	*Eucopia grimaldii*	52.1
600-700	*Eucopia grimaldii*	43.1	600-700	*Eucopia grimaldii*	47.9
700-800	*Eucopia grimaldii*	46.4	700-800	*Eucopia grimaldii*	31.5
800-900	*Eucopia grimaldii*	54.4	800-900	*Hymenodora frontalis*	50.0
900-1000	*Eucopia grimaldii*	51.6	900-1000	*Eucopia grimaldii*	41.4

CSA

Day			Night		
0-20	*Thysanoessa inspinata*	88.9	0-20	*Euphausia pacifica*	65.8
20-100	*Thysanoessa inspinata*	75.0	20-100	*Euphausia pacifica*	97.8
100-150	*Thysanoessa inspinata*	100.0	100-150	*Euphausia pacifica*	53.1
150-200	*Thysanoessa inspinata*	55.3	150-200	*Euphausia pacifica*	100.0
200-300	*Euphausia pacifica*	98.4	200-300	*Bentheogennema borealis*	39.6
300-400	*Euphausia pacifica*	98.2	300-400	*Bentheogennema borealis*	32.5
400-500	*Sergestes similis*	62.6	400-500	*Hymenodora frontalis*	36.4
500-600	*Eucopia grimaldii*	51.6	500-600	*Eucopia grimaldii*	63.2
600-700	*Eucopia grimaldii*	56.0	600-700	*Eucopia grimaldii*	61.2
700-800	*Eucopia grimaldii*	56.4	700-800	*Eucopia grimaldii*	67.9
800-900	*Eucopia grimaldii*	54.2	800-900	*Eucopia grimaldii*	58.1
900-1000	*Eucopia grimaldii*	48.5	900-1000	*Eucopia grimaldii*	67.4

ESA

Day			Night		
0-15	*Euph pacifica & Thys inspinata*	57.1	0-15	*Thysanoessa inspinata*	56.3
15-90	*Thysanoessa inspinata*	86.2	15-90	*Euphausia pacifica*	66.7
90-120	*Stylocheiron maximum*	66.7	90-120	*Thysanoessa inspinata*	70.0
120-200	*Stylocheiron maximum*	24.0	120-200	*Thysanoessa inspinata*	67.2
200-300	*Euphausia pacifica*	98.0	200-300	*Thysanoessa inspinata*	31.1
300-400	*Euphausia pacifica*	74.6	300-400	*Thysanoessa inspinata*	39.3
400-500	*Tessarabrachion oculatum*	26.1	400-500	*Thysanoessa inspinata*	59.0
500-600	*Eucopia grimaldii*	63.8	500-600	*Eucopia grimaldii*	30.9
600-700	*Eucopia grimaldii*	57.5	600-700	*Eucopia grimaldii*	68.7
700-800	*Eucopia grimaldii*	46.5		ND	
800-900	*Eucopia grimaldii*	62.3		ND	
900-1000	*Eucopia grimaldii*	47.2		ND	

BS

Day			Night		
0-20	*Thysanoessa longipes*	100.0	0-20	*Thysanoessa longipes*	74.7
20-50	*Thysanoessa longipes*	98.5	20-50	*Thysanoessa longipes*	65.2
50-180	*Thysanoessa longipes*	96.2	50-180	*Thysanoessa longipes*	79.3
180-300	*Thysanoessa longipes*	63.3	180-300	*Thysanoessa longipes*	84.7
300-400	*Thysanoessa longipes*	86.8	300-400	*Hymenodora frontalis*	34.0
400-500	*Hymenodora frontalis*	38.3	400-500	*Hymenodora frontalis*	43.2
500-600	*Eucopia grimaldii*	56.4		ND	
600-700	*Eucopia grimaldii*	61.3		ND	
700-800	*Eucopia grimaldii*	51.2		ND	
800-900	*Eucopia grimaldii*	43.0		ND	
900-1000	*Eucopia grimaldii*	41.3		ND	

Vertical patterns in the CSA were similar, with *Thysanoessa inspinata* dominating the 0 – 200 m depth layer and *Euphausia pacifica* dominating the 200 – 400 m layer by day (> 55%). *E. pacifica* was the only dominant euphausiid (>53%) at night (0 – 200 m layer). The only dominant decapod species during the day was *Sergestes similis,* in the 400 – 500 m depth layer (>62%). At night, *Bentheogennema borealis* dominated (>32%) the 200 – 400 m depth layer, and *Hymenodora frontalis* dominated the 400 – 500 m layer (> 36%). Mesopelagic depth layers below 500 m were dominated by *Eucopia grimaldii* (> 48%) both day and night.

There were more dominant species of euphausiids in the daytime epipelagic layers (0 – 400 m) of the ESA (n = 3) than in any other region; *Euphausia pacifica, Thysanoessa inspinata* and *Stylocheiron maximum.* The euphausiids were also dominant to a greater depth in the ESA (500 m) than in any other region. Only in the daytime were there depth layers (n=3) where 2 species shared co-dominance; in the 0 – 15 m layer by *Euphausia pacifica* and *Thysanoessa inspinata* (> 57%), and the 90 – 120 m and 120 – 200 m depth layers by *E. pacifica* and *Stylocheiron maximum* (> 66 and 24%, respectively). The daytime 400 – 500 m layer was the only one where *Tessarabrachion oculatum* dominated (> 26%) in any region. No decapods were dominant at any layer, day or night, while *Eucopia grimaldii* was the dominant species from 500 – 1000 m during the day (>46%), and 500 – 700 m at night (>30%).

Surface layers in the BS were dominated by *Thysaonoessa longipes* (> 60%) both day and night (0 – 400 m and 0 – 300 m, respectively). *Hymenodora frontalis* was the only dominant decapod (> 30%) in the daytime 400 – 500 m layer and in the 300 – 500 m layers at night (>34%). Due to a net malfunction while sampling layers deeper than 500 m, there are no data available below 500 m at night.

DISCUSSION

Sampling

The differences in species composition and the number of species between the RMT 8 and IKMT nets (Table 3-III) may be a result of the differing casting strategies used by these different gears. Moreover, while dominant MNC species were collected via both nets, differences in minor constituent species between the two trawling regimes more likely reflects their low abundances and overall rarity.

Only two of the four species identified as transitional or subtropical were found in both IMKT and RMT 8 casts, *Pasiphaea japonica* and *Stylocheiron elongatum.* The other two transitional or subtropical species were only collected in the IKMT casts, which also involved

sampling at a greater number of stations (n=19), and each cast was much longer than RMT 8 casts. Therefore, since these transitional or subtropical species are rare in these waters, it may be that the greater sampling effort over a greater geographic range accounts for the differences in species diversity between the two sampling regimes. It also shows that possible influences on species diversity and distribution due to the strong El Nino of 1997 were weak. Off Oregon during the same time period, the zooplankton and nektonic communities were heavily influenced by the advection of offshore warm oceanic waters by atmospheric forcing in conjunction with weak coastal upwelling, so that the usual boreal copepod species were greatly reduced by transitional or subtropical species (Pearcy 2002; Peterson *et al* 2002), and the resultant community persisted for one year. The open ocean is more resistant to these changes in physical structure than coastal regions such as that off Oregon or the shelf region of the BS.

Many of the mysids and shrimp collected here are meso- or bathypelagic in distribution, with only their upper ranges coming within the depths sampled here (e.g. *Eucopia grimaldii* and *Hymenodora gracilis*). The vertical distribution data presented here, showing that daytime density and biomass remain at high values up to the 900 - 1000 m depth layer, confirms that the population centers for many mysids and shrimps are located in the bathypelagic zone, as has been reported elsewhere (Kikuchi and Omori 1986, Vinogradov 1997). The mesopelagic shrimps, *H. frontalis* and *Bentheogennema borealis*, showed size depth trends where larger individuals are found deeper than smaller, younger shrimps. When compared to the IKMT casts, there were far fewer mysids collected with the RMT 8+1. Therefore, as suggested in Chapter 2, the diversity of the mysid population was augmented by the presence of coastal species, which influenced the faunal composition of IKMT stations outside the sampling area covered by the RMT 8+1 nest.

Biomass and Abundance

Biomass, abundance and vertical distribution of micronekton and large gelatinous zooplankton in the SAP and BS were described and discussed in Nishikawa *et al.* (2001). They also noted the negative influence on MNC vertical distribution in the WSA and CSA by the cold intermediate water, which was also reported by Vinogradov (1972) in the Kurile-Kamchatka region. Nishikawa *et al*, (2001) reported the range of total biomass in the 0 – 1000 m water column as 2.9 – 5.1 g DW/m2, and that biomass in the ESA was dominated by a preponderance of thaliaceans. When they removed thaliaceans and euphausiids from the biomass of primary consumers, they found that the total micronektonic biomass in the BS was highest within the study area. In this study, the WSA was greatest in biomass (5.0 gWW/m^2) then the CSA (4.5 gWW/m^2), ESA (2.9 gWW/m^2)

and BS (1.9 gWW/m^2).

Zooplankton biomass and abundance in the 4 regions (WSA, CSA, ESA, and BS) simultaneously collected by the RMT 1 net will be discussed in detail in Chapter 5. However, day and night mean biomass across the study area was approximately one order of magnitude (10x) greater that of MNC biomass, as has been reported by other workers (e.g. Brodeur 1996; Goldblatt et al., 1999; Mackas and Tsuda 1999). Copepods, chaetognaths and cnidarians comprised approximately 70% of the total biomass, day or night at all stations. The distribution of zooplankton, with the exception of thaliaceans, in the ESA was similar to that of MNC species ordinarily found in the upper 200 m at night, (e.g. *Euphausia pacifica*, *Thysanoessa inspinata*). Presumably due to the influence of the strong 1997 ENSO (> 5C in the top 100 m, 12C in the top 50 m), these species were absent from the 0 – 120 m surface layer. The main effect of the ENSO seems to have been the "depression" the normal daytime vertical distribution patterns downward by 120-200 m, and affected the species composition of the surface layers.

MNC biomass and abundance were dominated by the euphausiids *Euphausia pacifica* and *Thysanoessa inspinata*, the decapods *Sergestes similis*, *Hymenodora frontalis* and *Bentheogennema borealis*, and the mysid *Eucopia grimaldii*. In the upper epipelagic zone euphausiids are the probable main vector of vertical flux in the study area, due to their dominance in both abundance and biomass. Although *Euphausia pacifica* and *Thysanoessa inspinata* were relatively uncommon in the BS, *T. longipes* was present in great abundance and biomass, providing an abundant amount of food for predators (Nemoto, 1977; Mackas and Tsuda, 1999).

Previous studies in the ESA (Pearcy and Forss, 1966, 1969; Krygier and Pearcy, 1981) reported that *Sergestes similis* was by far the most numerous species (76% of all IKMT captured shrimp), with *Hymenodora frontalis* a distant second. Because *S. similis* is a well-known epipelgic migrator, higher catches in their study were found in the upper 50 m at night and between 200 – 300 m during the daytime. *Sergestes similis* is the most abundant pelagic shrimp in the North Pacific Drift (Omori and Gluck, 1979), and comprises a substantial proportion of all micronekton in the cooler part of the California Current. In contrast, total shrimp abundance and biomass peaks in this study were consistently below 400 m day or night, due to the relatively low abundance and biomasses of the epipelagic *S. similis*. In the WSA, Kikuchi and Omori (1985), reported that *S. similis* was a minor member of the pelagic shrimp population, and that *Bentheogennema borealis* and *Hymenodora frontalis* (in that order) were more abundant. They reported that the transitional

depth between migratory mesopelagic and non-migratory bathypelagic decapods was around 600 m, and that vertical migrants have potential influence on organic flux larger than animals of similar standing crop that have low frequency vertical migration. Comparing the abundance and biomasses of migrants to non- or slight migrants in this study to previous work shows that the average potential impact of vertical flux from migrating epipelagic shrimp is low in the WSA, compared to the non- or slight lower mesopelagic shrimps, and increases across the SAP towards the ESA. However, IKMT data from the previous chapter (Chapter 2), reported abundance of *S. similis* comparable to that of *H. frontalis*, but not biomass. This was supported by the fact that *S. similis* was dominant only in the WSA, and only at two stations. Therefore, *S. similis* may have a very strong local effect on the vertical flux of organic material within the SAP and BS as a whole. On the other hand, Nemoto (1977) in a study of feeding in baleen whales in the SAP found that *S. similis* is a major component of some whale's gut contents. Since whales only feed on prey that are densely concentrated, it supports the idea that *S.similis* concentrates in highly localized dense aggregates.

Similar to the decapods, the majority of mysid abundance and biomass was concentrated below 500 m and the BS had the highest abundance and biomass of mysids compared to that of the euphausiids. This may reflect sampling error, since the lower nighttime mesopelagic layers went unstapled due to equipment malfunctions. However, if the usual trend of large mysid biomass below 500 m in the SAP holds true for the BS, then mysids may be as important as decapods in that region. There have been very few studies examining mysids in the open ocean, and therefore finding such a large contribution to biomass and abundance is a new and important finding. Pearcy *et al* (1977) in an examination of vertical distribution of oceanic micronekton off Oregon reported that *Eucopia unguiculata* and *Boreomysis californica* exhibited no diel vertical displacement, also observed here, and their abundance and biomass peaks were consistently below 600 m, about 200 m deeper than described here. Although this was the third dominant mysid in the SAP, it was the least abundant. The abundance and biomass of *Eucopia grimaldii* were nearly equivalent to that of the mesopelagic shrimp *Hymenodora frontalis* (Table 3-II), and occurred within similar depth ranges. This mysid was the dominant MNC below 500 m throughout the SAP and BS, and therefore is potentially a very important member of the mesopelagic MNC, with a subsequent potential contribution to vertical flux. There are no ecological studies of this mysid in the SAP, and even the taxonomy of this genus is in some dispute (Casanova *et al*, 1998). It is important to examine feeding patterns in this species in order to better understand its' potential impact within the SAP food web. Cartes and Sorbe (1998) and Cartes and Maynou (2001) examined the distribution and

ecology of *Boreomysis arctica* in the western Mediterranean, where it has a bathypelagic distribution. They found that even though daytime densities were slightly higher in the water column compared to nighttime, there was no significant difference. They found peak feeding during the day, while it decreased at night; however, despite its numerical dominance in bathyal assemblages, its trophic impact was low, even lower than other mesopelagic species. Although the impact of *Eucopia grimaldii* is unknown, it may have a similarly low trophic impact, despite its numerical dominance in the lower mesopelagic zone.

Vertical patterns and resource partitioning

The total surface productivity will determine the amount of organic material available for transport into deeper water (Angel, 1989). The stepped vertical migration patterns of MNC within the 0 – 1000 m water column can act as a method of transport for this material from the surface epipelagic layers into the deeper mesopelagic and bathypelagic layers. The effectiveness of this transport depends on the time, gut fullness and gut retention times. In *Meganyctiphanes norvegica* gut retention times have been reported to be as much as 30 minutes in the largest individuals (Angel, 1989), while these rates in decapods have been variously reported as 6 – 8 hours (Omori 1974; Roe 1984; Mincks *et al*, 2000), and 2.89 hours in the bathypelagic mysid *Boreomysis arctica* (Cartes and Maynou 2001). Roe (1984) examined the vertical migrations and feeding patterns of MNC in the North Atlantic and reported that feeding in *Eucopia unguiculata* and numerically dominant decapod species was continuous throughout the diel cycle and fed upon different prey at each end of the migration cycle. He also determined that it was unlikely that *E. unguiculata* competed with decapods for resources due to differences in migration patterns in combination with differences in body size. Therefore, the diel vertical migration patterns of the MNC need to be considered in conjunction with feeding intensity and periodicity along with and gut passage times in order to better understand vertical flux in the SAP and BS.

Vertical distribution patterns of epipelagic species are strongly influenced by the physical characteristics of their resident water masses. In the SAP, there was a relatively sharp distinction between the vertical distribution of peak abundances of euphausiids and decapods in the WSA that gradually weakened towards the ESA. This may have been primarily due to higher temperatures in the top 300 m combined with lower salinity in the top 150 m, presumably the result of the strong the El Nino. While the thermoclines and haloclines in the WSA and CSA were very well defined compared to the ESA and BS, the vertical ranges of the epipelagic euphausiids were 100 m deeper in the ESA water column compared to the WSA and CSA. Nevertheless, the main connection

between the epipelagic and mesopelagic MNC was *Sergestes similis*, which was the only shrimp with a large enough abundance and biomass to be an important vector for the transport of material from the surface to deeper waters.

In the eastern Gulf of Mexico, midwater fishes and decapods consume similar amounts of daily ration, and are likely competitors for food. Ponomareva (1963) discussed the feeding habits of *E. pacifica* and *T. longipes*, with the latter feeding mainly on amphipods and ostracods rather than on detritus and phytoplankton like *E. pacifica*. *Boreomysis* has been described as omnivorous on the basis of stomach contents and mandible morphology (Mauchline 1980). In the Northeast Atlantic, *Eucopia unguiculata* was described by Roe (1984b) as a predator of copepods and coelenterates on the basis of gut content analysis. No data is available on the feeding habits of *G. gigas*. These factors will be examined and discussed in the next chapter.

This chapter has established that numerically, the primary members of the pelagic MNC community are the euphausiids in the epipelagic zone, the mysids in the lower mesopelagic zone, and the decapods are dominant in between, but to a much lesser extent. The dominant MNC in the vertical 0 – 1000 m water column are the same as those identified in horizontal geographic distribution in the SAP and BS in the previous chapter. Species exhibiting significant diel vertical migration patterns were few, and mainly limited to the dominant euphausiids and the decapod *Sergestes similis*. Diversity in the 0 – 1000 m water column tended to be lowest in the epipelagic zone, and higher in the upper mesopelagic before dropping off in the lower mesopelagic. The cold intermediate layer, as reported by Nishikawa *et al* (2001) had a negative effect on the vertical distribution of MNC and zooplankton, which tended to avoid this layer. The 1997 ENSO seems to have had a significant effect on the vertical distribution of MNC in the epipelagic zone of the ESA due to higher water temperatures in the upper mesopelagic zone and the shallower gradient of dissolved oxygen and temperature clines with depth.

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