

ZOOPLANKTON ABUNDANCE, COMMUNITY STRUCTURE, AND
OCEANOGRAPHY NORTHEAST OF KODIAK ISLAND, ALASKA

By

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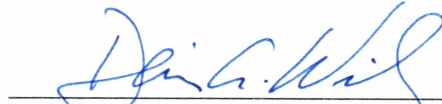


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OCEANOGRAPHY NORTHEAST OF KODIAK ISLAND, ALASKA

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Presented to the Faculty
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for the Degree of

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By

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Abstract

Zooplankton community dynamics and correlations with physical characteristics of the water were studied in the northwestern Gulf of Alaska. Zooplankton were collected systematically northeast of Kodiak Island, Alaska in March, May, August and November of 2002 to 2004. Species composition, total abundance and spatial community structure were correlated to physical variables. Small copepods (numerically >50%) dominated the zooplankton composition and were most abundant in August. Average biomass was 48.7 g WW m⁻² in May and 52.0 g WW m⁻² in August in Kodiak region. Interannual zooplankton abundance variations were large, with May 2003 having a dramatically higher abundance (2×10^4 individual m⁻³ higher) than 2002 and 2004, probably due to the higher temperature (1 °C higher) and lower salinity in May 2003. Small to moderate correlations ($r < 0.7$) were found between temporal zooplankton abundance and selected physical variables. Spatial patterns in zooplankton composition among stations were more discernable in May than in August, likely due to water column stability in the spring and more dynamic influences in the summer, but revealed no consistent spatial patterns. The zooplankton community patterns in this region thus appear to arise due to complex oceanographic and bathymetric interactions, and suggest high variability can occur in the availability of prey for higher trophic levels.

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General Introduction

Zooplankton occupy a key position in the pelagic food web as they transfer the organic energy produced by primary producers through photosynthesis to higher trophic levels such as fish, marine birds and mammals (Lindeman, 1942; Platt et al., 1981; Lenz, 2000). Zooplankton abundance and biomass are direct indices of food web structure and carrying capacity for higher trophic level predator species (Mackas, 1995). The planktonic early life history of finfish and shellfish is dependent on zooplankton availability during this critical period (Damkaer, 1977; Dunn et al., 1979). In the Gulf of Alaska (GOA), specifically in Prince William Sound (PWS), zooplankton abundance has been correlated to changes in pink salmon (*Oncorhynchus gorbuscha*) and juvenile herring (*Clupea pallasii*) diets and their subsequent recruitment success and fish survival (Foy and Norcross, 2001; Boldt and Haldorson, 2003; Armstrong et al., 2005). In the Shelikof Strait in the GOA, copepod nauplii, and *Pseudocalanus* spp. were the main prey items for pollock larvae (Kendall et al., 1987). Longer term studies in the North Pacific have also shown positive correlations between zooplankton biomass and abundance of pelagic fish and squid (Brodeur and Ware, 1992).

To understand the role of zooplankton in the food web, large scale environmental forcing has been assessed in the North Pacific Ocean (McGowan et al., 1996; Mackas & Tsuda, 1999; Peterson & Schwing, 2003; Chiba et al., 2006). The summer zooplankton biomass in the North Pacific subarctic gyre fluctuates on interannual and interdecadal time scales, correlated to the winter wind intensity in the northern GOA (Brodeur and Ware, 1992) and in the western subarctic North Pacific (Odate, 1994). At finer scales,

zooplankton community heterogeneity is often the result of physical and biological interactions (Pinel-Alloul, 1995). Fluctuations in temperature and salinity, water column stratification, tidal mixing and excursion, currents, fresh water inflow, advection and turbidity, front formation and wind variability have all been found to affect zooplankton community structure to varying extents (Brodeur and Ware, 1992; Roman et al. 2001; Coyle and Pinchuk, 2003; Basedow et al., 2004; Rawlinson et al., 2005). Water temperature is a major factor affecting copepod distribution (Lee et al., 1999), likely due to the strong dependence of copepod growth on temperature, especially for earlier life stages (Hirst and Bunker, 2003; Liu and Hopcroft, 2006a,b). Upwelling caused by wind forcing, shelf break front, and coastal topology can also directly or indirectly affect zooplankton abundance and species composition (Cunha 1993; Danielsen et al., 1998; Keister and Peterson, 2003) and biomass (Brodeur and Ware, 1992). Biological processes such as top-down control by fish species are also known to affect zooplankton abundance, biomass and spatial distribution (e.g. in the Oyashio region of the North Pacific - Tadokoro et al., 2005).

In the GOA, small and large scale variability in the physical environment strongly influences the seasonal abundances of zooplankton, fish, and upper trophic levels. The GOA sustains an abundant and diverse zooplankton community dominated by about 30 species, with copepods being predominant (Cooney, 1986; Cooney, 2005). This abundant zooplankton and higher trophic community in the GOA are surprising given that the coastal GOA is classically considered a predominately downwelling system, but during the summer months significant periods of upwelling occur (Stabeno et al., 2004).

In the western GOA, the Kodiak Archipelago is surrounded by a bathymetrically and hydrographically complex shelf. The inshore area is influenced primarily by the Alaska Coastal Current (ACC) and local factors such as winds, complex bathymetry, and freshwater inputs (Kendall et al., 1980; Stabeno et al., 2004). The ACC dominates the GOA shelf circulation controlling the transport of dissolved substances and planktonic materials (Reed, 1984; Reed and Stabeno, 1989; Stabeno et al., 1995). In this productive and hydrographically complex region of Kodiak Archipelago, high temporal variability in the zooplankton stocks has been found at oceanic, shelf and coastal locations (Frost, 1993; Mackas, 1995; Coyle and Pinchuk, 2003; Mackas and Coyle, 2005). The majority of zooplankton research around the Kodiak Archipelago was conducted during Fisheries Oceanography Coordinated Investigations (FOCI) by the National Marine Fisheries Service. Abundance and species composition of zooplankton were assessed in Shelikof Strait, on the west side of Kodiak Island, between 1984 and 1989 (Incze and Ainaire, 1994; Napp et al., 1996; Incze et al., 1997).

The goal of this study was to describe and assess correlations between the zooplankton community structure and the oceanography northeast of Kodiak Island. Specifically, the objectives were to: observe seasonal and interannual zooplankton abundance variability and spatial zooplankton community structure, describe the interactions between zooplankton and specific oceanographic factors, and compare results with concurrent data collected by Global Ocean Ecosystems Dynamics (GLOBEC) program adjacent to this study. Finally, this effort contributes to the Gulf Apex Predator–prey (GAP) study, focused on the interactions among apex predators (upper trophic

levels), their prey (i.e. zooplankton and fish), and the oceanographic conditions near the Kodiak Archipelago (Wynne and Foy, 2002). In particular, this project seeks to provide a better understanding of the prey resources available to fish to better understand their ultimate influence on the apex predators near Kodiak Island.

Chapter 1

Zooplankton abundance, community structure, and oceanography northeast of Kodiak Island, Alaska *

Abstract

Zooplankton community dynamics and correlations with physical characteristics of the water were studied in the northwestern Gulf of Alaska. Zooplankton were collected systematically northeast of Kodiak Island, Alaska in March, May, August and November of 2002 to 2004. Species composition, total abundance and spatial community structure were correlated to physical variables. Small copepods (numerically >50%) dominated the zooplankton composition and were most abundant in August. Average biomass was 48.7 g WW m⁻² in May and 52.0 g WW m⁻² in August in Kodiak region. Interannual zooplankton abundance variations were large, with May 2003 having a dramatically higher abundance (2×10^4 individual m⁻³ higher) than 2002 and 2004, probably due to the higher temperature (1 °C higher) and lower salinity in May 2003. Small to moderate correlations ($r < 0.7$) were found between temporal zooplankton abundance and selected physical variables. Spatial patterns in zooplankton composition among stations were more discernable in May than in August, likely due to water column stability in the spring and more dynamic influences in the summer, but revealed no consistent spatial patterns. The zooplankton community patterns in this region thus appear to arise due to complex

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Introduction

Zooplankton occupy a key position in the pelagic food web as they transfer the organic energy produced by primary producers through photosynthesis to higher trophic levels such as fish, marine birds and mammals (Lindeman, 1942; Platt et al., 1981; Lenz, 2000). Zooplankton abundance and biomass are direct indices of food web structure and carrying capacity for higher trophic level predator species (Mackas, 1995). The planktonic early life history of finfish and shellfish is dependent on zooplankton availability during this critical period (Damkaer, 1977; Dunn et al., 1979). In the south-eastern Bering Sea, abundance of walleye pollock (*Theragra chalcogramma*) and yellowfin sole (*Limanda aspera*) were found to be correlated with the abundance of *Eucalanus bungii* and *Metridia pacifica* (Lee, 1980). In the Gulf of Alaska (GOA), specifically in Prince William Sound (PWS), zooplankton abundance has been correlated to changes in pink salmon (*Oncorhynchus gorbuscha*) and juvenile herring (*Clupea pallasii*) diets and their subsequent recruitment success and fish survival (Foy and Norcross, 2001; Boldt and Haldorson, 2003; Armstrong et al., 2005). In the Shelikof Strait in the GOA, copepod nauplii, and *Pseudocalanus* spp. were the main prey items for pollock larvae (Kendall et al., 1987). Longer term studies in the North Pacific have also shown positive correlations between zooplankton biomass and abundance of pelagic fish and squid (Brodeur and Ware, 1992).

To understand the role of zooplankton in the food web, large scale environmental forcing has been assessed in the North Pacific Ocean (McGowan et al., 1996; Mackas & Tsuda, 1999; Peterson & Schwing, 2003; Chiba et al., 2006). The summer zooplankton biomass in the North Pacific subarctic gyre fluctuates on interannual and interdecadal time scales, correlated to the winter wind intensity in the northern GOA (Brodeur and Ware, 1992) and in the western subarctic North Pacific (Odate, 1994). Studies on spatial zooplankton community fluctuations have largely focused on inshore-offshore gradients (Morgan et al., 2003; Mackas and Coyle, 2005). The shelf zooplankton community consists of a mixture of oceanic and neritic species due to the complex cross-shelf circulation patterns (Coyle and Pinchuk, 2005).

At finer scales, zooplankton community heterogeneity is often the result of physical and biological interactions (Pinel-Alloul, 1995). Fluctuations in temperature and salinity, water column stratification, tidal mixing and excursion, currents, fresh water inflow, advection and turbidity, front formation and wind variability have all been found to affect zooplankton community structure to varying extents (Brodeur and Ware, 1992; Roman et al. 2001; Coyle and Pinchuk, 2003; Basedow et al., 2004; Rawlinson et al., 2005). Water temperature is a major factor affecting copepod distribution (Lee et al., 1999), likely due to the strong dependence of copepod growth on temperature, especially for earlier life stages (Hirst and Bunker, 2003; Liu and Hopcroft, 2006a,b). Upwelling caused by wind forcing, shelf break front, and coastal topology can also directly or indirectly affect zooplankton abundance and species composition (Cunha 1993; Danielsen et al., 1998; Keister and Peterson, 2003) and biomass (Brodeur and Ware, 1992). Biological processes

such as top-down control by fish species are also known to affect zooplankton abundance, biomass and spatial distribution (e.g. in the Oyashio region of the North Pacific - Tadokoro et al., 2005). Primary production availability is also very important to zooplankton because herbivorous zooplankton growth rates are dependent on phytoplankton and chlorophyll a concentration, and chlorophyll a concentration is a proxy for phytoplankton concentration (Liu and Hopcroft, 2006a, b). The distribution of water types and nutrients in the GOA has also been coupled to zooplankton abundance, in part due to their impact on phytoplankton production (Coyle and Pinchuk, 2003).

In the GOA, small and large scale variability in the physical environment strongly influences seasonal abundances of zooplankton, fish, and upper trophic levels. The GOA sustains an abundant and diverse zooplankton community dominated by about 30 species, with copepods being predominant (Cooney, 1986; Cooney, 2005). This abundant zooplankton and higher trophic community in the GOA are surprising given that the coastal GOA is classically considered a predominately downwelling system, but during the summer months significant periods of upwelling occur (Stabeno et al., 2004).

In the western GOA, the Kodiak Archipelago is surrounded by a bathymetrically and hydrographically complex shelf. The inshore area is influenced primarily by the Alaska Coastal Current (ACC) and local factors such as winds, complex bathymetry, and freshwater inputs (Kendall et al., 1980; Stabeno et al., 2004). The ACC dominates the GOA shelf circulation controlling the transport of dissolved substances and planktonic materials (Reed, 1984; Reed and Stabeno, 1989; Stabeno et al., 1995). The ACC flows westward along the Kenai Peninsula and bifurcates at Kennedy-Stevenson Entrance with

the majority of transport continuing down the Shelikof Strait and with less than half of the transport continuing along the northeast of Kodiak Island. Ecological processes on the offshore shelf at the shelf break are strongly affected by the Alaska Stream which follows the 1000 m isobath southwestward from the head of the GOA. The Kodiak shelf is also influenced by current close to the Kodiak Archipelago through numerous canyons adjoining the nearshore shelf areas with the shelf break.

In this productive and hydrographically complex region of Kodiak Archipelago, high temporal variability in the zooplankton stocks has been found at oceanic, shelf and coastal locations (Frost, 1993; Mackas, 1995; Coyle and Pinchuk, 2003; Mackas and Coyle, 2005). The majority of zooplankton research around the Kodiak Archipelago was conducted during Fisheries Oceanography Coordinated Investigations (FOCI) by the National Marine Fisheries Service. Abundance and species composition of zooplankton were assessed in Shelikof Strait, on the west side of Kodiak Island, between 1984 and 1989 (Incze and Ainaire, 1994; Napp et al., 1996; Incze et al., 1997). During springtime in Shelikof Strait, copepod copepodites typically dominate the mesozooplankton (0.2-2 mm) taxa, while copepod nauplii dominate the microzooplankton (20-200 μm). Biomass can be even greater than in the highly productive Bering Sea, presumably due to higher productivity in the shallow coastal area of Shelikof Strait (Howell-Kubler et al., 1996; Napp et al., 1996), and than other nearby regions during spring time such as PWS, Cook Inlet, and GOA station P as well (Incze et al., 1997). Although there was no difference in species diversity between the inshore and offshore study areas near Kodiak Island, the inshore zooplankton abundance in various bays was higher than abundance at the shelf

break. On the east side of the Kodiak Archipelago, zooplankton density was positively correlated with average temperature in the late 1970s (Kendall et al., 1980; Vogel and McMurray, 1982). The region's unique and complex bathymetry may provide increased production as a result of water column mixing and localized upwelling (Stabeno et al., 2004) but overall, the mechanisms underlying these distributions were never fully established.

Temporal and mesoscale zooplankton patterns and their relationship to the underlying physical environment are not well documented on the GOA shelf northeast of the Kodiak Archipelago. The goal of this study was to describe and assess correlations between the zooplankton community structure and the oceanography northeast of Kodiak Island. Specifically, the objectives were to: observe seasonal and interannual zooplankton abundance variability and spatial zooplankton community structure, describe the interactions between zooplankton and specific oceanographic factors, and compare results with concurrent data collected by Global Ocean Ecosystems Dynamics (GLOBEC) program adjacent to this study. Finally, this effort contributes to the Gulf Apex Predator–prey (GAP) study, focused on the interactions among apex predators (upper trophic levels), their prey (i.e. zooplankton and fish), and the oceanographic conditions near the Kodiak Archipelago (Wynne and Foy, 2002). In particular, this project seeks to provide a better understanding of the prey resources available to fish to better understand the ultimate influence of prey on apex predators near Kodiak Island.

Methods

Study location

Kodiak Island is the largest island in the Kodiak Archipelago located in the northwestern GOA. The archipelago is approximately 285 km long and 108 km across, extending from the Barren Islands on the north, to Chirikof Island and the Semidi Islands group on the south. The Kodiak shelf area is hydrographically complex influenced by the Alaska Stream, Alaska Coastal Current, wind intensity, bathymetry and freshwater inputs (Kendall et al., 1980). Basic features of the sea floor northeast of Kodiak Island include a number of shallow banks at depths of 50 to 100 m separated by troughs at depths of 200 m or more (Hampton, 1983) (Fig. 1). These topographic features lead to complex mixing of water masses and therefore distribution of plankton.

Sample collection and analyses

Oceanography

Temperature and salinity data of the entire water column were collected using a SeaBird19 CTD at systematically distributed stations spaced ~7.5 km apart within Marmot Bay and Chiniak Bay area and spaced ~10 km apart in the Portlock Bank area. CTD data of August 2003 were lost due to equipment failure. Fluorometry data was collected with a WETSTAR mini- fluorometer interfaced with the CTD. The fluorometer has an output of 0-5 VDC, which is proportional to the amount of fluoresced light emitted at 695 nm. The CTD was deployed at a speed of 0.5 ms⁻¹. The data series were processed using SBEDataProcessing-Win32 software.

Zooplankton

Zooplankton samples were collected in Chiniak Bay and Marmot Bay northeast of Kodiak Island from March to August (2002 to 2004). In 2004, “offshore” sampling stations were added in the Portlock Bank area (Fig. 1). Sampling stations were systematically distributed at regular intervals of ~15 km within Chiniak Bay and Marmot Bay area and intervals of ~20 km near Portlock Bank area. Not all stations were sampled in each cruise due to inclement weather conditions and sea state.

A 0.75 m diameter, 130 μm mesh ring net was deployed vertically to a depth of 25 m at multiple stations to collect zooplankton specimens at day time. The depth of the tows was originally chosen based on the average maximum depth of the acoustic (38 kHz) scattering layer in this region. The ring net was retrieved at a speed of 0.5 ms^{-1} through a volume of water estimated as the product of mouth area and the 25m depth, assuming that all tows were vertical (tows that had a larger angle than 30° away from vertical were not used for analysis). In May 2005, additional flowmeter data from 28 tows were collected from 50 m of the water column to the surface to estimate variability in water volume filtered. Net filtration efficiency was calculated to be 135% (SD = 31%) of the expected volume based on a truly vertical tow when the net was lowered to 50 m. Since the tows during the rest of the study were taken from 25 m to the surface the actual net filtration efficiency during this study was likely better than 135%. Filtration efficiency higher than 100% indicates that not all tows were truly vertical during the study. Upon retrieval, zooplankton samples were preserved immediately in 10% buffered formalin.

In the laboratory, each preserved sample was poured into a sorting tray where large animals (size larger than 1 cm) were counted and removed before splitting the samples. The samples were sequentially split using a Folsom splitter until the smallest subsample contained approximately 100 specimens of the most dominant taxa, then the plankton in the smallest subsample were identified, staged and enumerated, followed by analysis of subsamples of increasing size for less abundant taxa (Coyle and Pinchuk, 2003).

Data analyses

After the zooplankton samples were analyzed, the abundance and biomass of each taxa were calculated. Species that accounted for less than 1% of the total abundance and biomass in each sample were grouped together as the “other” zooplankton category for species composition description. Estimated average wet weights (WW) of different zooplankton taxa collected from the North Pacific between 1997 and 2003 were used to calculate zooplankton WW biomass in this study (Coyle, K. unpublished data, Appendix A.5).

Seasonal (among months) and interannual (among years) variation in average total zooplankton abundance was assessed among similar stations from 2002 to 2004 (only data from nearshore Marmot and Chiniak Bay stations were used for these analyses to maintain a more balanced design, Fig. 1) with a one factor ANOVA test and post hoc Tukey’s test, the significance level is $\alpha = 0.05$. Zooplankton abundance data were $\log(y+1)$ transformed to meet assumptions of ANOVA.

Variations in average temperature above 25 m (T_{25}), average salinity above 25 m (S_{25}), average fluorometry above 25 m (F_{25}), average stratification parameter and pycnocline depth among months and years were analyzed using a one factor ANOVA and post hoc Tukey's test (again restricted to Marmot and Chiniak Bay stations were used to calculate these averages in order to keep consistent with seasonal and interannual zooplankton abundance comparison). Trends in oceanographic factors among months and years were correlated to the variation in average total zooplankton abundance. As a measure of stratification parameter (Φ) we used the potential energy

$$\bar{v} = \frac{1}{h} \int_h^0 (\rho - \bar{\rho})gzdz; \bar{\rho} = \frac{1}{h} \int_h^0 \rho dz; \Phi = \bar{\rho} \bar{v} \quad (1.1)$$

where z is the vertical coordinate, h is the depth, ρ is the density, $\bar{\rho} \bar{v}$ (Φ) is the work which would be done in redistributing the mass in bringing about complete vertical mixing (Simpson et al., 1977). Pycnocline depth was defined as the maximum change of water density based on 1 m depth increments. Stratification parameter (Φ) and pycnocline depth data were $\log(y+1)$ transformed to meet assumptions of correlation.

Correlations between total zooplankton abundance and T_{25} , S_{25} , F_{25} , stratification parameter (Φ), and pycnocline depth were assessed in order to check for possible influential factors that could influence zooplankton abundance in specific time of the year in Marmot and Chiniak Bay. Initial plots of distance from shore and station depth showed that neither factor was related to zooplankton abundance, and they were therefore removed from further analysis.

The spatial structure of the zooplankton community composition was assessed in May and August each year. Cluster analysis and non-metric multidimensional scaling (NMDS) ordination based on a Bray-Curtis similarities matrix were performed on zooplankton species composition and abundance (individual m^{-3}) data. Similarity matrices were calculated using zooplankton species abundance transformed by $\log(y+1)$. All analyses were carried out using the software package PRIMER v6 (Clark and Warwick, 2001). Cluster analysis and the similarity profile test (SIMPROF) of the PRIMER software were used to group sites based on the similarity of zooplankton abundance and species composition. The similarity profile test is a permutation test of the null hypothesis that the rankings of a specified set of samples that are not *a priori* divided into groups do not differ from a random grouping. The similarity profile itself is the set of all dissimilarities between the specified samples, ranked from smallest to largest, and the ordered dissimilarities then plotted against their rank. An “expected” profile obtained by permuting the entries for each variable across that subset of samples provide a null condition in which samples have no group structure. The mean values of a random rearrangement of the entries across the samples carried out 1000 times and the mean values out of the 1000 times provide the “expected” profile. The similarity percentages routine (SIMPER) of the PRIMER software was used to determine which species contributed most to the separation between groups. The similarity percentage routine decomposes average Bray-Curtis dissimilarities among samples within a group into percentage contributions from each species, listing the species in decreasing order of each

contribution. Bubble plots of the top three species that contribute to the separation of the groups were superimposed on NMDS ordinations.

Correlation between zooplankton community composition and T_{25} , S_{25} , F_{25} , stratification parameter, and pycnocline depth were also assessed to check for which factors could explain the patterns in spatial zooplankton composition. The BEST (Bio-Env) tool of the PRIMER software was used for this analysis. The purpose of this analysis is to search for high rank correlations between a matrix generated from different variables subsets of physical variables and groupings from a biotic ordination. The output is a list of variables sorted according to their correlations to the biotic ordination.

Lastly, the biomass of dominant taxa from this study were compared to the biomass of dominant taxa collected concurrently during the GLOBEC studies on the Seward line 350 km north-east of Kodiak Island. During GLOBEC, mesozooplankton were collected from 13 stations using the 150 μ m CalVET net in May and August 2002 and 2003 according to the methods described in Coyle and Pinchuk (2005) (Appendix A.2). Previous studies have found significant differences in nearshore versus offshore species composition on the Seward line (Coyle and Pinchuk, 2005). Therefore only data from stations in the inner shelf and mid-shelf transition region on Seward line were compared to Kodiak data when collection times were similar. To make the biomass data from the two study locations comparable, biomass units were converted to $WW \text{ g m}^{-2}$ ($WW \text{ g m}^{-2} = WW \text{ g m}^{-3} * \text{sampling depth m}$).

Results

General Trends

Oceanographic data

CTD casts were taken at 11 to 49 nearshore stations in 2002-2004 and from 38 to 40 offshore stations in 2004 northeast of Kodiak Island (Table 1, Table 2, Fig. 1). The mean and standard deviation of T_{25} , S_{25} , F_{25} , stratification parameter, and pycnocline depth are summarized in Table 2.

Average temperature above 25 m was about 1 °C greater in May 2003 than in May 2002 and May 2004 and average salinity above 25 m was lower in May 2003 than in May 2002 and May 2004. Average temperature above 25 m was lower in August 2002 than August 2004 and average salinity above 25 m was higher in August 2002 than August 2004.

Zooplankton species composition

Zooplankton were sampled from 4 to 31 nearshore stations in 2002-2004 and from 18 to 19 offshore stations in 2004 northeast of Kodiak Island (Table 2, Fig. 1). A total of 34 zooplankton taxa were encountered from 206 zooplankton tows. The most species rich taxonomic group collected was copepods (14 species) (Appendix Table A.1).

Overall, copepods were the dominant zooplankton taxa both in time and space during this study (Fig. 2). *Oithona* spp. was the only cyclopoid copepod found in our samples. Among the copepod taxa, small copepods such as *Pseudocalanus* spp., *Oithona* spp., and *Acartia* spp. were more abundant than large copepods such as *Neocalanus* spp., *Eucalanus* sp. and *Calanus* sp. in every sampling season. In general, zooplankton

abundance was highest in August within each year while zooplankton biomass was highest in August in 2002 and 2003 but highest in May in 2004.

Barnacle larvae were the most numerically abundant taxa in March 2002 (36.3%) and March 2003 (32.0%). Other numerically abundant taxa in March were *Oithona* spp., copepod nauplii, and *Pseudocalanus* spp. In May, euphausiid larvae, *Oithona* spp., copepod nauplii, and *Pseudocalanus* spp. were dominant taxa. Euphausiid larvae abundance was greater in May 2002 (21.1%) and May 2004 (18.3%) than in May 2003 (<1%). In August and November, the numerically dominant zooplankton species were similar to those in May, although the total abundance was lower in November.

Barnacle larvae had the highest biomass of any taxa in spring and early summer. They accounted for 60.1% of total biomass in March 2002 and 84.2% of total biomass in March 2003. Barnacle larvae, *Oikopleura* spp., and *Clione limacina* were dominant taxa based on biomass in May 2002, May 2003, and May 2004. Total zooplankton biomass was higher in May 2004 (85.5 g WW m⁻²) than May 2002 (21.8 g WW m⁻²) and May 2003 (38.9 g WW m⁻²) due to higher *Clione limacina* biomass in May 2004. Polychaete juvenile, *Oikopleura* spp., and adult female (AF) *Pseudocalanus* spp. were the dominant taxa in zooplankton biomass in August 2002, August 2003, and August 2004. The total biomass in August 2003 (89.1 g WW m⁻²) was higher than in August 2002 (33.1 g WW m⁻²) and August 2004 (33.7 g WW m⁻²) due to a higher biomass of *Oikopleura* spp. in August 2003. *Oikopleura* spp. (44.7%) was the most dominant taxa in total biomass in November 2002.

Total zooplankton abundance: monthly comparison (2002, 2003 and 2004)

In 2002, average total nearshore zooplankton abundance among stations varied significantly among May, August and November months ($p < 0.001$, $F = 73.6$, $n = 53$; Fig. 3). Zooplankton abundance was significantly higher in August (1.91×10^4 individual m^{-3}) than in May (4.72×10^3 individual m^{-3}) and November (2.46×10^3 individual m^{-3}). There was no significant difference in zooplankton abundance between May and November (Although in March 2002 zooplankton were sampled, due to the small sample size, March 2002 data were not included in the ANOVA test). In 2003, total nearshore zooplankton abundance varied significantly among March, May and August ($p < 0.001$, $F = 84.0$, $n = 28$; Fig. 3). Zooplankton abundance was significantly higher in August (5.36×10^4 individual m^{-3}) than in March (950 individual m^{-3}), was significantly higher in May (3.62×10^4 individual m^{-3}) than in March, but not significantly different in zooplankton abundance between August and May. In 2004, total nearshore zooplankton abundance was significantly higher in August (4.43×10^4 individual m^{-3}) than in May (1.81×10^4 individual m^{-3} , $p < 0.001$, $F = 22.9$, $n = 29$; Fig. 3).

Total offshore zooplankton abundance in the Portlock Bank area was significantly higher in August 2004 (3.10×10^4 individual m^{-3}) than in May 2004 (1.03×10^4 individual m^{-3} ; $p = 0.005$, $F = 8.96$, $n = 37$; Fig. 4). There was no significant difference between the nearshore and offshore total zooplankton abundance in either May ($p > 0.05$, $F = 3.47$, $n = 35$) or August 2004 ($p > 0.05$, $F = 1.03$, $n = 40$).

Total zooplankton abundance: interannual comparison (May and August)

In May, average total zooplankton abundance among stations varied significantly among 2002, 2003, and 2004 ($p < 0.001$, $F = 117$, $n = 44$; Fig. 3). Total zooplankton abundance was significantly higher in May 2003 than in May 2004, and zooplankton abundance was significantly higher in May 2004 than in May 2002. Copepod nauplii, *Pseudocalanus* spp., *Oithona* spp., and *Acartia* spp. numerically accounted for the significant interannual variations in zooplankton abundance in May. Abundance of those species was higher in May 2003 than in May 2002 and 2004. Conversely, euphausiid larvae abundance was lowest in May 2003.

In August, total zooplankton abundance varied significantly among 2002, 2003 and 2004 ($p = 0.01$, $F = 5.16$, $n = 43$; Fig. 3). Zooplankton abundance in August 2004 was significantly higher than in August 2002. Zooplankton abundance in August 2003 was significantly higher than in August 2002. There was no significant difference in zooplankton abundance between August 2003 and 2004. Copepod nauplii, *Pseudocalanus* spp., *Oithona* spp., and *Acartia* spp. also numerically accounted for the significant interannual variations in zooplankton abundance in August. Abundance of those species was much lower in August 2002.

Correlation of total zooplankton abundance with physical and biological factors

Physical and biological factors significantly correlated to total zooplankton abundance varied among months and years (Table 4).

Zooplankton abundance was significantly correlated to S_{25} , T_{25} , F_{25} , and Φ in

different months and years, but without consistent pattern. In May, zooplankton abundance was negatively correlated to S_{25} in 2002 and Φ in 2004. In August, zooplankton abundance was positively correlated to T_{25} and Φ in 2002. In November, zooplankton abundance was positively correlated to F_{25} in 2002. In 2003, no biological or physical factors were significantly correlated with zooplankton abundance.

Spatial zooplankton community structure

May 2002 stations clustered into three groups at 70% similarity based on cluster analysis and ordination of zooplankton species composition and abundance. Euphausiid eggs, euphausiid nauplii, and copepod nauplii contributed most to the separation of groups based on similarity percentage by the SIMPER algorithm in PRIMER (Fig. 5, Table 5). The rank correlation (ρ) between the biotic and the physical ordination matrices suggested that the species ordination was slightly correlated to S_{25} ($r=0.28$). However, spatial patterns based on visual representation of the ordination clusters were not discernable (Fig. 6).

May 2003 stations clustered into two groups at 40% similarity based on cluster analysis and ordination of zooplankton species composition and abundance. *Acartia* spp., copepod nauplii and euphausiid eggs contributed most to the separations of groups based on similarity percentage (Fig. 7, Table 6). The species composition ordination was most correlated to T_{25} and S_{25} ($r=0.46$). However, spatial patterns based on visual representation of the ordination clusters were not discernable (Fig. 8).

May 2004 stations clustered into two groups at 50% similarity based on cluster analysis and ordination of zooplankton species composition and abundance. Euphausiid larvae, Barnacle larvae and *Neocalanus* spp. contributed most to separation of groups based on similarity percentage (Fig. 9, Table 7). All correlations between species composition ordination and physical or biological variables were negligible in May 2004. Spatial patterns based on visual representation of the ordination clusters suggested some discernable patterns with the nearshore stations clustered in the lower temperature zone and the offshore stations clustered in the higher temperature zone of the study area (Fig. 10).

In August, there were no significant station clusters based on zooplankton species composition and abundance in any year.

Regional zooplankton composition comparison

Not surprisingly, there is great similarity in the species composition between the Kodiak study area and the Seward line study area (Table 8, Appendix A.3). It is notable that biomass of more oceanic *Neocalanus* spp. and *Metridia pacifica* biomass on Seward line were higher than in the Kodiak study area. Similarly biomass of the more neritic *Pseudocalanus* spp., *Oithona* spp. and *Oikopleura* spp. biomass were higher in the Kodiak than on the Seward line with the exception of 2002. *Clione limacina* biomass in Kodiak was higher than on the Seward line.

Discussion

Regional zooplankton comparison

The overall numerical dominance of small copepods *Pseudocalanus* spp., *Oithona* spp., and *Acartia* spp. within the holozooplankton northeast of Kodiak Island was similar to that found in the northern GOA study sites near Seward (May and July 1998-2000; Coyle and Pinchuk, 2003), in PWS (spring and summer 1994; Cooney et al., 2001), in Shelikof Strait (May 1994-1997; Incze et al., 1997), and on the Kodiak Island shelf (fall 1977 to winter 1979; Kendall et al., 1980). Large interzonal copepod species such as *Neocalanus* spp. and *Eucalanus* sp. were not abundant in this study likely due to their deeper distributions (Damkaer, 1977). However, relatively higher abundance of these species in May was expected due to their seasonal ontogenetic migration and advection onto shallower shelf waters (Coyle and Pinchuk, 2003, 2005). This seasonal increase was more pronounced in the offshore waters of Portlock Bank in 2004 likely due to the proximity of deep gullies that favor the movement of deeper water masses onto the shelf. This process may be enhanced through the interaction of the Alaskan Stream with the dynamic bathymetry on the Kodiak shelf (Kendall et al., 1980). The relative abundance of meroplankton such as barnacle larvae decreased between March and May as they metamorphosed to benthic life stages.

There are several possible factors affecting the high abundance of zooplankton in this study region. Although zooplankton abundance in the Kodiak region may be a result of local production, zooplankton distributions may also be influenced by oceanographic currents and tides outside the immediate study area. Zooplankton from the Kodiak Shelf

may be transported to the study area by the Alaska Stream, and the ACC may transport zooplankton from the central GOA into the study area as well. Studies in the Gulf of Maine suggest zooplankton distribution is influenced by deep flow, advection from upstream areas, and regional bathymetry (Johnson et al. 2006). Tidal currents originating in Cook Inlet, north of the study area, might also influence the small scale zooplankton community (Stabeno et al. 2004). Tidal affects on zooplankton distribution have been noted in the Gulf of Maine and the tidal forcing “sloshes” water masses along the shelf, and the tidal sloshing could effect the temporal distribution of zooplankton (Wishner et al. 2006). Tides could also affect current speeds and a change in current speed could influence zooplankton distribution (Foreman, et al. 2006; http://www.pac.dfo-mpo.gc.ca/sci/osap/people/foreman_e.htm).

Zooplankton biomasses estimated in this study were within the range of that found in other studies (Table 9). This general agreement is surprising given the difference methods of biomass determination, and different sampling depth ranges (e.g. 100 m or 200 m) between studies, both of which hamper direct comparison. Zooplankton biomass in the upper 200 m ranges from 0.01 to 0.08 g WW m⁻³ in the fall and winter and from 0.2 to 5 g WW m⁻³ in the spring and summer in GOA coastal, shelf, and oceanic regions (Incze et al., 1997; Coyle and Hunt, 2000; Cooney et al., 2001; Coyle and Pinchuk, 2003, 2005). Zooplankton biomass data in other regions of GOA from other studies and biomass data from this study were listed in the same biomass unit (WW g m⁻²) in Table 9. In some studies, samples were not taken to a consistent depth, so there are potential sources of bias in the biomass information provided in Table 9. The average March zooplankton

biomass in this study near Kodiak Island (3.3 g WW m^{-2}) was lower than in Shelikof Strait between 1985 and 1989 (58.2 g WW m^{-2}), and PWS in 1977 (56.2 g WW m^{-2} ; Damkaer, 1977) in early April. In May, the average zooplankton biomass in Shelikof Strait between 1985 and 1989 ($178.5 \text{ g WW m}^{-2}$; Incze et al., 1997) was similar to this study (48.7 g WW m^{-2}), and was higher than in the northern GOA between 1997 and 1999 (18.5 g WW m^{-2} ; Coyle and Pinchuk, 2003). While differences among zooplankton studies in the GOA existed, comparisons are confounded by interannual and spatial variability.

One of the goals of this study was to compare zooplankton biomass and species composition data collected in the Kodiak region to data collected concurrently on the Seward line in the GOA. Bathymetric and oceanographic differences between the two regions likely influenced the zooplankton biomass and species composition differences observed. Relatively higher abundance of small copepod species such as *Pseudocalanus* spp. and *Oithona* spp. in the Kodiak region could be due to higher plankton production from increased water column mixing (Stabeno et al., 2004). Differences between study methodologies may also have influenced measure of zooplankton biomass and species composition. The plankton net mesh size in this study ($130\mu\text{m}$) was smaller than that used during the Seward line study ($150\mu\text{m}$), but probably close enough not to result in major differences in catch. Sampling depth during this study (25 m) was much shallower than the Seward line study (100 m), and likely biases direct comparisons between these two regions for larger species with significant abundances below 25 m (see Coyle and Pinchuk, 2005). For instance, higher *Metridia pacifica* abundance in May and August on

the Seward line was likely the result of deeper sampling depths. *Metridia pacifica* was found to inhabit in deeper water as day-length increased (Batchelder, 1985; Hirakawa and Imamura, 1993). Higher biomass of *Neocalanus* spp., and in particular *N. cristatus*, on Seward line than Kodiak region also arise in part due to the differences in sampling depths (Coyle and Pinchuk, 2005).

The productivity of the shelf area around Kodiak Island was historically greater than other regions in the GOA, even during peak summer stratification (Stabeno et al., 2004). A spring (May) along-shelf gradient in chlorophyll was found between Prince William Sound (2.0 mg m^{-3}) and Kodiak Island ($2.5\text{-}3.0 \text{ mg m}^{-3}$) where chlorophyll was highest near Kodiak Island from 1997 to 2001 (Brickley and Thomas, 2004). From 1998 to 2002 chlorophyll concentrations ranged from 2.9 to 4.0 mg m^{-3} near Kodiak Island and from 0.7 to 2.5 mg m^{-3} near Seward line between June 15 and August 30 (Stabeno et al., 2004). During this study from 2002 to 2004, chlorophyll concentrations were between 1.7 and 12.2 mg m^{-3} which is similar to or greater than the previous studies. In a concurrent study, estimated chlorophyll concentrations from satellite data were from 0.2 to 11 mg m^{-3} in this study area (Montes-Hugo et al., 2005). It should be noted that the vertical structure of chlorophyll concentration is not represented by SeaWiFs satellite data and may account for differences between sites. Fluorometry profiles from 25 m of the water column to the surface of the water column in this study revealed chlorophyll concentration was lower on the surface than at depth in the water column (Appendix A.4), consistent with summertime observations along the Seward Line (Childers et al., 2005; Whitledge, unpublished). The likely cause of this western GOA production is increased nutrient

supply as a result of water mass movement influenced by gullies and banks (Stabeno et al., 2004). The relatively higher zooplankton abundance and biomass in this study supports the hypothesis that the Kodiak region is relatively more productive than other regions in the GOA, at least during summer.

Zooplankton abundance, related oceanography and ecosystem considerations

Correlations of physical and biological factors with total zooplankton abundance partially explain significant interannual variability in zooplankton abundance observed in this study. Higher T_{25} and lower S_{25} in May 2003 coincided with the highest May zooplankton abundances from 2002 to 2004 (Table 3 and Fig. 3). The possible cause for temperature and salinity abnormalities in May 2003 was relatively high freshwater discharge and high winds in winter 2002-2003 in the GOA region (Royer, personal communication). Temperature may have been more important in affecting zooplankton abundance than other factors in early spring because of the relationship between increased stratification in the surface layer and increased phytoplankton and zooplankton production (Eslinger et al., 2001). Similarly, higher T_{25} and lower S_{25} in August 2003 and 2004 compared to 2002 may have caused higher zooplankton abundance. During summer months, salinity might become more important in affecting zooplankton abundance because of the larger influence of freshwater from snowmelt, glacial runoff, and precipitation on the GOA ecosystem (Reed, 1987). Similar relationships between temperature and salinity with zooplankton abundance have been found in previous years and in other GOA regions (Vogel and McMurray, 1982; Foy and Norcross, 2001; Coyle

and Pinchuk, 2003).

Interannual and seasonal variability in the zooplankton community impacts the availability of zooplankton as prey for higher trophic levels. For example, in Shelikof Strait, reduced copepod nauplii concentrations in the spring were correlated to low indices of larval feeding (Canino et al., 1991). On Georges Bank, cod and haddock larval production were linked to zooplankton biomass increases (Sherman et al., 1984). In the subarctic Pacific (1956-1962 and 1980-1989) pelagic fish and squid abundances were positively correlated with zooplankton biomass (Brodeur and Ware, 1992). In the GOA, walleye pollock, Pacific herring, rainbow smelt (*Osmerus mordax*), eulachon (*Thaleichthys pacificus*) and capelin (*Mallotus villosus*) principally feed on the zooplankton resources in this region. Specifically, copepod nauplii and *Pseudocalanus* spp. were found to be main prey items for larval walleye pollock (Kendall et al., 1987), Pacific herring, and capelin (Vogel and McMurray, 1982). Therefore, the seasonal and interannual variability in these copepod taxa observed in this study may impact the abundances of these forage species in this region. Other commercial fishes, sea birds, and mammals that consume zooplankton could also be influenced by zooplankton abundance trends quantified in this region (Vogel and McMurray, 1982; Anderson and Piatt, 1999).

Spatial zooplankton community structure and related oceanography

Spatial patterns in the zooplankton community among stations changed seasonally: where stations could be aggregated based on similar zooplankton community structure in May, but not in August of each year (2002- 2004). In August, a lack of spatial

zooplankton community organization among stations coincided with decreased salinity as a result of fresh water inputs through the ACC. This fresh water increase might increase zooplankton advection and provide better mixing and exchange of zooplankton species assemblages in this area (Stabeno et al., 1995; Stabeno et al., 2004). Similar to this study, station groupings on the northern GOA shelf between 1998 and 2000 were also seasonal, occurring primary in May and July, but largely absent by August and October (Coyle and Pinchuk, 2005). This study did not fully support the hypothesis that there is a nearshore-offshore gradient in species composition on the shelf near Kodiak Island. Although stations could be aggregated in May 2002 - 2004, the aggregations were not correlated to bathymetry or distance from shore. Although spatial patterns were observed in May 2002 and 2003, relationships to physical variables were not discernable and the ecological significance of the patterns was not clear.

The correlations of zooplankton species composition with physical and biological factors were weak, suggesting that temperature, salinity, fluorometry, stratification, pycnocline depth, and station depth do not independently influence the aggregation of species on the northeast side of Kodiak Island. It is likely that a combination of factors or other factors not addressed in this study such as wind forcing, freshwater discharge, circulation pattern of the upper layers, and the topology of the coast and continental shelf might better explain species community structure (Hubbard and Agard, 1991; Cunha, 1993; Sugimoto and Tadokoro, 1998). Tidal currents interacting with complex topographies also influence zooplankton community structure in coastal environments. In the San Juan Islands the median densities of weekly sampled copepods were 42 to 252

individual m^{-3} greater during flood tides than ebb tides during July-October of 1995 to 1997 (Zamon, 2002). Although we did not examine the influence of tidal currents on the zooplankton community structure, tidal cycles may be responsible for some of the variability in zooplankton distribution and abundance. However, current structure influences associated with seasonal changes in the ACC, as indicated by temperature and salinity data were assumed to be greater than tidal influences for this study.

Potential Sources of errors and further investigations

To adequately assess mesozooplankton the sampling gear should be the proper size to target the entire size range of the species present. Variability in net filtration efficiency due to phytoplankton clogging the small mesh size net may have biased the abundance estimation. To address flow through our nets, in August 2005, a flowmeter was used to calculate the filtered water volume while we sampled zooplankton at 28 stations. Based on the flowmeter data, our net filtration rate ranged between 75% and 200%. The assumption in this study that each plankton net was deployed vertically either underestimates or overestimates the water filtered through the plankton net, and thus impacts our estimates of abundance. Future zooplankton studies should adequately quantify the net filtration efficiency as well as assess the catchability of all size classes of mesozooplankton.

Future studies should incorporate additional factors that may affect zooplankton abundance on seasonal and interannual scales. These include predation (Vogel and McMurray, 1982) and additional environmental effects, such as wind intensity (Brodeur

and Ware, 1992). Also, the timing and intensity of eddies that propagate along the GOA shelf break are known to influence zooplankton composition and abundance (Mackas and Coyle, 2005) and likely affect the Kodiak region (Ladd et al., 2005). Lastly, future studies should consider correlations among physical factors that may interact to affect zooplankton abundance in a more complex analysis than in this study. A larger geographic extent with more stations could also be added to future study and probably sampling zooplankton from both 25 m and 100m to make results more comparable to other studies in this region.

To adequately understand temporal zooplankton abundance and biomass variation, vertical migration of zooplankton taxa should be taken into account with depth specific studies. Zooplankton could be sampled from different depth intervals of the water column to understand specific zooplankton taxa's depth preferences, which could make our study more comparable to other similar studies in other regions. Diurnal activity of zooplankton species should also be taken into account.

Zooplankton should be more frequently sampled in the future to increase the resolution of zooplankton data in the Kodiak region. Sampling zooplankton monthly or even bi-weekly consecutively in a period of one or two years would help to locate when the zooplankton population reaches its maximum and minimum abundances in the Kodiak region, or whether there is a secondary peak in the zooplankton population in this area.

Conclusions

Studies on temporal and spatial zooplankton species composition, abundance, and biomass are important to better understand interactions among trophic levels in the marine ecosystem (Vogel and McMurray, 1982; Mackas et al., 1998; Anderson and Piatt, 1999). This study provides evidence that the zooplankton community structure and oceanographic factors are highly variable on the shelf northeast of Kodiak Island, implying that the availability of prey for upper trophic levels such as commercially important fish, seabirds, and mammals may fluctuate on similar temporal and spatial scales. Correlations between oceanographic factors and the zooplankton community structure were weak in this study, likely a result of the complex interactions between physical processes and biological production on the western GOA shelf. Specifically, additional factors more complex than temperature and salinity such as bathymetry, dynamic currents, and variable climate forcing may be more influential in driving zooplankton community structure. Zooplankton advections from other regions may also play an important role in local zooplankton community structure and confound relationships with local environmental conditions. It is therefore not surprising that local physical features would not necessarily correlate strongly with zooplankton density in a small study area like this Kodiak study site where localized conditions may be different from those of the broader geographic areas.

Acknowledgements

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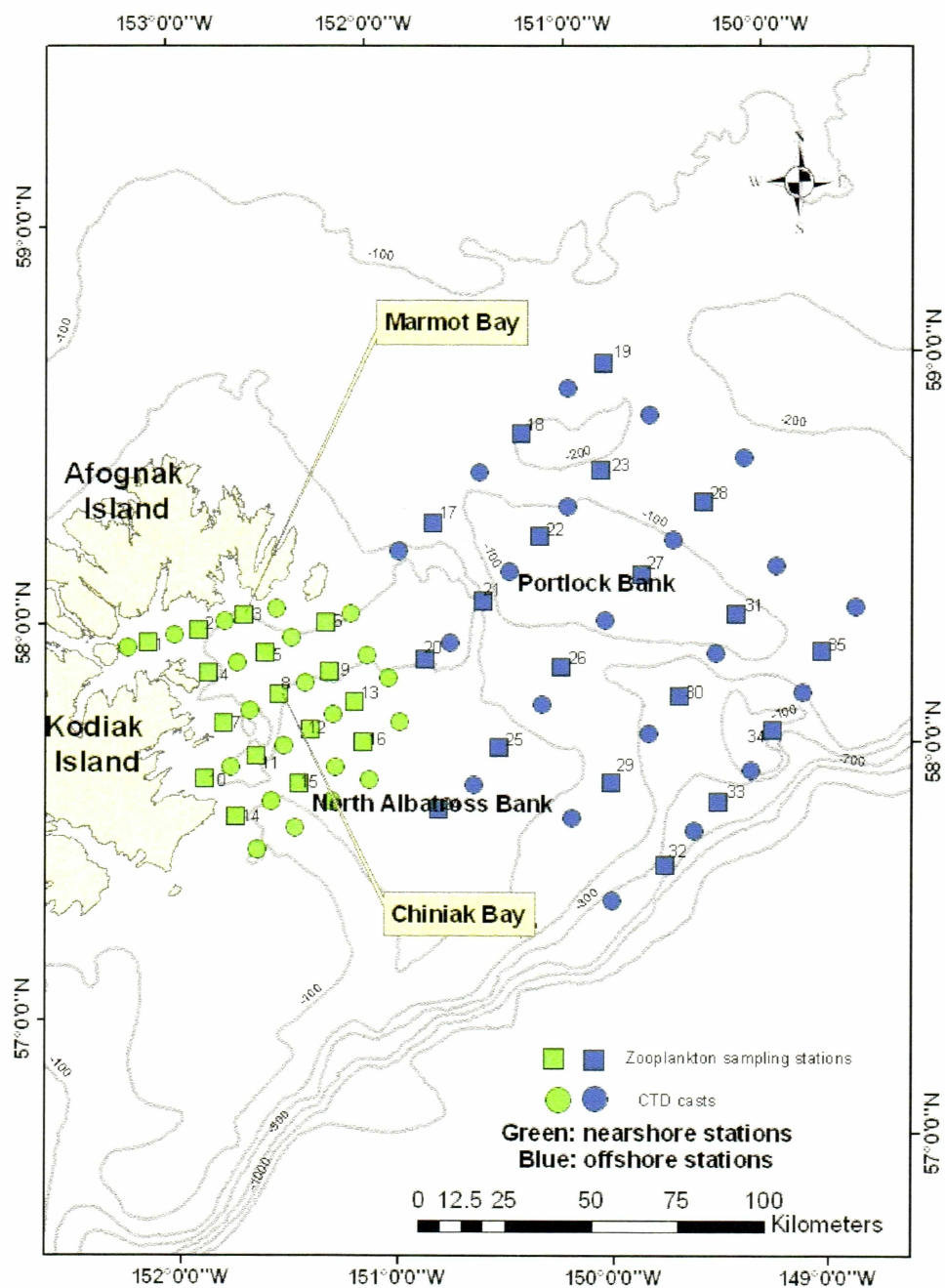


Fig. 1. Locations of systematically sampled stations and CTD casts in Chiniak Bay, Marmot Bay and Portlock Bank 2002-2004, northeast of Kodiak Island, Alaska.

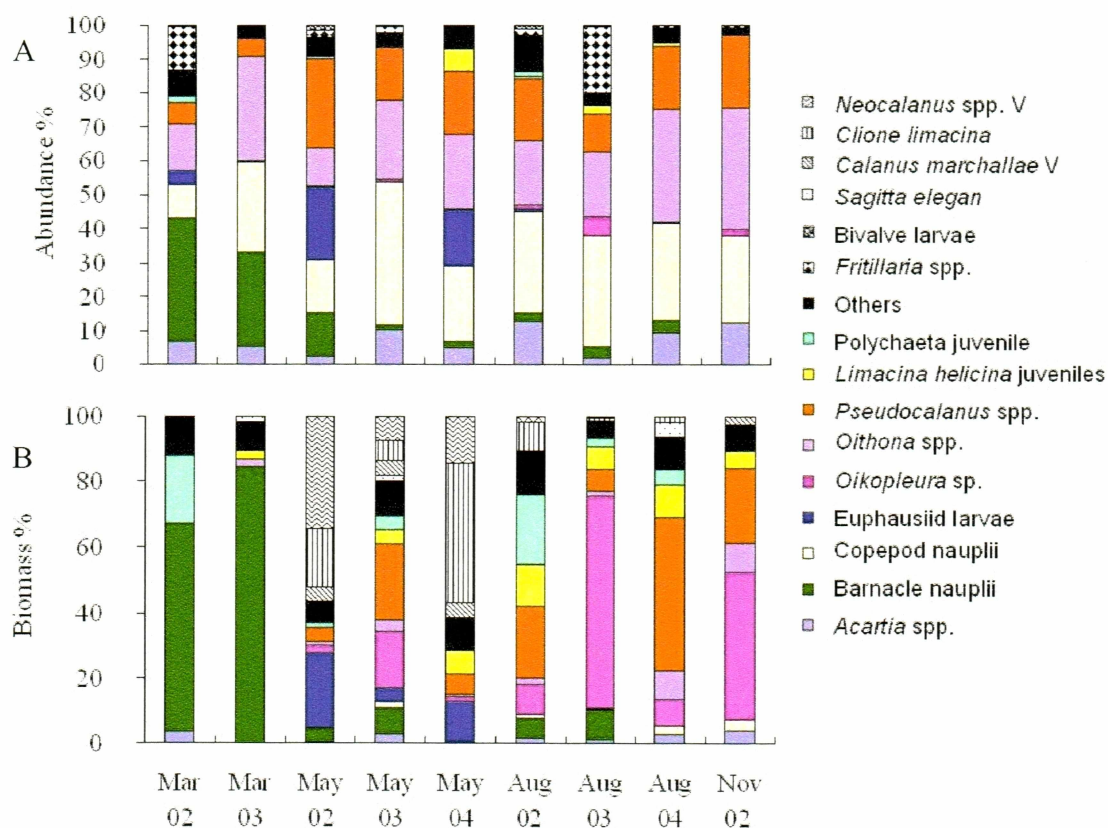


Fig. 2. Percent abundance (A) and percent biomass (B) of zooplankton in March, May, August and November of 2002-2004, for Chiniak and Marbot Bay region, Kodiak Island, Alaska.

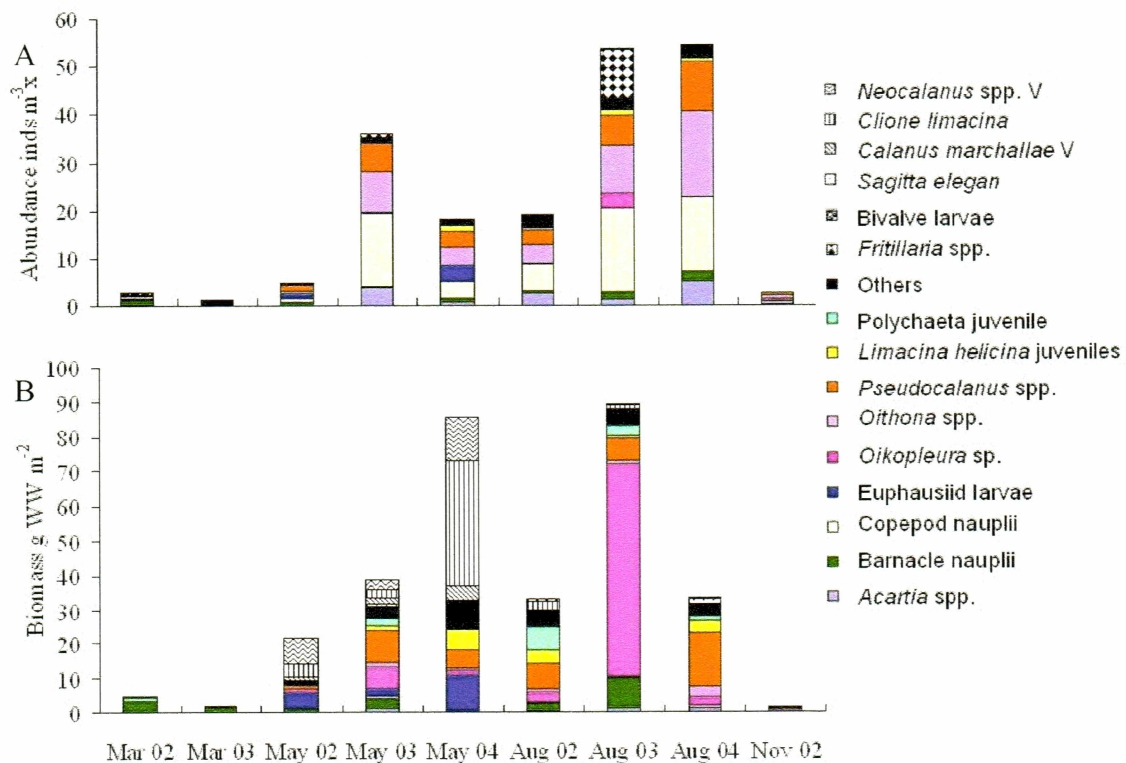


Fig. 3. Total zooplankton abundance (A) and biomass (B) in March, May, August and November of 2002-2004, for Chiniak and Marmot Bay region, Kodiak Island, Alaska

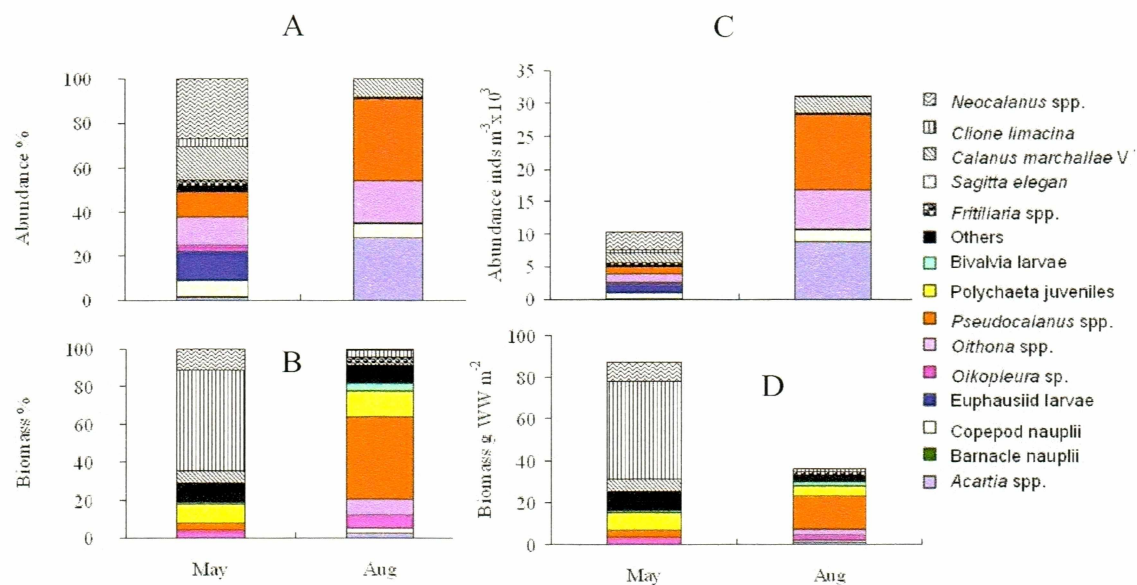


Fig. 4. Percent abundance (A) and percent biomass (B), abundance (C) and biomass (D) of zooplankton, for Portlock Bank, northeast of Kodiak Island, Alaska, in May and August 2004.

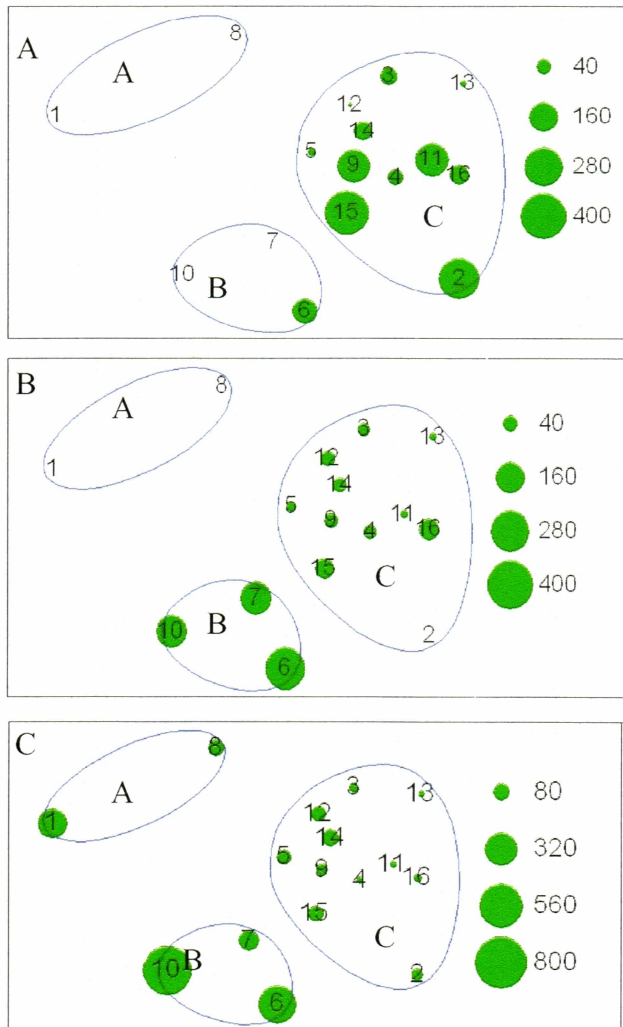


Fig. 5. May 2002 bubble plots of species abundance (individual m^{-3}) (A= euphausiid eggs, B= euphausiid nauplii, C= euphausiid calyptopis) superimposed on MDS ordination, for Chiniak and Marbot Bay region, Kodiak Island, Alaska.

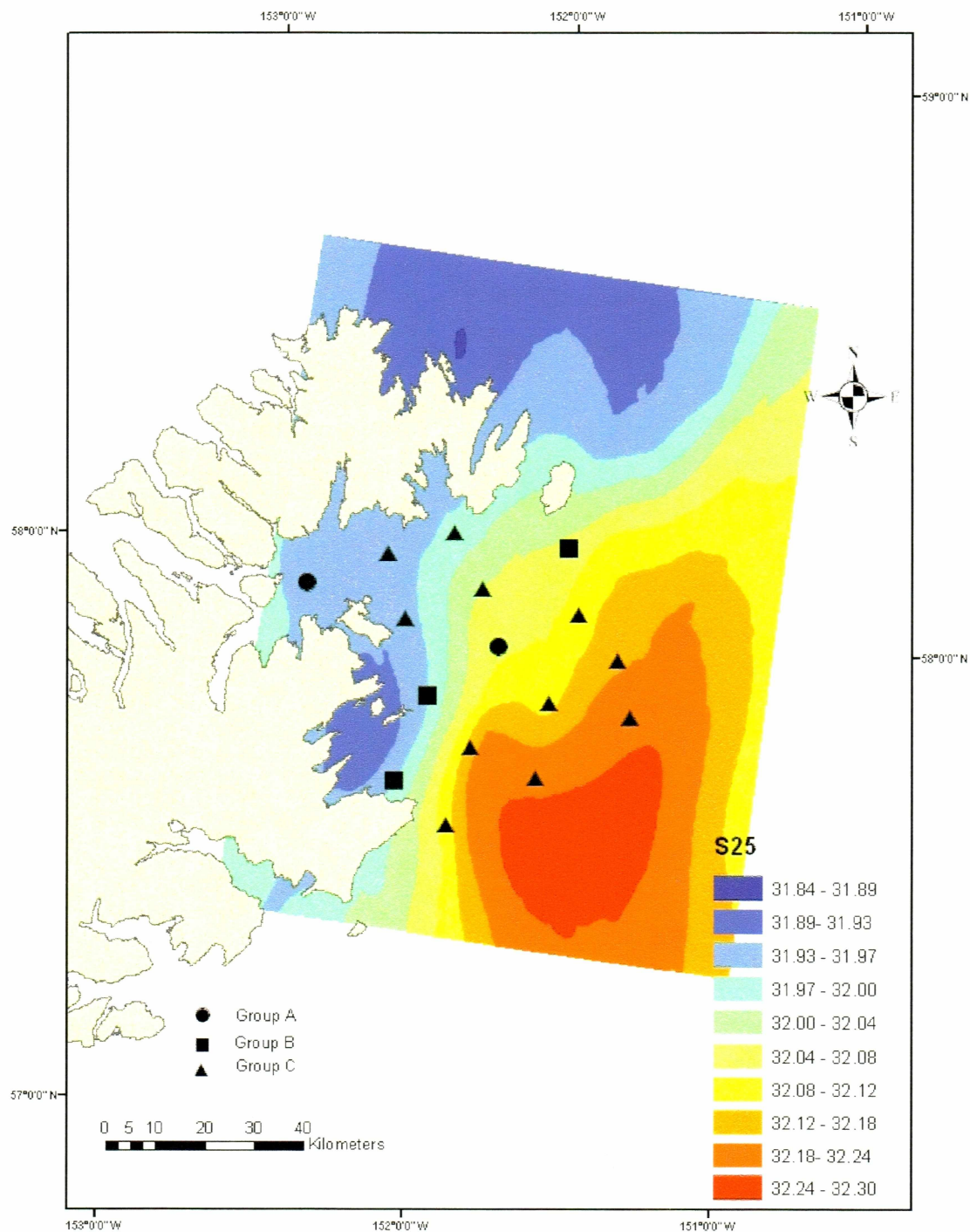


Fig. 6. May 2002 MDS ordination superimposed on S_{25} , northeast of Kodiak Island

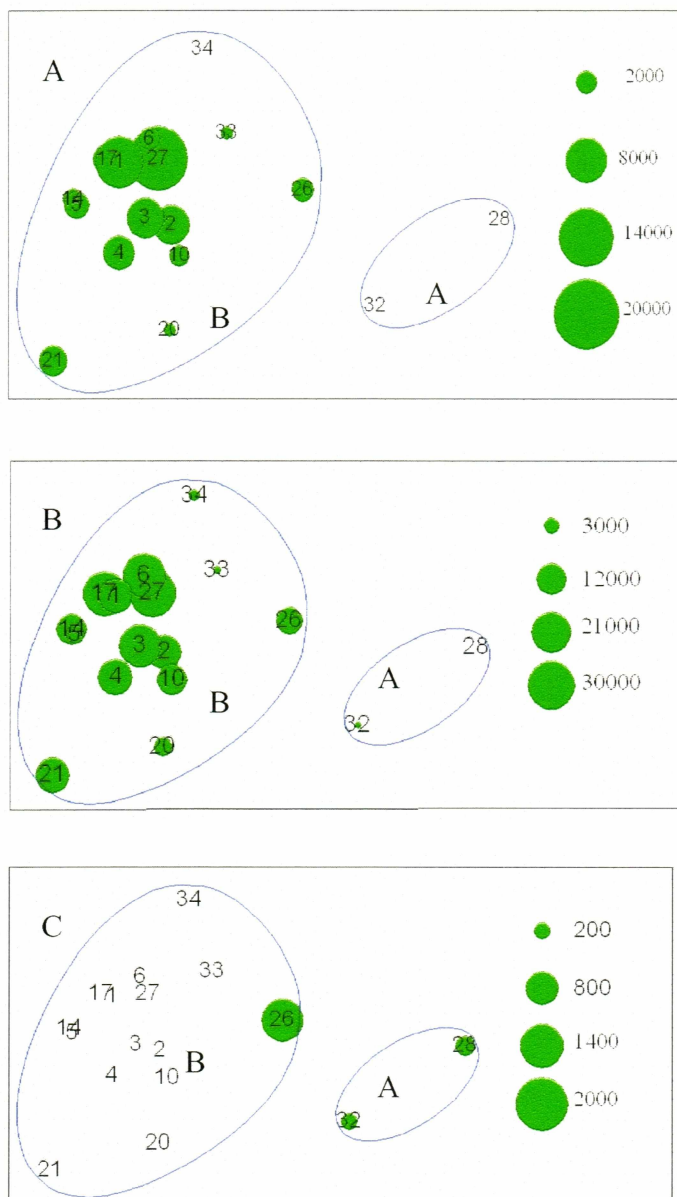


Fig. 7. May 2003 bubble plots of species abundance (individual m^{-3}) (A= *Acartia* spp., B= copepod nauplii, C= euphausiid eggs) superimposed on MDS ordination, for Chiniak and Marbot Bay region, Kodiak Island, Alaska

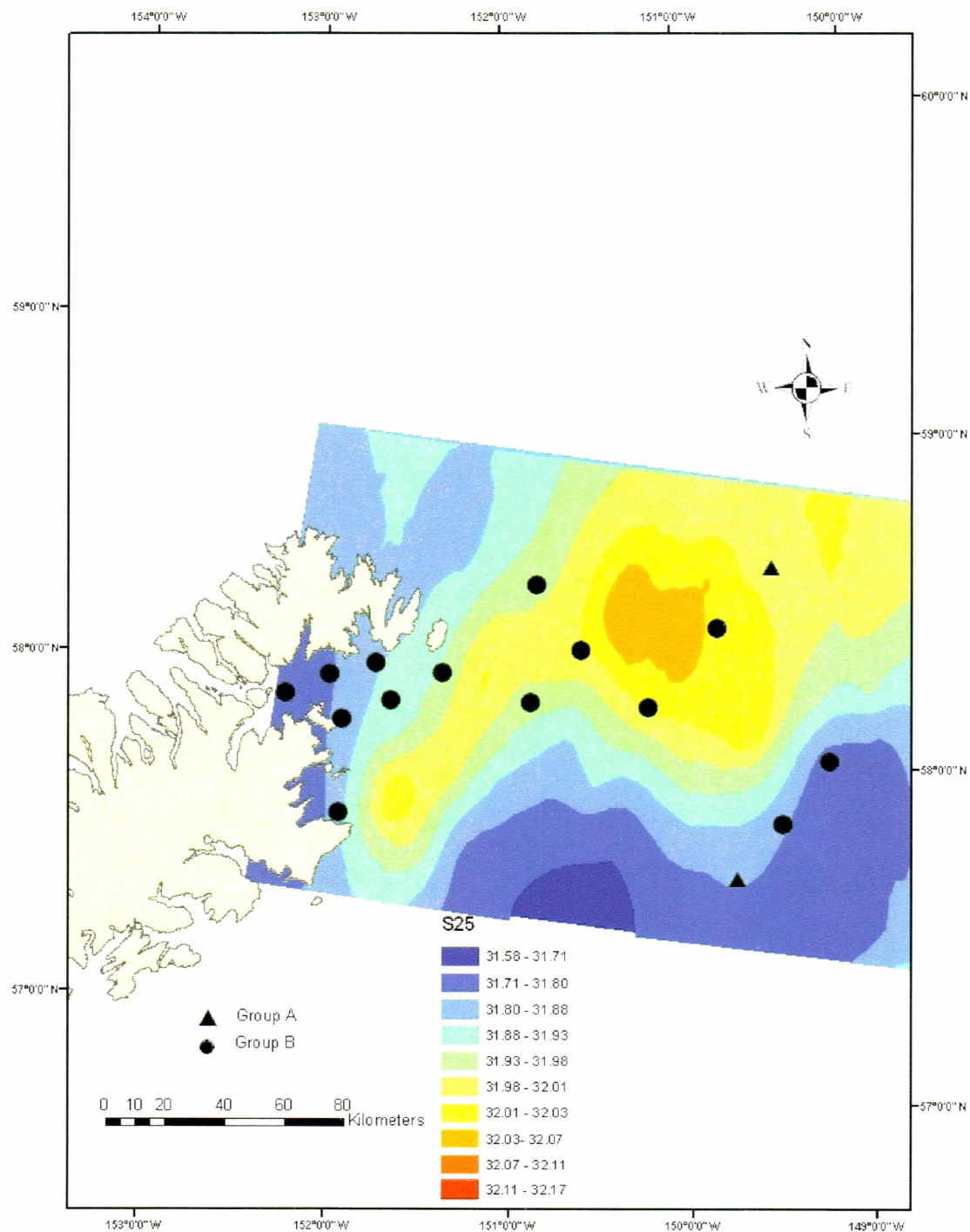


Fig. 8. May 2003 MDS ordination superimposed on S₂₅, northeast of Kodiak Island

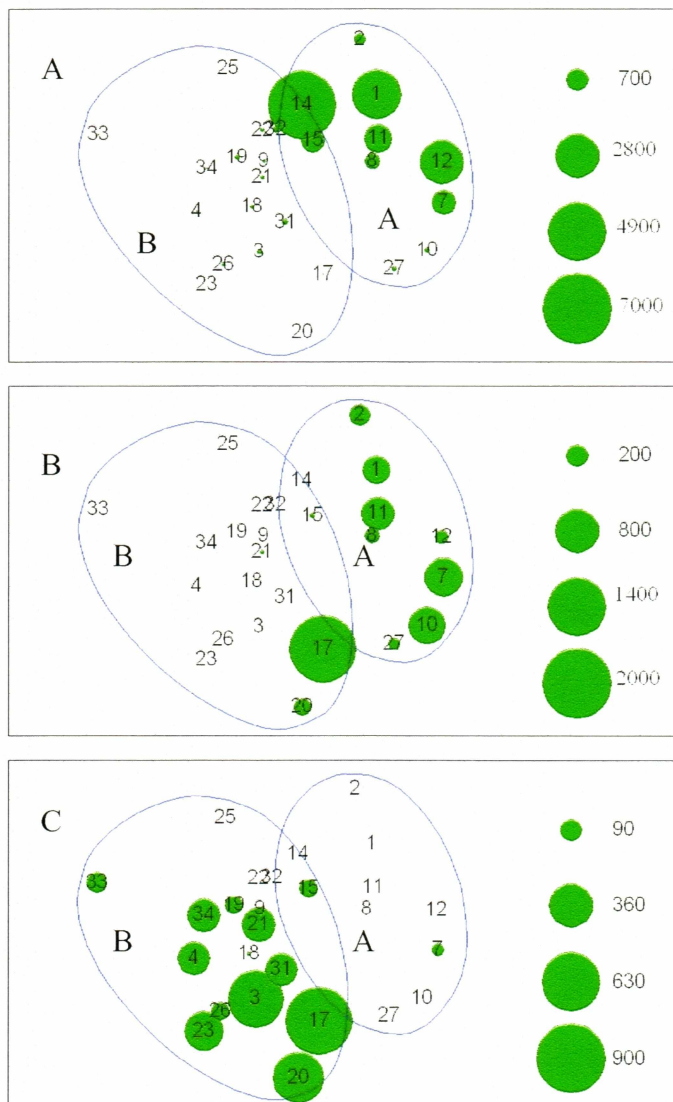


Fig. 9. May 2004 bubble plots of species abundance (individual m⁻³) (A= euphausiid furcilia, B= barnacle larvae, C= *Neocalanus* spp.) superimposed on MDS ordination, for Chiniak and Marbot Bay and Portlock Bank region, Kodiak Island, Alaska

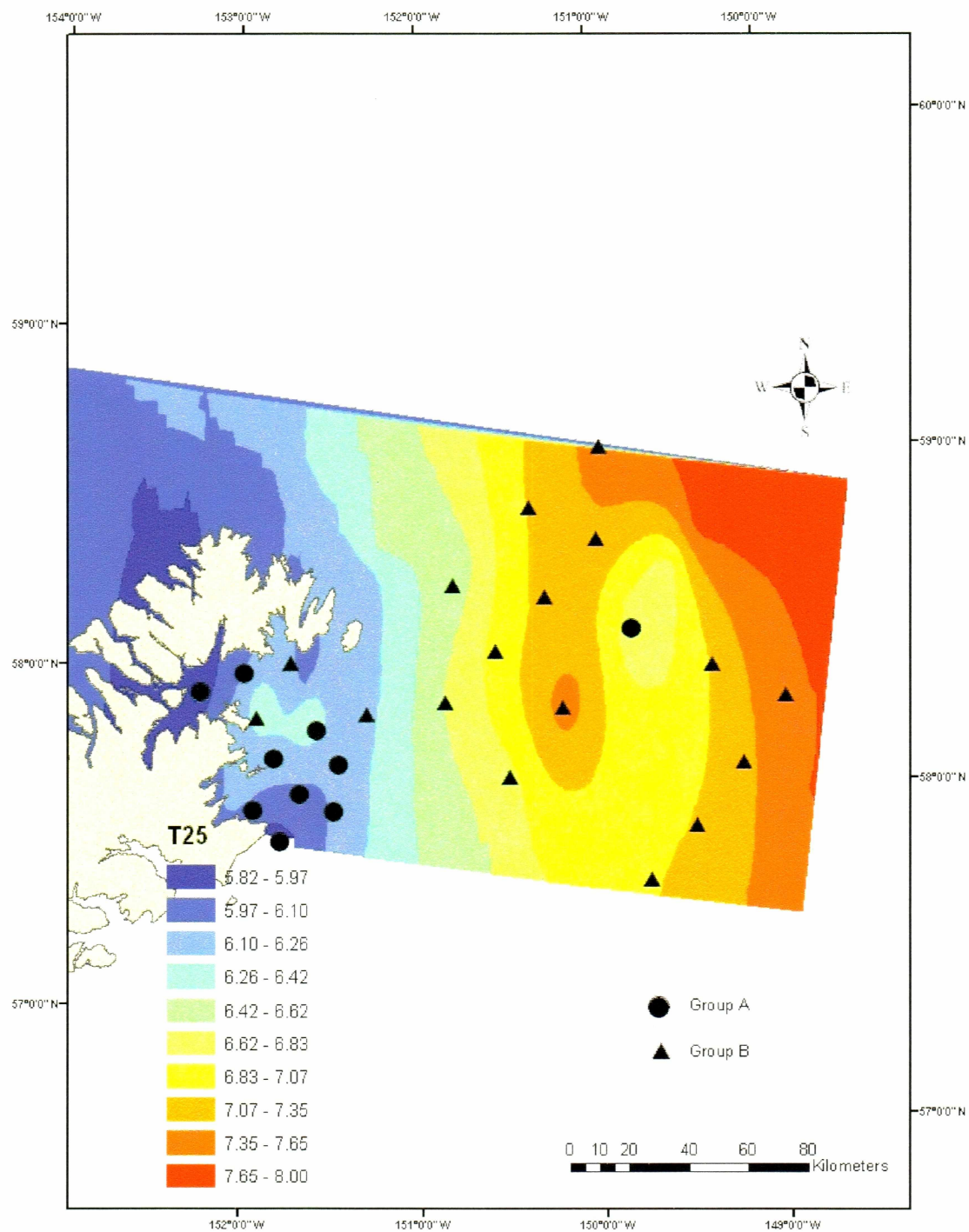


Fig. 10. May 2004 MDS ordination superimposed on T_{25} , northeast of Kodiak Island

Table 1. Sampling periods and locations from March 2002 to August 2004, northeast Kodiak Island, Alaska. M = Marmot Bay stations (nearshore), C = Chiniak Bay stations (nearshore) and P = Portlock Bank stations (offshore).

Cruises	Dates	Locations
2002 March	1-5 April	M & C
2002 May	16-28 May	M & C
2002 Aug	18-30 July	M & C
2002 Nov	11-23 November	M & C
2003 March	5-9 March	M & C
2003 May	22 May-4 June	M & C
2003 Aug	1-17 August	M & C
2004 May	17-29 May	M & C & P
2004 Aug	28 July- 9August	M & C & P

Table 2. Number of CTD casts and zooplankton samples conducted in this study northeast of Kodiak Island, Alaska.

	2002		2003		2004			
	nearshore		nearshore		nearshore		offshore	
	CTD	Zoop	CTD	Zoop	CTD	Zoop	CTD	Zoop
March	11	4	24	12	N/A	N/A	N/A	N/A
May	48	37	42	19	34	17	40	18
August	49	31	N/A	16	42	21	38	19
November	29	12	N/A	N/A	N/A	N/A	N/A	N/A

Table 3. Average (SD) temperature above 25 m (T_{25}), salinity above 25 m (S_{25}) and chlorophyll fluorescence above 25 m (F_{25}), average (SD) stratification parameter (Φ) and pycnocline depth, for Chiniak and Marbot Bay region, Kodiak Island, Alaska.

	March		May		August		November
year	2003	2002	2003	2004	2002	2004	2002
	5.63	6.21	7.11	6.14	8.95	9.79	6.95
T_{25} (°C)	(0.33)	(0.64)	(0.15)	(0.20)	(0.43)	(0.71)	(0.48)
	31.90	32.09	31.92	31.99	31.97	31.72	31.81
S_{25}	(0.11)	(0.14)	(0.16)	(0.12)	(0.20)	(0.13)	(0.36)
	1.73	14.32	9.08	12.21		9.72	4.91
F_{25} (mg m ⁻³)	(1.88)	(1.63)	(1.88)	(1.86)	n/a	(1.58)	(2.60)
	7.5	24.1	29.4	80.4	105.1	72.7	43.6
Φ (J m ⁻³)	(5.1)	(19.0)	(19.6)	(79.0)	(82.4)	(54.4)	(39.6)
Pycnocline	35.2	18.6	11.3	18.5	22.9	17.4	58.6
depth (m)	(51.8)	(28.3)	(8.2)	(27.5)	(16.6)	(17.6)	(45.8)

Table 4. Environmental factors having significant correlations ($p < 0.05$) with zooplankton community abundance on the northeast side of Kodiak Island (r value of non significant correlation were not listed).

Cruise	Variables (average)	r value
May 2002	Salinity (S_{25})	-0.47
August 2002	Temperature (T_{25})	0.52
	Stratification (Φ)	0.53
November 2002	Fluorometry (F_{25})	0.64
March 2003	n/a	n/a
May 2003	n/a	n/a
May 2004	Stratification (Φ)	-0.57
August of 2004	n/a	n/a

Table 5. Relative contributions of each zooplankton species to the MDS separation of stations, May 2002, northeast of Kodiak Island, Alaska.

	Group A&C	Group A&B	Group B&C
Species	%	%	%
Euphausiid eggs	16.18	5.48	12.62
Euphausiid nauplii	12.41	18.76	9.31
Copepod nauplii	11.48	12.73	4.13
<i>Fritillaria</i> spp.	8.07	17.31	11.96
Barnacle larvae	7.98	6.82	6.49
Euphausiid furcilia	7.37	6.04	7.77
<i>Centropages</i> sp.	6.44	3.61	9.14
Euphausiid calytopis	5.95	3.84	9.3
<i>Acartia</i> spp.	5.64	6.47	8.43
<i>Oithona</i> spp.	4.41	<1	<1
Polychaete juvenile	4.24	5.01	6.73

Table 6. Relative contributions of each zooplankton species to the separation of stations, May 2003, northeast of Kodiak Island, Alaska.

Species	%
<i>Acartia</i> spp.	17.28
Copepod nauplii	13.56
Euphausiid eggs	12.07
Euphausiid furcilia	7.58
Euphausiid calytopis	6.78
Barnacle larvae	6.75
<i>Oikopleura</i> spp.	6.63
<i>Eucalanus</i> sp.	6.48
Euphausiid nauplii	5.72
<i>Calanus</i> sp.	5.5
<i>Pseudocalanus</i> spp.	5.1

Table 7. Relative contributions of each zooplankton species to separation of stations, May 2004, northeast of Kodiak Island, Alaska.

Species	%
Euphausiid furcilia	15.75
Barnacle larvae	15.48
<i>Neocalanus</i> spp.	12.95
<i>Calanus</i> spp.	10.25
<i>Oikopleura</i> spp.	8.47
Copepod nauplii	7.58
<i>Acartia</i> spp.	7.43
<i>Eucalanus</i> sp.	7.35
<i>Fritillaria</i> spp.	5.87

Table 8. Zooplankton biomass (WW g m⁻²) of Kodiak region and on Seward line, May and August in 2002 - 2004.

	May 2002		August 2002	
	Kodiak	Seward	Kodiak	Seward
<i>Acartia</i> spp.	0.10	0.17	0.52	0.15
<i>Oithona</i> spp.	0.20	0.77	1.13	0.62
<i>Pseudocalanus</i> spp.	1.13	4.84	7.14	2.36
<i>Neocalanus cristatus</i>	0.84	8.63	0.50	2.05
<i>Neocalanus</i> spp.	6.36	26.57	0.11	1.14
<i>Eucalanus bungii</i>	0.09	8.48	0.47	1.28
<i>Metridia pacifica</i>	0.37	2.55	0.09	0.77
<i>Clione limacina</i>	3.84	0.16	2.76	0.18
<i>Limacina helicina</i> juvenile	0.04	0.09	0.55	0.02
<i>Fritillaria</i> spp.	0.04	0.09	0.13	0.02
<i>Oikopleura</i> spp.	0.58	1.07	3.16	0.07
Euphausiid larvae	4.93	14.38	1.52	0.07
<i>Calanus marshallae</i>	0.98	2.19	0.74	2.63

Table 8. Continued.

	May 2003		August 2003	
	Kodiak	Seward	Kodiak	Seward
<i>Acartia</i> spp.	1.08	0.86	1.38	0.22
<i>Oithona</i> spp.	1.47	1.54	1.51	0.81
<i>Pseudocalanus</i> spp.	10.64	4.24	6.35	3.41
<i>Neocalanus cristatus</i>	2.23	15.57	0.01	0.41
<i>Neocalanus</i> spp.	0.73	12.05	0.14	0.26
<i>Eucalanus bungii</i>	3.88	2.72	0.02	0.90
<i>Metridia pacifica</i>	0.07	5.64	0.00	0.77
<i>Clione limacina</i>	1.56	0.36	0.79	0.42
<i>Limacina helicina</i> juvenile	1.70	0.98	0.34	0.02
<i>Fritillaria</i> spp.	0.15	0.28	0.50	0.10
<i>Oikopleura</i> spp.	6.66	1.54	61.4	0.64
Euphausiid larvae	1.81	3.78	0.44	0.71
<i>Calanus marshallae</i>	1.90	2.73	0.20	2.00

Table 8. Continued.

	May 2004	
	Kodiak	Seward
<i>Acartia</i> spp.	0.32	0.71
<i>Oithona</i> spp.	0.77	1.17
<i>Pseudocalanus</i> spp.	5.19	4.06
<i>Neocalanus cristatus</i>	2.36	10.68
<i>Neocalanus</i> spp.	9.92	21.14
<i>Eucalanus bungii</i>	1.93	6.14
<i>Metridia pacifica</i>	0.54	5.24
<i>Clione limacina</i>	36.6	0.46
<i>Limacina helicina</i> juvenile	8.25	0.49
<i>Fritillaria</i> spp.	0.13	0.03
<i>Oikopleura</i> spp.	2.41	1.01
Euphausiid larvae	10.52	3.17
<i>Calanus marshallae</i>	3.73	3.10

Table 9. Zooplankton biomass (WW g m^{-2}) of Kodiak region and other similar studies in the literature. Where necessary biomass was converted into WW g m^{-3} using the regression functions provided in Wiebe (1988).

Location	Month	Year	Biomass	Depth (m)	Citations
Kodiak	March	2002-2004	3.3	25	this study
Shelikof	April	1985-1989	58.2	250	Incze et al. 1997
PWS	April	1976	56.2	700	Damkaer 1977
Kodiak	May	2002-2004	48.7	25	this study
Shelikof	May	1985-1989	178.2	250	Incze et al. 1997
northern					Coyle and
GOA	May	1997-1999	18.5	100	Pinchuk 2003
Station P	May	1956-1980	7.5	150	Fulton 1983
Kodiak	August	2002-2004	51.97	25	this study

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General Conclusions

It is important to study temporal and spatial zooplankton species composition, abundance, and biomass, in order to better understand interactions among trophic levels in the marine ecosystem (Vogel and McMurray, 1986; Mackas et al., 1998; Anderson and Piatt, 1999). This study provides evidence that the zooplankton community structure and oceanographic factors are highly variable on the shelf northeast of Kodiak Island, implying that the availability of prey for upper trophic levels such as commercially important fish, seabirds, and mammals may fluctuate on similar temporal and spatial scales.

Correlations between oceanographic factors and the zooplankton community structure were weak in this study, likely due to complex interactions between physical processes and biological production on the western GOA shelf. Additional factors more complex than temperature and salinity such as bathymetry, dynamic currents, and variable climate forcing may be more influential in affecting zooplankton community structure. Zooplankton advections from other regions may also influence local zooplankton community structure and confound relationships with local environmental conditions. It is therefore not surprising that local physical features would not necessarily correlate strongly with zooplankton density in a small study area like this Kodiak study site where localized conditions may be different from those of the broader geographic region.

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Appendices

Appendix A. 1. Zooplankton taxa sampled on northeast side of Kodiak Island, Alaska,
March 2002 to August 2004 by taxonomic category.

Annelida

Polychaeta

Cnidaria

Hydrozoa

Hydromedusae

Leptomedusae

Mollusca

Bivalvia

Gastropoda

Clione limacina

Limacina helicina

Echinodermata

Echinodermata larvae

Arthropoda

Crustacean

Amphipoda

Parathemisto pacifica

Cladocera

Podon sp.

Evadne sp.

Copepoda

Acartia longiremis

Acartia tumida

Calanus marshallae

Calanus pacificus

Centropages abdominalis

Eucalanus bungii

Euchaeta elongate

Metridia pacifica

Neocalanus cristatus

Neocalanus plumchrus/flemingeri

Oithona similis

Oithona spirostris

Oncaea spp.

Pseudocalanus spp.

Decapoda

Hippolytidae zoea

Brachyrrhyncha zoea

Oregoninae zoea

Paguridae zoea

Pinnotheridae zoea

Euphausiacea

Euphausia pacifica

Euphausiid calytopis larvae

Euphausiid furcilia larvae

Thysanoessa raschii

Chaetognatha

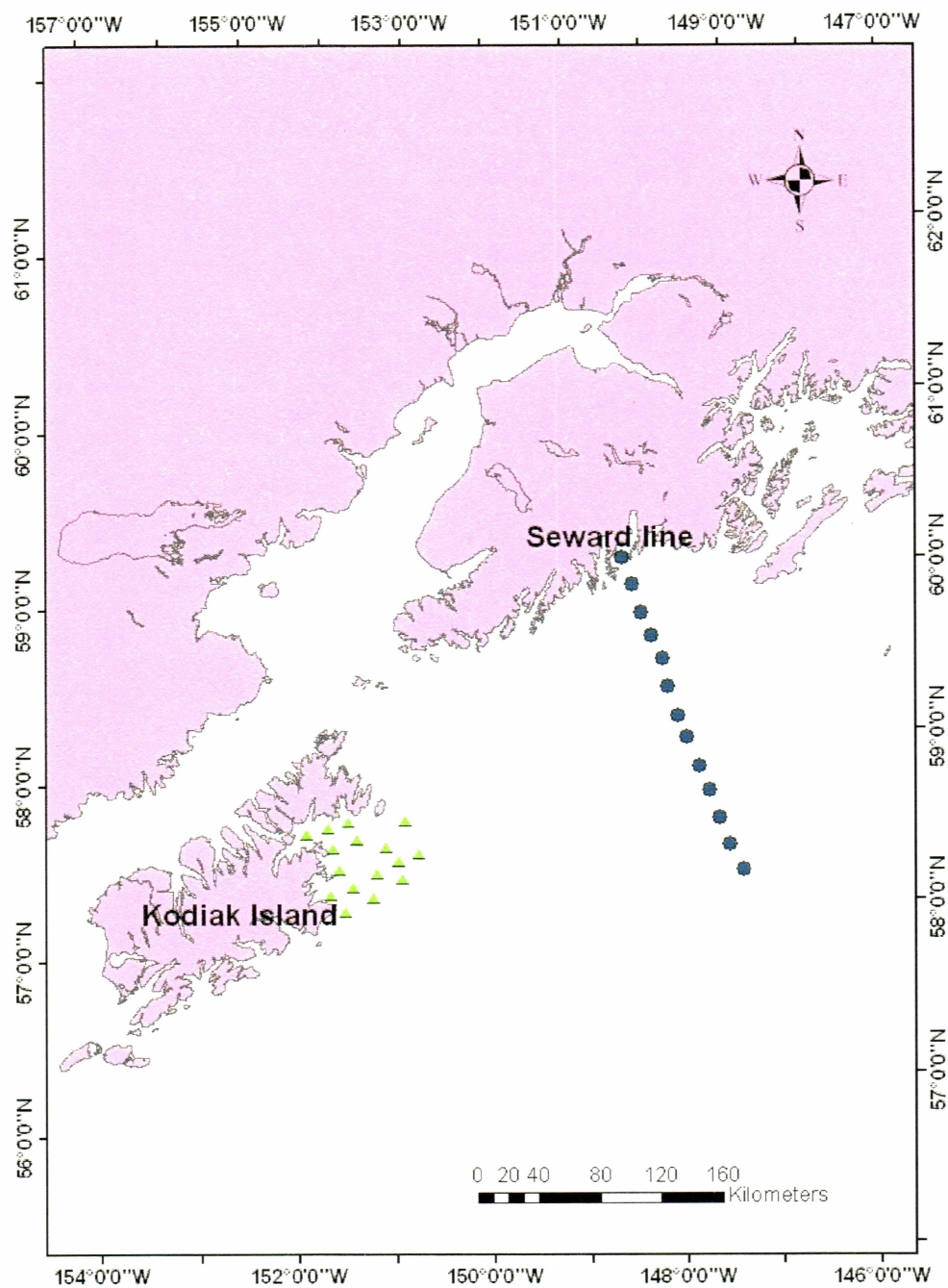
*Eukrohnia hamata**Sagitta* spp.

Chordate

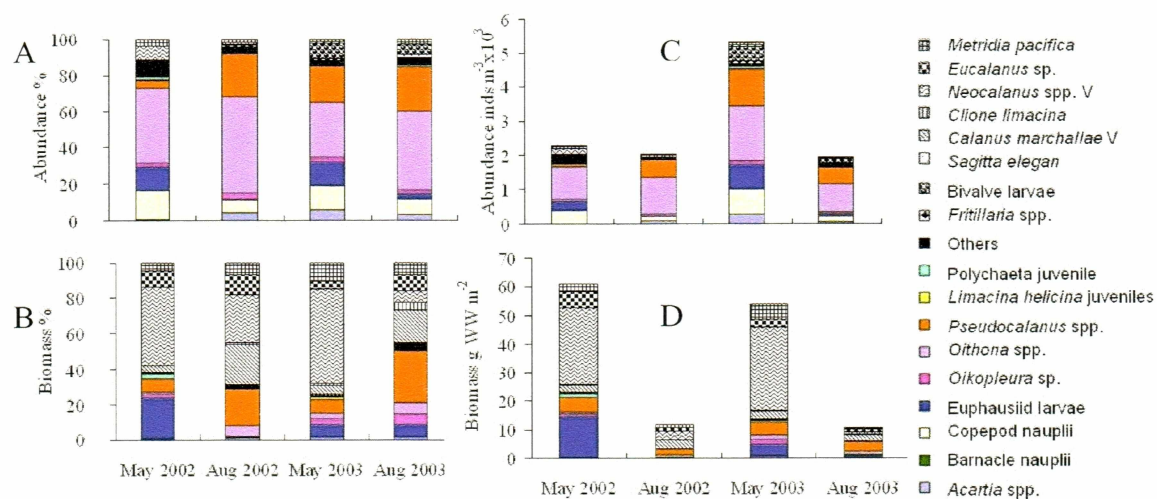
Larvacea

Oikopleura spp.*Fritillaria* spp.

Appendix A. 2. Map showing Kodiak stations (triangles) and Seward line (circles)
stations, Alaska

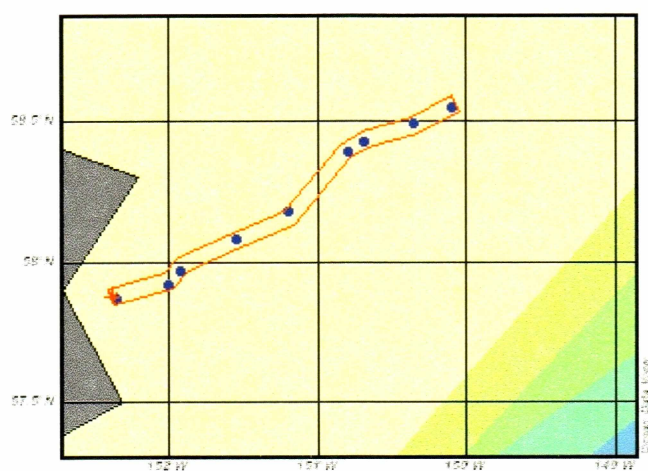
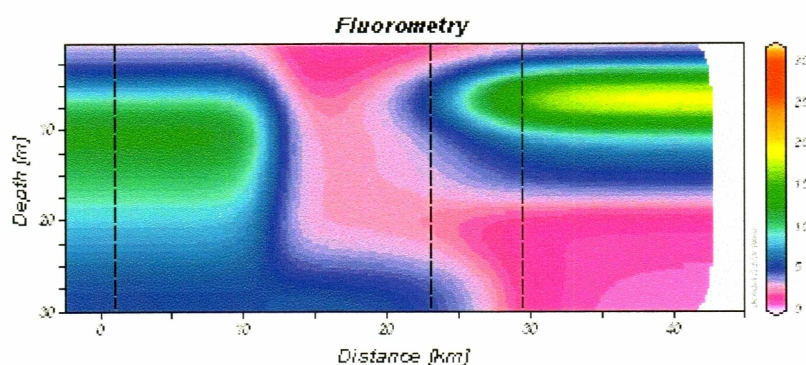


Appendix A. 3. Percent abundance (A) and percent biomass (B) of zooplankton, abundance (C) and biomass (D) of zooplankton in May and August 2002 and 2003, on Seward line, Alaska.



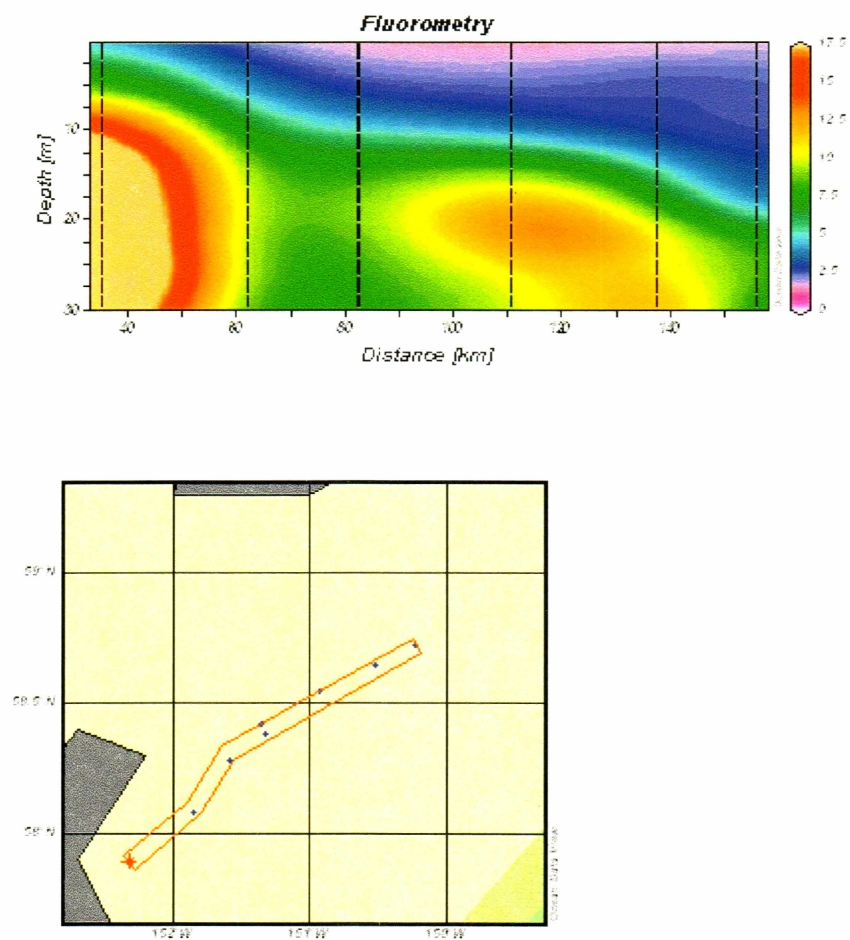
Appendix A. 4. Fluorometry profiles over sampling areas above 25 m depth of the water column, northeast of Kodiak Island, May and August in 2003 and 2004 (gridding algorithm: VG Gridding of the ODV software).

Fluorometry profiles over a transect line within the sampling areas above 25 m depth of the water column, northeast of Kodiak Island, May 2003.



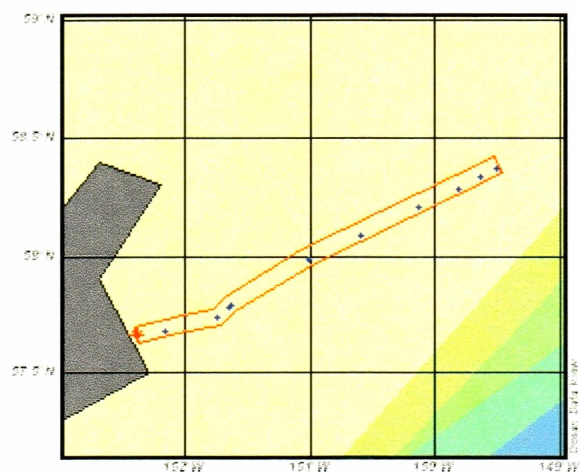
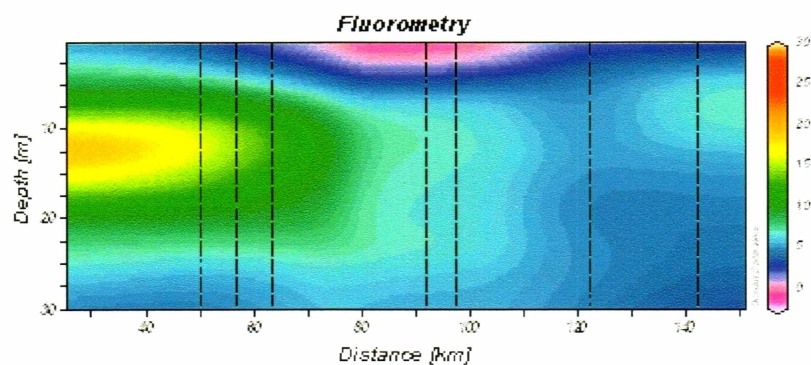
Appendix A. 4. Continued.

Fluorometry profiles over a transect line within the sampling areas above 25 m depth of the water column, northeast of Kodiak Island, August 2003.



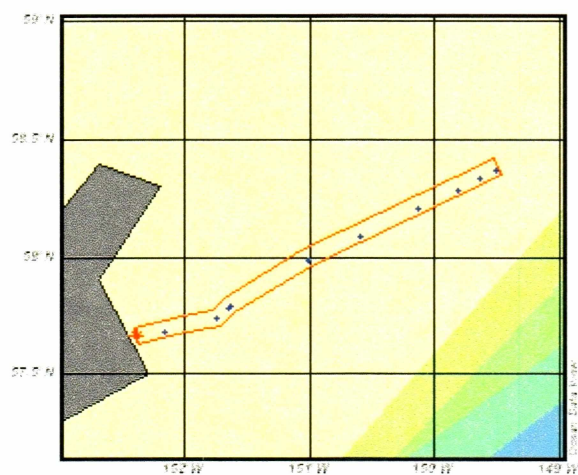
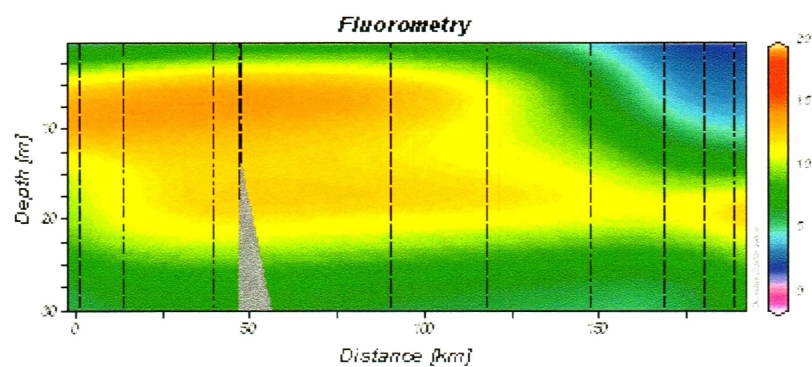
Appendix A. 4. Continued.

Fluorometry profiles over a transect line within the sampling areas above 25 m depth of the water column, northeast of Kodiak Island, May 2004.



Appendix A. 4. Continued.

Fluorometry profiles over a transect line within the sampling areas above 25 m depth of the water column, northeast of Kodiak Island, August 2004.



Appendix A. 5. Estimate average wet weight per individual (mg WW) for major zooplankton taxa encountered between 2002 to 2004, northeast of Kodiak Island, Alaska (estimated by Coyle data collected from the North Pacific between 1997 and 2003) (AF: adult female, AM: adult male, I: copepodites stage I, II: copepodites stage II, III: copepodites stage III, IV: copepodites stage IV, V: copepodites stage V).

Zooplankton taxa	Average biomass (mg WW)
<i>Acartia clausi</i> AF	0.075
<i>Acartia clausi</i> AM	0.061
<i>Acartia longiremis</i> AF	0.071
<i>Acartia longiremis</i> AM	0.044
<i>Acartia</i> spp. I	0.002
<i>Acartia</i> spp. II	0.003
<i>Acartia</i> spp. III	0.003
<i>Acartia</i> spp. IV	0.022
<i>Acartia</i> spp. V	0.035
<i>Acartia tumida</i> AF	0.287
<i>Acartia tumida</i> AM	0.152
<i>Acartia tumida</i> IV	0.100
<i>Acartia tumida</i> V	0.145
Barnacle cyprid	0.209
Barnacle nauplii	0.177
Bivalve larvae	0.034
Brachyrrhyncha zoea	0.906
Calanoida nauplii	0.002
<i>Calanus marshallae</i> AF	1.846
<i>Calanus marshallae</i> AM	1.486
<i>Calanus marshallae</i> I	0.053
<i>Calanus marshallae</i> II	0.122
<i>Centropages abdominalis</i> III	0.013
<i>Centropages abdominalis</i> IV	0.030
<i>Centropages abdominalis</i> V	0.097
<i>Clione limacina</i> (medium)	17.731
<i>Clione limacina</i> (small)	1.637
Echinodermata larvae	0.045

Appendix A.5. Continued

<i>Eucalanus bungii</i> AF	5.372
<i>Eucalanus bungii</i> AM	2.624
<i>Eucalanus bungii</i> I	0.048
<i>Eucalanus bungii</i> II	0.160
<i>Eucalanus bungii</i> III	0.376
<i>Eucalanus bungii</i> IV	0.972
<i>Eucalanus bungii</i> V	2.211
<i>Euchaeta elongata</i> AF	8.654
<i>Euchaeta elongata</i> AM	5.775
<i>Euchaeta elongata</i> I	0.120
<i>Euchaeta elongata</i> II	0.161
<i>Euchaeta elongata</i> III	0.433
<i>Euchaeta elongata</i> IV	1.419
<i>Euchaeta elongata</i> V	4.364
Euphausiid calyptopis	0.141
Euphausiid eggs	0.095
Euphausiid furcilia	0.553
Euphausiid nauplii	0.028
<i>Evadne</i> spp.	0.056
<i>Fritillaria</i> sp.	0.017
Hippolytidae zoea	1.825
<i>Limacina helicina</i> (medium)	1.787
<i>Limacina helicina</i> (small)	0.221
<i>Metridia ochotensis</i> AF	1.873
<i>Metridia ochotensis</i> AM	0.569
<i>Metridia ochotensis</i> III	0.095
<i>Metridia ochotensis</i> IV	0.279
<i>Metridia ochotensis</i> V	0.742
<i>Metridia pacifica</i> AF	0.746
<i>Metridia pacifica</i> AM	0.198
<i>Metridia pacifica</i> III	0.051
<i>Metridia pacifica</i> IV	0.117
<i>Metridia pacifica</i> V	0.232
<i>Metridia</i> spp. I	0.014
<i>Metridia</i> spp. II	0.050
<i>Metridia</i> spp. III	0.083
<i>Metridia</i> spp. IV	0.205

Appendix A.5. Continued

<i>Metridia</i> spp. V	0.253
<i>Neocalanus</i> spp. AF	3.212
<i>Neocalanus cristatus</i> AF	10.899
<i>Neocalanus cristatus</i> I	0.135
<i>Neocalanus cristatus</i> II	0.253
<i>Neocalanus cristatus</i> III	1.006
<i>Neocalanus cristatus</i> IV	3.803
<i>Neocalanus cristatus</i> AM	9.544
<i>Neocalanus cristatus</i> V	13.905
<i>Neocalanus</i> spp. III	0.298
<i>Neocalanus</i> spp. IV	0.967
<i>Neocalanus</i> spp. V	2.202
<i>Oikopleura</i> spp.	0.815
<i>Oithona similis</i> AF	0.009
<i>Oithona similis</i> AM	0.006
<i>Oithona similis</i> V	0.009
<i>Oithona spirostris</i> AF	0.018
<i>Oithona spirostris</i> AM	0.008
<i>Oithona</i> spp. copepodites	0.006
<i>Oncaea</i> sp.	0.014
Oregoninae zoea	1.025
Paguridae zoea	1.378
Pandalidae zoea	0.648
<i>Podon</i> spp.	0.124
Polychaete juvenile	0.855
Polychaete larvae	0.150
<i>Pseudocalanus</i> spp. AF	0.152
<i>Pseudocalanus</i> spp. AM	0.086
<i>Pseudocalanus</i> spp. I	0.006
<i>Pseudocalanus</i> spp. II	0.010
<i>Pseudocalanus</i> spp. III	0.012
<i>Pseudocalanus</i> spp. IV	0.031
<i>Pseudocalanus</i> spp. V	0.125

Appendix A.5. Continued

<i>Sagitta elegans</i> (extra small)	0.067
<i>Sagitta elegans</i> (large)	31.735
<i>Sagitta elegans</i> (medium)	12.764
<i>Sagitta elegans</i> (small)	2.192
<i>Sagitta scrippsae</i> (large)	215.806
<i>Sagitta scrippsae</i> (medium)	43.402
<i>Sagitta scrippsae</i> (small)	4.818
