

# Seasonal differences in the distribution, density and scale of zooplankton patches in the upper mixed layer near the western Aleutian Islands

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**Abstract:** Spatial statistics based on 420 kHz acoustic measurements and net samples were used to look for significant local interannual and seasonal differences in the distribution of zooplankton biomass relative to water mass distribution, pycnocline depth and intensity, and species composition in the western Aleutian Islands near Buldir, Kiska and Gareloi Island in June 1992 and July 1993. Zooplankton species composition and water mass type indicated the presence of Alaska Stream water north of the Aleutians near Gareloi Island and Bering Sea water north of Kiska Island in July 1993. Spatial analysis revealed significant interannual and seasonal differences in the distribution of ADB (acoustically determined zooplankton biomass) in the upper mixed layer north of Kiska Island. Dense layers of *Neocalanus* occurred in Bering Sea water north of Kiska in June 1992. Weak zooplankton scattering layers having a patchy distribution occurred in July 1993. Highest overall ADB north of the Aleutians in July 1993 occurred north of Gareloi Island, where Alaska Stream water was moving northward through Amchitka Pass. Elevated zooplankton densities north of the Aleutians in June 1992 were apparently promoted by a large-scale spring-bloom condition in the Bering Sea water mass. Small patches of elevated zooplankton biomass in July 1993 occurred near the north slope of the Aleutian ridge, where fronts and turbulent flow through the passes apparently generated localized areas of elevated production or convergence. Although discrete patches of high biomass were observed, mean ADB for the sampling grids was within the range observed by previous studies for the Gulf of Alaska and western Aleutians.

**Key words:** zooplankton, acoustics, Aleutians

## Introduction

Zooplankton distribution and abundance in the western Aleutian Islands is influenced by a variety of physical and biological processes. The physical environment includes the Alaska Stream south of the islands, turbulent flow through the passes and Bering Sea water to the north of the islands (Reed & Stabeno 1994; Pavlov & Pavlov 1996). In addition, the seasonal zooplankton succession is delayed in Bering Sea water relative to Pacific water (Coyle et al. 1998). Thus, spring bloom conditions may result in large-scale zooplankton patches to the north of the islands in June, but much lower zooplankton densities in Pacific water to the south (Coyle et al. 1998). Summer conditions, however, are prob-

ably very different. Many of the interzonal copepods, which dominate the biomass in spring, migrate below the pycnocline to overwintering depth following the spring bloom (Coyle et al. 1996). Therefore, the large-scale patches observed in June are likely to absent later in the summer.

In spring 1992 and summer 1993 we examined the spatial distribution of water masses and fronts relative to the distribution of zooplankton forage for the least auklet (*Aethia pusilla*). During June 1992, least auklets in the western Aleutians were feeding primarily north of the islands in resident Bering Sea water, however, in July 1993, they had shifted their foraging to the passes and regions south of the islands (Hunt et al. 1998; Hunt & Coyle, unpublished manuscript). The above shift seemed to be related to changes in oceanographic conditions affecting the distribution and abundance of the zooplankton prey. In this

paper, we document those changes in zooplankton abundance and biomass using acoustics, net tows and spatial statistics, and we examine the physical and biological processes producing those differences.

### Materials and Methods

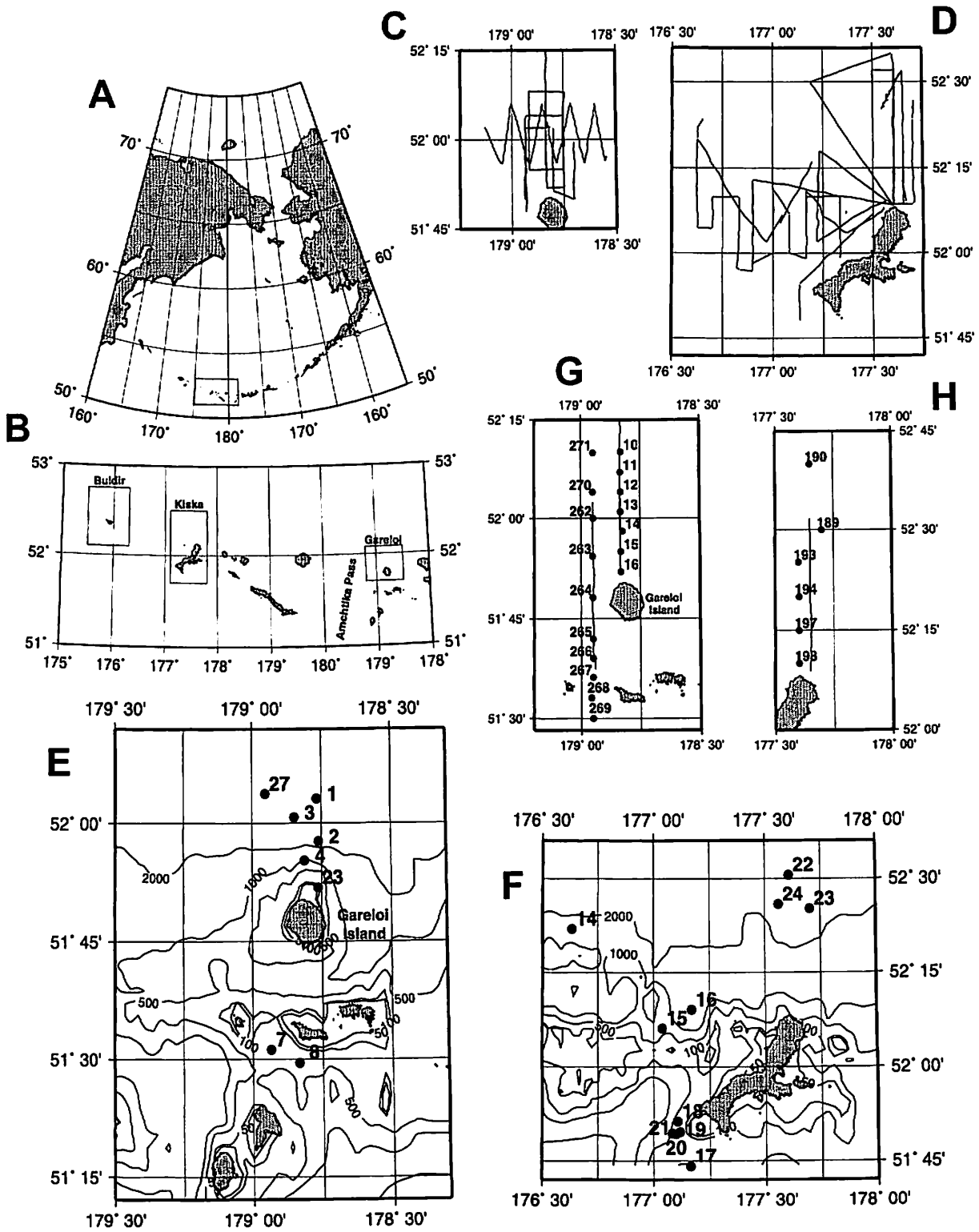
Data collection methods in both 1992 and 1993 were identical (Coyle 1998; Coyle et al. 1998), thus facilitating direct comparison of the 1992 and 1993 data sets. The study area included regions around Kiska and Gareloi Islands (Fig. 1A, B). The distribution and density of transect lines were dictated by the requirements of the bird surveys. All acoustic and net data were collected in the upper 160 m during the daylight. Deep nocturnal vertical migrators were therefore not sampled in this survey. Zooplankton were collected with a 1-m MOCNESS system with 0.5 mm mesh nets. Volume scattering intensity was measured along transects at frequencies of 200 and 420 kHz at integration interval of 30 s (horizontal distance of 120 m) using a Biosonics model 120 echosounding system and integration board (Coyle 1998; Coyle et al. 1998). The effective range of the 200 and 420 kHz systems was 160 and 45 m respectively. In addition, acoustic data were also collected concurrently with net tows to permit direct comparison of net-caught biomass and volume scattering. The net tow data were pooled and regressions of net caught biomass against volume scattering were used to generate a scaling factor to convert volume scattering to ADB (acoustically determined biomass) (Coyle 1998). The scaling factors are therefore averages for the entire sampling area. Due to the limited range of the 420 kHz system, only those nets which fished between 45-m and 5-m depth were used in scaling the 420 kHz acoustic data. The scaling factors for the 1993 data were  $-71$  and  $-72$  dB/g for 420 and 200 kHz data respectively. Volume scattering in excess of  $-68$  dB in the upper mixed layer could not be accounted for by net samples and was therefore deleted from the data. The above precaution minimized the possibility of including fish and other large nekton in the acoustic estimates of zooplankton biomass. The net sample is therefore the ultimate standard for scaling the acoustic data and the resulting ADB are conservative measure of zooplankton biomass.

The acoustic grids north of Gareloi and Kiska Islands are shown in Fig. 1C and D. Acoustic grids north of Kiska in 1992 are shown in Coyle et al. (1998) (see also Fig. 6B, C). The tow locations are shown in Fig. 1E and F. The zooplankton samples were preserved in formalin for later processing. All taxa were identified to the lowest taxonomic level possible, enumerated and the wet weight was measured on the individual taxa. *Neocalanus* in the plots refers primarily to *N. plumchrus*, which dominated *Neocalanus* populations in July 1993. CTD (Conductivity-temperature-depth) measurements were taken with a Neil Brown CTD (Coyle et al. 1998). In situ fluorescence was measured with a model Q fluorometer mounted on the CTD. The fluo-

rometric data were converted to chlorophyll concentrations as outlined in Parsons et al. (1984). In addition, sea surface temperature and salinity along the cruise track was measured using a continuous-flow seawater system. Measurements were taken every 1–2 min using Seabird sensors and written to disk. Time and position data from the ships GPS system were written to all data files to facilitate comparison of data sets.

The 420 kHz acoustic data were analyzed for statistically-significant differences in ADB in the upper 45 m between years. Due to the close proximity of adjacent measurements in the acoustic transects, the data were auto-correlated. Therefore, treatment of each acoustic measurement as independent would be a form of pseudoreplication (Hurlbert 1984). Since discrete data points were not statistically independent, spatial covariance models were fit to the data and geostatistical techniques (Isaaks & Srivastava 1989) were used to predict the mean and 95% confidence intervals at specific locations on a grid encompassing the transects. Because the magnitude of the confidence intervals at each grid point is a function of the variability of the surrounding measurements (the nugget effect) and the density of measurements, the confidence interval at any given grid point widens as the density of measurements around the grid point declines. The power of the statistical technique to discriminate differences at any given point is therefore a function of both the sample variability and the sample density. In mapping the distribution of ADB, we used the lower 95% confidence interval. The above convention may underestimate biomass in regions of low sample density, but has minimal effect on the distributional maps at regions of high sample density. The biomass maps are therefore conservative estimates of ADB. Geostatistical analyses were done on 420 kHz measures of ADB only.

Tests for statistically significant differences in the distribution of zooplankton biomass between June 1992 and July 1993 were done as follows. The ADB between 7- and 45-m depth was integrated to produce biomass estimates in  $\text{g m}^{-2}$ . The data were log transformed and the position coordinates were converted to distance (km) from the southeast corner of the grid in the  $x$  (east-west) and  $y$  (north-south) directions. The distances between all grid data points were computed, bin averaged into 1-m bins and the variance with respect to distance was modeled using standard spherical or exponential geostatistical models (Isaaks & Srivastava 1989), depending on which best fit the data. A two dimensional kriging algorithm was used to generate 40 by 40 point grids of the upper and lower 95% confidence intervals for regions where the study grids in 1992 and 1993 overlapped. The upper and lower confidence intervals for the corresponding grid cells for the different sampling periods were subtracted to produce regional plots showing the magnitude of the differences between sampling periods in the upper and lower confidence intervals. Kriging was also used to generate single estimates of the spatial mean and its 95% confidence intervals for the different regions to look



**Fig. 1.** The study area in the western Aleutians (A); sample regions near Buldir, Kiska and Gareloi Islands (B); acoustic transects taken north of Gareloi (C) and Kiska (D) during July 1993; location of MOCNESS tows taken during July 1992 (tows 23 and 27) and July 1993 (tows 1-4, 7-8) in the Gareloi Island region (E) and during July 1993 near Kiska (F), depth contours in meters; CTD and acoustic transects taken north of Gareloi (G) and north of Kiska (H). Stns 262-271 and accompanying transect (G) taken 1 July 1992, all other stations and transects taken July, 1993.

for regional differences in ADB. Spatial statistics was done with software written in Matlab programming language with calls to C subroutines. Map plots were produced with GMT (Generic Mapping Tool) software.

MDS (Multidimensional scaling) was used to group the data based on taxonomic categories and developmental stages. A list of the nine most abundant taxa or stage in the upper 45 m in each tow was generated. The analysis treated developmental stages and taxonomic categories equally. The tows were therefore grouped both by taxonomic composition and successional stage of the community. The Bray Curtis index (Clarke & Warwick 1994) was used to compute dissimilarity between the tows and MDS was run on the dissimilarity matrix to look for taxon groups. The taxon groups were compared with water column properties to categorize the group as of Pacific or Bering Sea origin.

All transect contours were generated with 200 kHz data only, using a minimum curvature gridding algorithm. The greater effective range of the 200 kHz data permitted us to plot vertical distribution of ADB to about 160-m depth. The temperature, salinity and fluorescence data from the MOCNESS were averaged into 1-m depth increments before plotting.

## Results

CTD and acoustic transects were run north of Gareloi and Kiska Islands to contrast the distribution of water masses and ADB (Fig. 1C, D, G, H). Temperatures below the pycnocline north of Gareloi Island were above 4°C, except within a small pocket of cold water at 52.00–52.05°N (Fig. 2A). Chlorophyll concentrations along the transect north of Gareloi were under  $1 \mu\text{g l}^{-1}$ . Most of the ADB was above the pycnocline or below 120-m depth. In contrast, 1993 temperatures below the pycnocline north of Kiska Island were primarily below 4°C (Fig. 2B). Although small patches of elevated ADB occurred in the pycnocline, most of the ADB was below 100-m depth. ADB along the same transect in June 1992 was above the pycnocline (Fig. 2C). Maximum chlorophyll concentrations along the transect north of Kiska were over  $3.5 \mu\text{g l}^{-1}$  in June 1992 but under  $2 \mu\text{g l}^{-1}$  in July 1993 (Fig. 2B, C). A front separating the mixed region in the passes from the stratified region north of Kiska occurred in both 1992 and 1993. The front in both years is characterized by the upward sloping isohaline and isothermal lines near the south end of the transect (Fig. 2B, C).

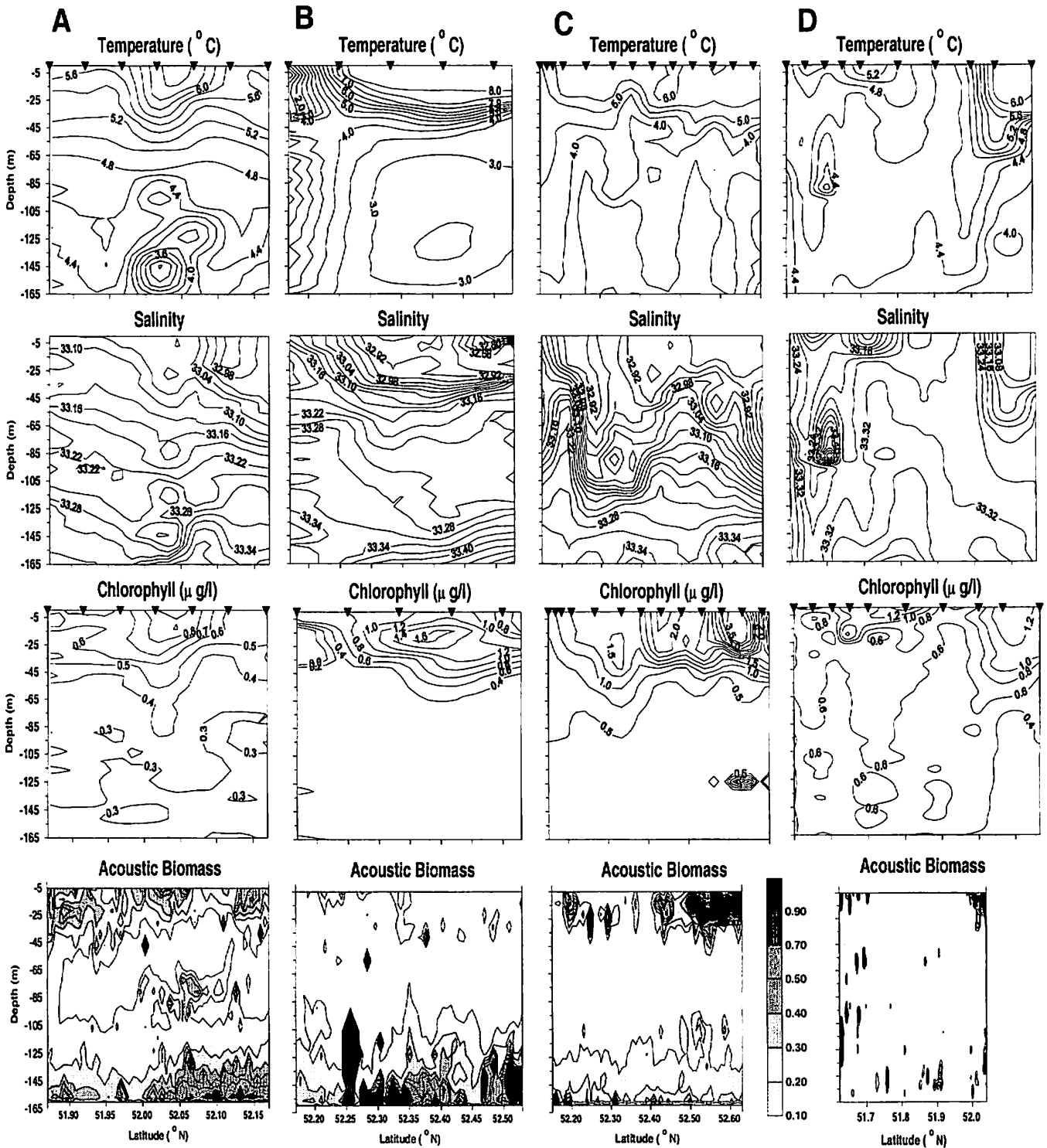
In July 1993, most of the biomass in the upper 50 m north of Gareloi Island occurred in a band extending from the surface to the top of the pycnocline (Fig. 2A) and consisted primarily of *Neocalanus plumchrus* and *Eucalanus bungii* (Fig. 3A). The scattering layer at 80 m had elevated concentrations of *Dimophyes arctica*, *Eukhronia hamata* and *E. bungii*. In contrast to July 1993, elevated biomass in July 1992 occurred in the upper 40 m in isolated patches associated with warm water pools in the surface (Fig. 2D).

The warm surface pools had elevated chlorophyll concentration relative to the surrounding colder water (Fig. 2D). Most of the biomass in the patches occurred around 15-m depth in a narrow band at a weak thermocline and was dominated by *Neocalanus cristatus* and *Neocalanus flemingeri* (Fig. 3B). We saw no evidence of substantially different salinity-temperature regimes between years (Fig. 2A, D).

Zooplankton north of Kiska Island were patchily distributed, both vertically and horizontally (Fig. 4). When present, elevated ADB and zooplankton densities were commonly observed in the pycnocline. Sound scattering above the pycnocline was often close to background levels. Zooplankton within the pycnocline scattering layer at 30–40-m depth consisted primarily of *N. plumchrus* and *E. bungii*. The scattering layer below 120 m depth contained *Thysanoessa longipes*, *E. hamata*, *N. cristatus*, *Metridia pacifica* and *Dimophyes arctica*.

Multidimensional scaling indicated some regional differences in faunal composition. The dimension 1 MDS point values for tows from the Gareloi Island region and south of Kiska Island (Pacific water mass) were negative while those for tows from north and west of Kiska (Bering Sea water mass) were positive (Fig. 5). Dimension 2 tended to separate samples in well stratified regions (positive values) from less stratified regions (negative values). The thermocline in Tow 2 was pushed up near the surface (surface temperature under 6°C); Tow 19 was taken in a surface pocket of unusually warm water (surface temperature over 8°C). Tows 14–16 were taken over the north side of the Aleutian ridge where tidal effects weakened stratification. In contrast, tows 22–24 were taken north of the ridge where a warm surface layer over the cold intermediate layer produced an intense thermocline. Tows 1, 3 and 4 from the north side of Gareloi Island and Tows 7 and 8 from south of Gareloi had almost identical species composition (Fig. 5). Analysis of variance on the data extracted for MDS revealed that late stage *E. bungii*, *Oikopleura* spp. and *Limacina helicina* were more abundant in the Gareloi region and south of Kiska than north and west of Kiska (Table 1). Negative values on dimension 2 of the MDS plot tended to have higher abundance of early stage copepodids of *E. bungii*, *N. cristatus*, and *Neocalanus*, *M. pacifica* stages IV and V, and *E. hamata*, although the differences were generally not statistically significant. No significant differences in the concentration of *N. plumchrus* stage V were observed.

Spatial statistics was applied to ADB grids north of Gareloi Island in 1993 and north of Kiska in 1992 and 1993. There was not enough data collected in the Gareloi Island region in 1992 to permit statistical analysis. The exponential and spherical variance models produced the best fit to the data (Table 2). Shaded contours of the lower 95% confidence interval of ADB north of Kiska and Gareloi Islands in July 1993 are shown in Fig. 6A. The plots are overlain with contours of sea surface temperature. Highest overall biomass was observed north of Gareloi Island. Elevated



**Fig. 2.** Temperature, salinity (psu), chlorophyll and acoustic biomass from (A) north of Gareloi, 10–11 July 1993 (Stns 10–16, Fig. 1G); (B) north of Kiska Island, 29 July 1993 (Stns 189–198, Fig. 1H); (C) north of Kiska Island in 26 June 1992 (Stns 225–237, see Coyle et al., 1998); (D) west of Gareloi Island, 1 July 1992 (Stns 262–271, Fig. 1G). Triangles along the upper axes mark CTD station locations. Horizontal axes on upper and lower figures aligned. Scale bar for acoustic biomass in  $\text{g m}^{-3}$ .

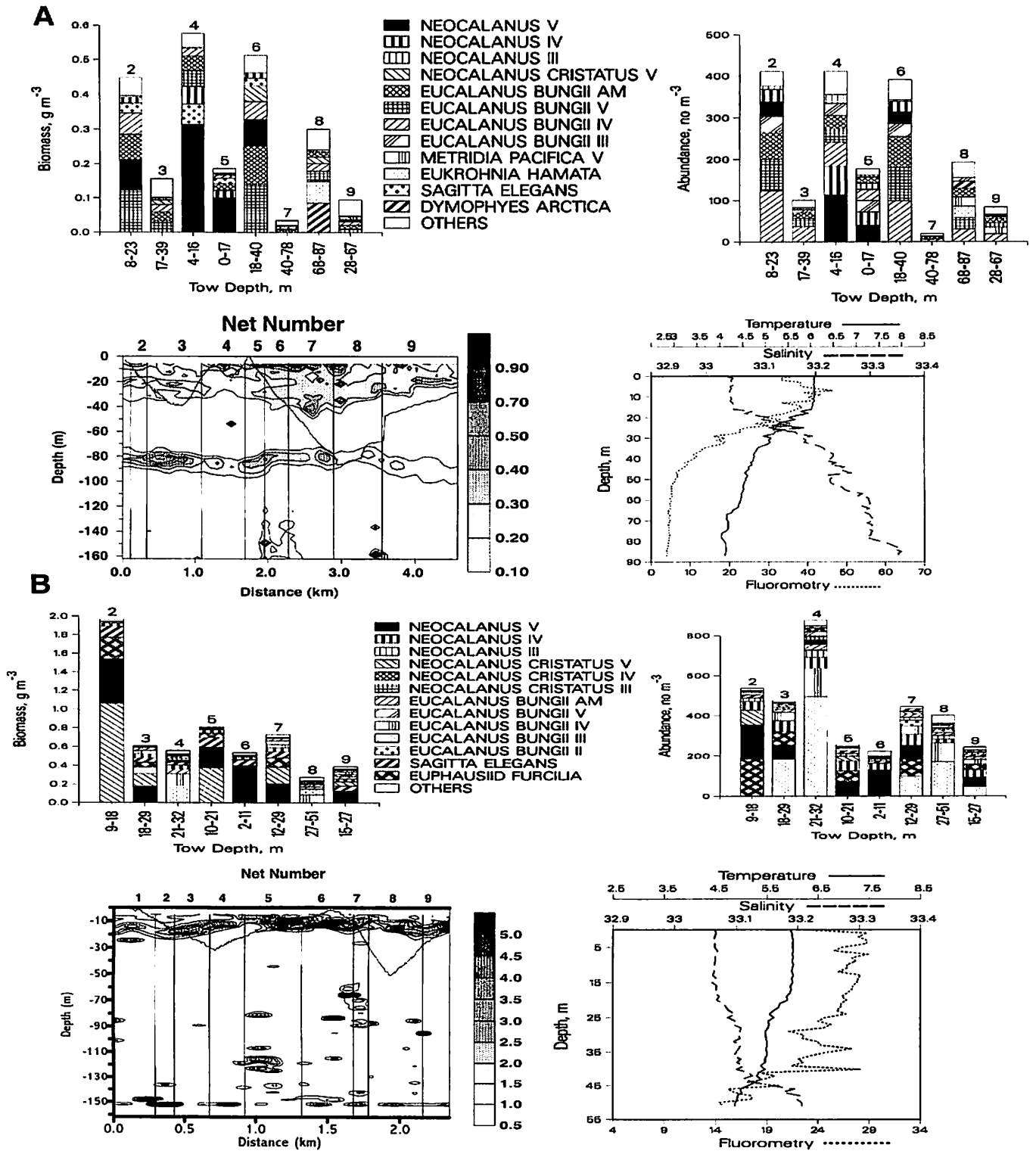


Fig. 3. Zooplankton wet weight biomass (upper left), abundance (upper right), acoustic biomass ( $\text{g m}^{-3}$ , lower left) and temperature ( $^{\circ}\text{C}$ ), salinity (ppt) and fluorescence (relative units) (A) from MOCNESS Tow 1, taken north Gareloi, 10 July 1993; (B) from MOCNESS Tow 27, taken north of Gareloi Island, 1 July 1992.

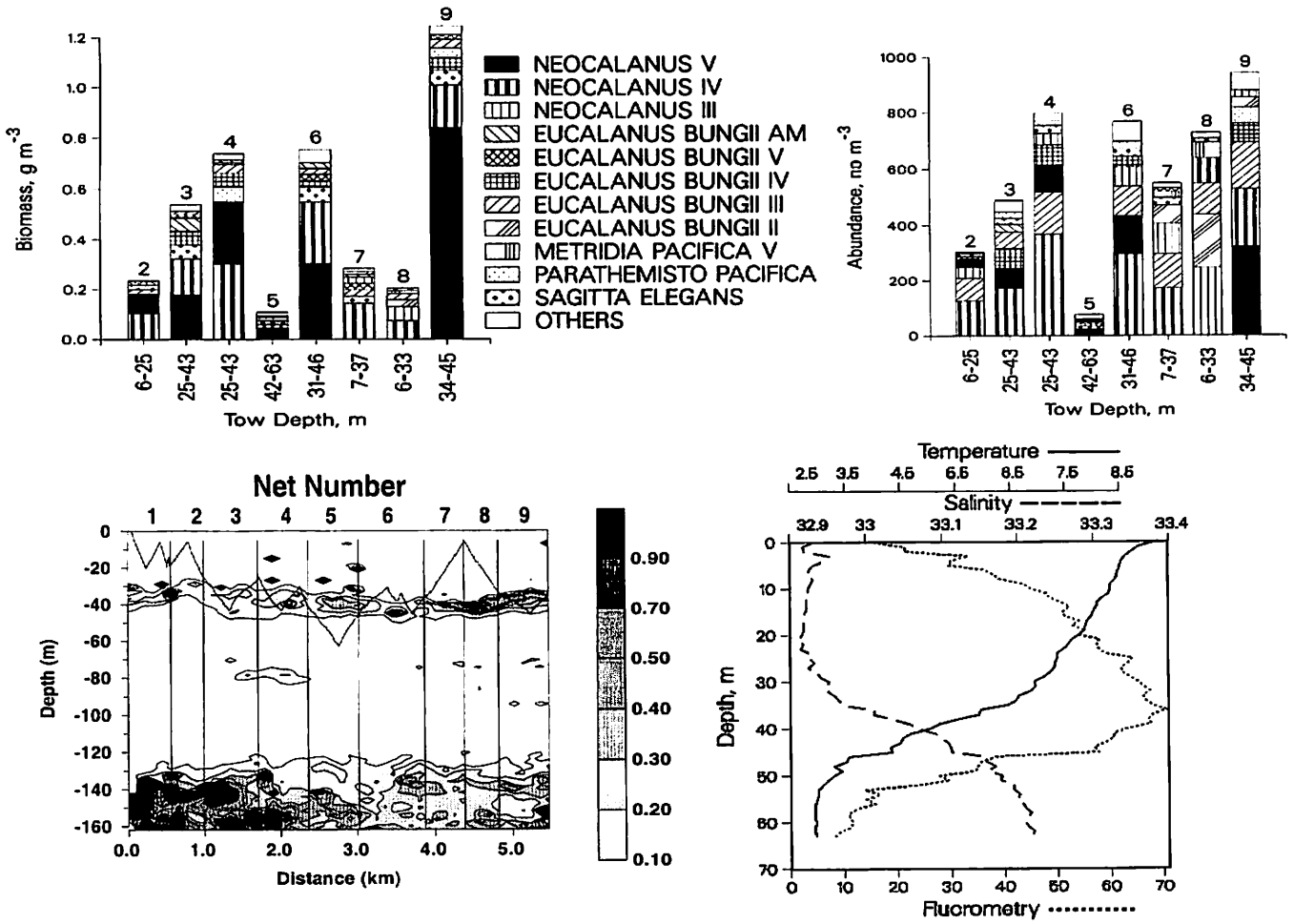


Fig. 4. Zooplankton wet weight biomass (upper left), abundance (upper right), acoustic biomass ( $\text{g m}^{-3}$ , lower left) and temperature ( $^{\circ}\text{C}$ ), salinity (ppt) and fluorescence (relative units) from MOCNESS Tow 22, taken north of Kiska, 28 July 1993.

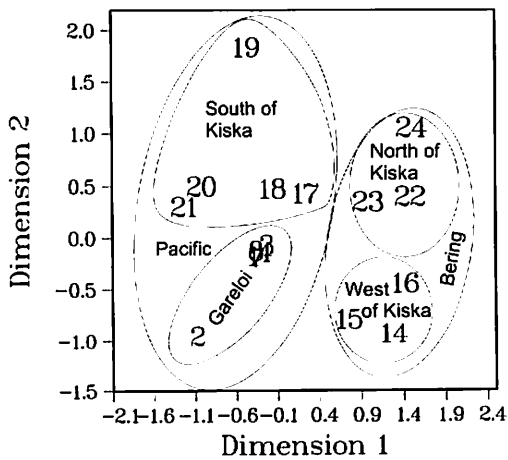


Fig. 5. Multidimensional scaling plot of tows taken in the Gareloi Island region (1-4, 7, 8), south of Kiska (17-21), west of Kiska (14-16) and north of Kiska (22-24) during July 1993 (Fig. 1E, F).

ADB in the Kiska region occurred to the west of the island along the  $8^{\circ}\text{C}$  isotherm, where surface contours of temperature tended to converge in the front separating the mixed regime in the pass from the stratified regime to the north.

Regions north of Kiska where the lower 95% confidence interval in the 1992 data exceeded the upper 95% confidence interval in the 1993 data are plotted in Fig. 6B. ADB in the upper 40 m was significantly higher in June 1992 than in July 1993 for much of the region. The largest differences occurred to the west of Kiska along  $52^{\circ}15'\text{N}$  during early June but had shifted eastward and to the north of  $52^{\circ}20'\text{N}$  by late June. Thus, dense patches of ADB, significantly higher than that for the same region in 1993, were measured to the northwest of Kiska in early June 1992 and to the northeast of Kiska in late June 1992. Regions where ADB during July 1993 was significantly higher than in June 1992 occurred primarily south of  $52^{\circ}15'\text{N}$  (Fig. 6C). In June 1992 ADB was greater by up to  $20 \text{ g m}^{-2}$  in those regions where it exceeded the July 1993 values. In those regions where ADB in July 1993 exceeded that of June 1992, differences were under  $2 \text{ g m}^{-2}$  (note the differences in scale

**Table 1.** Analysis of variance (abundance, no. m<sup>-3</sup>) on the nine most abundant species in any tow at stations grouped by region and water-mass type. Samples were collected in July 1993 from south and north of both Gareloi and Kiska Islands. *P* is the probability of equal means. "TUKEY" is a Tukey test for equal means ( $P \leq 0.05$ ). Table lists those taxa where differences were statistically significant ( $P \leq 0.05$ ). Group 1 (Pacific Water south of Kiska): Tows 17, 18, 19, 20, 21. Group 2 (Bering Sea Water west of Kiska): Tows 14, 15, 16. Group 3 (Bering Sea Water north of Kiska): Tows 22, 23, 24. Group 4 (Pacific Water in the Gareloi Island region): Tows 1, 2, 3, 4, 7, 8. AM: adult males. AF: adult females.

Taxa	Group number				<i>P</i>	TUKEY
	1	2	3	4		
<i>Eucalanus bungii</i> IV	19.14	11.88	20.54	51.48	0.002	4>1 & 2 & 3
<i>Eucalanus bungii</i> V	27.18	5.81	3.90	26.80	0.001	1 & 4>2 & 3
<i>Eucalanus bungii</i> AM	21.91	5.12	5.03	31.81	0.000	1 & 4>2 & 3
<i>Eucalanus bungii</i> AF	6.35	0.23	0.12	1.99	0.007	2 & 3<1
<i>Neocalanus</i> IV	13.06	27.18	63.07	22.66	0.029	3>1
<i>Neocalanus</i> V	17.88	24.90	23.74	20.68	0.898	
<i>Metridia pacifica</i> IV	0.19	0.00	2.16	0.00	0.025	3>2 & 4
<i>Metridia pacifica</i> AF	2.12	0.04	0.06	0.00	0.036	1>4
Euphausiid furcilia	2.93	1.04	2.02	6.73	0.001	4>1 & 2 & 3
<i>Eukrohnia hamata</i>	4.18	0.13	1.53	0.08	0.000	1>2 & 4
<i>Oikopleura</i> sp.	2.61	0.01	0.37	3.21	0.007	1 & 4>2
<i>Limacina helicina</i>	2.68	0.16	0.48	1.48	0.000	1>3 & 2

in the plots).

Comparisons of ADB from the various regions sampled in June 1992 and July 1993 are tabulated (Table 3). Highest biomass was recorded north of Kiska and Buldir Islands in June 1992. A polygon surrounding the region of maximum biomass in the northeast corner of the Kiska grid for June 26–28 (Fig. 6B) produced a mean ADB of 16 g m<sup>-2</sup> with an upper confidence interval of 20 g m<sup>-2</sup>. Lowest overall biomass occurred in July 1993 in the region north of Kiska where the 1992 and 1993 sampling grids overlapped (Figs 6B, C). Mean ADB for the whole sampling grid north of Kiska in July 1993 was higher than that of the overlapping region but was still significantly lower than for other sampling periods and regions (Table 3).

## Discussion

The observed differences in zooplankton distribution, abundance and species composition in the upper mixed

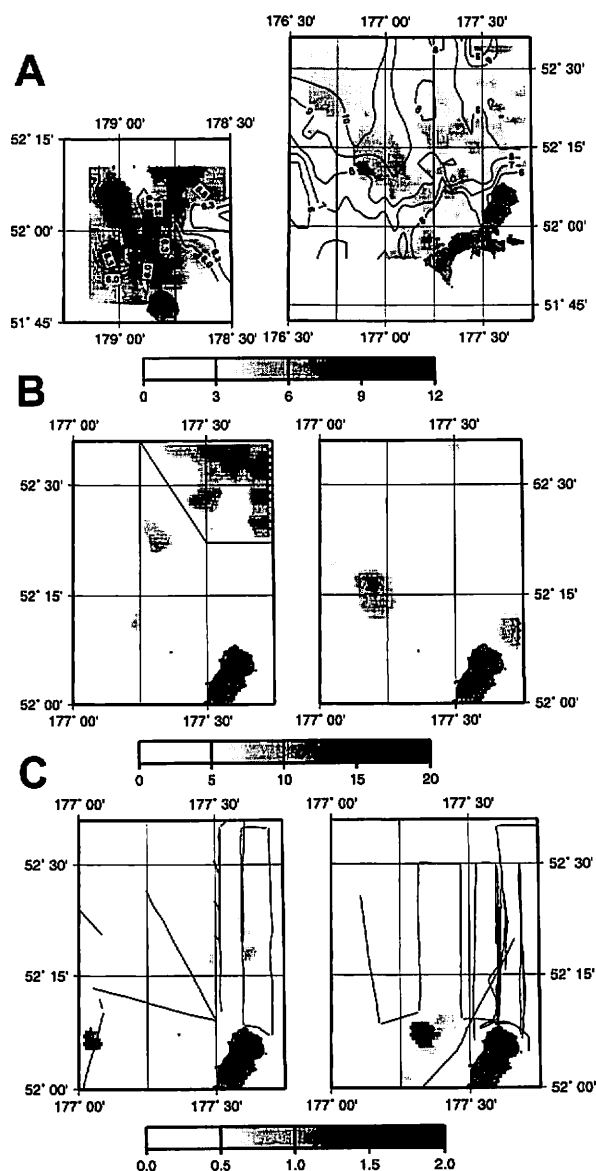
**Table 2.** Results from covariance models for acoustically determined biomass from Gareloi and Kiska Islands in 1992 and 1993.

Location	Model type	Nugget effect	Range (km)	<i>r</i> <sup>2</sup>
Kiska 6–11 June 92	Exponential	0.50	14	0.98
Kiska 24–28 June 92	Spherical	0.50	25	0.97
Kiska 22–29 July 93	Exponential	0.31	6	0.99
Gareloi 9–12 July 93	Exponential	0.40	13	0.98

layer between June 1992 and July 1993 are the result of both seasonal differences in the successional stage of the zooplankton community and interannual differences in the species composition and timing of successional cycles. Seasonal ontogenetic vertical migration of the dominant calanoid species is a major influence on zooplankton biomass in the upper mixed layer north and south of the Aleutian Islands (Coyle et al. 1996). The calanoid species undergoing interzonal ontogenetic migration include primarily *Neocalanus cristatus*, *Neocalanus plumchrus*, *Neocalanus flemingeri* and *Euclanus bungii*. Although the above species undergo ontogenetic vertical migrations each year, the exact timing of the migrations and the relative species composition of the interzonal copepods are subjected to influences which vary annually. Such interannual influences may include both climatic effects on the timing and intensity of the spring phytoplankton bloom, and water mass circulation and distribution.

Interannual differences in the direction and magnitude of water transport through the Aleutian passes may substantially influence zooplankton community composition around the Aleutian ridge (Coyle et al. 1998). Because northward transport of Pacific water through the Aleutian passes substantially influences both the faunistic and physical properties of water masses in the Bering Sea, a great deal of effort has been devoted to estimating the amount of flow through Aleutian passes (Stabeno & Reed 1994; Reed & Stabeno 1994; Stabeno & Reed 1992; Reed & Stabeno 1993). Given the faunistic differences observed on either side of the Aleutian ridge (Coyle et al. 1998), a clear physical marker for water of Pacific or Bering Sea origin would be useful in assessing the effect of flow in and out of the Bering on the zooplankton species composition and abun-





**Fig. 6.** A. Lower 95% confidence intervals of acoustically determined biomass (ADB) in the upper 45 m and contours of sea surface temperature ( $^{\circ}C$ ) for transects taken north of Gareloi Island (left) and north of Kiska (right). B. Locations north of Kiska Island where ADB in the upper 40 m in June 1992 exceeded that of July 1993 (the magnitude of the difference between the lower 95% confidence interval in June 1992 and the upper 95% confidence interval for July 1993). Comparison of July 1993 data with data taken 6–11 June 1992 (right) and 24–28 June 1992 (left). C. Locations north of Kiska Island where ADB in the upper 40 m in July 1993 exceeded that of June 1992 (the magnitude of the difference between the lower 95% confidence interval in July 1993 and the upper 95% confidence interval for June 1992). Comparison of July 1993 data with data taken 6–11 June 1992 (right) and 24–28 June 1992 (left). Lines indicate cruise track in June 1992. Scale bars: ADB in  $g\ m^{-2}$ .

dance both south and north of the Aleutians.

Resident Bering Sea water is characterized by a temperature minimum of under  $4^{\circ}C$  from the base of the seasonal thermocline to about 200-m depth (Reed & Stabeno 1993). The minimum is generated by deep mixing of cold surface water during winter storms following erosion of the seasonal thermocline (Pavlov & Pavlov 1996). The temperature minimum therefore marks a water mass as having resided in the Bering Sea for at least one winter season. By contrast, water along the south side of the Aleutian ridge originates in the eastern Pacific and is carried westward along the coast by the Alaska Stream (Reed 1984). It therefore lacks the low temperature marker characteristic of resident Bering Sea water (Reed & Stabeno 1993).

The water north of Kiska Island had a temperature minimum layer under  $4^{\circ}C$  in June, 1992, June 1995 (Coyle et al. 1998) and July 1993. Therefore, the presence of water which has been in the Bering Sea for at least one winter is apparently a fairly consistent feature north of Kiska Island in early summer. Nevertheless, drift buoys released in the Alaska Stream in September 1992 drifted through Buldir Pass northward into the eddy in Bowers Basin north of Kiska Island by October 1992 (Reed & Stabeno 1993). It is therefore probable that the plankton assemblage we encountered north of Kiska in July 1993 was at least partially influenced by plankton transported northward through the Aleutian passes during 1992 and retained in Bowers Basin for at least one winter. The marked contrast in species composition north of Kiska in July 1993 relative to June 1992 may have been at least partially due to the cessation of flow through the passes in 1990 and 1991 (Stabeno & Reed 1992; Coyle et al. 1998).

The greater abundance of later stage copepodids, larvaceans and pteropods in Pacific relative to Bering Sea water is indicative of retardation in the seasonal development of the zooplankton community in the Bering Sea relative to the northern Gulf of Alaska. The colder water temperatures north of Kiska in spring and early summer during all years could produce the apparent retardation of seasonal succession observed in the zooplankton community north of Kiska relative to that south of Kiska and Buldir and north of Gareloi (Coyle et al. 1998; this paper).

In contrast to waters north of Kiska, the water column north of Gareloi Island lacked a temperature minimum under  $4^{\circ}C$  in both July 1992 and July 1993 and had therefore probably originated in the Alaska Stream sometime after winter. The above conjecture is consistent with our interpretation of the MDS plot and with known circulation patterns in Amchitka pass (Stabeno & Reed 1994; Reed & Stabeno 1994). Nevertheless, the presence of *N. cristatus* patches in the seasonal pycnocline north of Gareloi Island in June 1992 is more characteristic of Bering Sea zooplankton than the Pacific zooplankton assemblage (Coyle et al. 1998). An intense southward transport on the west and northward transport on the east side of Amchitka Pass apparently produces eddies (Stabeno & Reed 1994; Reed &

**Table 3.** Mean acoustically determined biomass ( $\text{g m}^{-2}$ ) near the western Aleutian Islands. Kriging results on regions sampled in June 1992 and July 1993. Upper and lower limits are the upper and lower 95% confidence limits computed from kriging. Geom. Mean is the geometric mean of the acoustic data.

Region dates	Spatial mean	Lower lim	Upper lim	Geom. Mean
Kiska, 6–11 June '92	8.62	8.06	9.23	10.28
Kiska, 26–28 June '92	11.34	9.60	13.40	11.76
Kiska, June '92	9.87	9.07	10.47	11.56
Both periods pooled				
Kiska, 22–29 July '93	2.34	2.23	2.45	2.25
Overlapping area <sup>a</sup>				
Kiska, 22–29 July '93	6.90	6.57	7.25	7.22
Whole Region				
Gareloi, 9–12 July '93	10.05	9.35	11.03	9.41
Buldir, June '92	12.29	11.29	13.39	11.51
Buldir, North <sup>b</sup>	14.07	11.94	16.58	15.73
Buldir, South <sup>c</sup>	10.38	9.57	11.26	8.84

<sup>a</sup> That region north of Kiska where the sampling grid in 1993 overlapped the sampling grid in 1992.

<sup>b</sup> Region north of the front (Coyle et al. 1998)

<sup>c</sup> Region south of the front (Coyle et al. 1998)

Stabeno 1994) which may have mixed Bering and Pacific water and produced localized patches of *N. cristatus* north of Gareloi in June and July 1992. The presence of warm water eddies in the upper mixed layer north of Gareloi in 1992 is indicated by the warm, low-salinity surface patches with elevated chlorophyll concentration along the CTD transect (Fig. 2D).

Apparently, the cold Bering Sea water mass has markedly different influences on zooplankton distribution and development relative to the season. During June 1992, the spring bloom north of Kiska was ongoing, as indicated by elevated chlorophyll concentrations relative to that on transects taken in July 1993 (Fig. 2; see also Coyle et al. 1998). In addition, the lower water temperatures apparently prolong the development cycle of the large calanoids. As a result, large scale patches of late-stage *Neocalanus* were present in the developing seasonal pycnocline over a broad region north of Kiska Island in June 1992. However, as the season progresses, the overall zooplankton biomass above the seasonal pycnocline in the Aleutian Basin declines as the larger interzonal calanoid species migrate to their overwintering depth below 200 m (Coyle et al., 1996). In addition, the contrast between the colder Bering Sea Intermediate water mass and the overlying seasonal mixed layer produces a strong pycnocline north of Kiska. As a result, in July 1993 regions of elevated production and their associated zooplankton communities appeared as small patches of elevated ADB confined to the southern part of the Kiska grid, where the seasonal pycnocline was disrupted by fronts associated with the northern slope of the Aleutian ridge. The overall differences in patch size between years are indicated by the differences in the range of influence, which was 6 km in July 1993 but 14–25 km in June 1992 (Table 2). Thus, the large zooplankton patches north of Kiska in

June 1992 reflect large scale seasonal influences on zooplankton in the Bering Sea water mass, while the small scale zooplankton patches in July 1993 were apparently generated by localized conditions in the frontal regions on the north side of the Aleutian ridge. The small, isolated patches in July 1993 contributed little to the overall biomass of the whole grid, while the larger, denser layers in June 1992 substantially elevated the overall biomass over a greater area, particularly in the northeastern quadrant of the Kiska grid in late June. Mean ADB for the whole sampling grid at Kiska in late June 1992, Buldir in mid June 1992, and north of Gareloi in July 1993 was not significantly different. However, the Kiska grid in July 1993 had significantly lower ADB overall, particularly in the region where the 1992 and 1993 study grids overlapped. Turbulent mixing of the water column in the Gareloi region as it transited Amchitka Pass probably elevated nutrient concentrations in the surface water and enhanced productivity, resulting in higher overall zooplankton biomass under post-bloom summer conditions in the Gareloi region relative to north of Kiska in July 1993.

Direct comparisons of zooplankton densities reported in different studies are complicated by the many different units used to express abundance and biomass, and the various gear types and sampling strategies employed. While bearing in mind the effects of the above variables, some appreciation of the magnitude of variation in zooplankton biomass can be garnered by comparing the result of various studies. Zooplankton biomass estimates by a number of studies in the eastern Gulf of Alaska and eastern Bering Sea were recently tabulated and compared by converting the various units to  $\text{mg C m}^{-3}$  (Incze et al. 1997). We have modified the table in Incze et al. (1997) to include acoustic biomass estimates from this study and estimates by Motoda

**Table 4.** Comparison of zooplankton biomass estimates ( $\text{mg C m}^{-3}$ ) from the Gulf of Alaska and Bering Sea (modified from Incze et al. 1997).

Location	Month	Year	Biomass	Depth (m)	Source <sup>a</sup>
Station P	May	1956–1980	2.0	0–150	1
Prince William Sound	Early April–late May	1976	3.3–3.6	0–700	2
Kachemak Bay	Early April–early July	1976	0.8 (April), 17.5 (May)	0–72	2
Lower Cook Inlet	Early April–early July	1976	2.2 (April), 20.4 (July)	0–25	2
Shelikov Strait	Late April–late May	1985–1989	11.5 (April), 42.8 (May)	0 to bottom	3
Bering slope	April–May	1980	1.7 (April), 12.3 (May)	0–1200	4
Bering outer shelf	April–May	1980	15.4 (April), 30.8 (May)	0–150	4
Bering middle shelf	April–May	1980	21.4	0–70	4
North/south of Kiska & Buldir	Early–mid summer	1950s–1960s	8.8–15.7	0–80	5
Kamchatka Basin	Early–mid summer	1950s–1960s	28.6	0–80	5
North/south of Kiska & Buldir	Early–late June	1992	9.6–17.0	0–45	6
North of Kiska	July	1993	7.3	0–45	6
North of Gareloi	July	1993	11.4	0–45	6

<sup>a</sup> 1, Fulton (1983); 2, Damkaer (1977); 3, Incze et al. (1997); 4, Smith & Vidal (1986); 5, Motoda & Minoda (1974); 6, This study.

& Minoda (1974) from the western Aleutian Islands (Table 4). Wet weight ADB in  $\text{g m}^{-3}$  was converted to  $\text{mg C m}^{-3}$  using the regression equation of Wiebe et al. (1988).

Highest zooplankton biomass was reported from Shelikov Strait and the outer shelf of the Bering Sea in May and from the Kamchatka Basin in summer (Table 4). Average zooplankton biomass from the upper 150 m of the central Gulf of Alaska in 1957 and 1980 (Brodeur & Ware 1992) was 4.47 and 9.01  $\text{mg C m}^{-3}$ , respectively, when converted using the regression equation in Wiebe et al. (1988); the above values encompass ADB in the upper mixed layer north of Kiska in July 1993. The low values from the central Gulf of Alaska may be partially due to the depth of the tows relative to the depth of the mixed layer, where greatest zooplankton densities probably occur. The grid averages of ADB for the Buldir and Kiska regions in 1992 and the Gareloi Island region in 1993 are between the long term overall averages reported by Motoda and Minoda (1974) for the regions north and south of Kiska and Buldir. However, in regions of highest ADB during June 1992, the biomass would average 20–30  $\text{mg C m}^{-3}$ , with values as high as 790  $\text{mg C m}^{-3}$  measured by nets towed through *Neocalanus* scattering layers. The above averages are commensurate with the highest reported values in Table 4.

Although the average ADB we measured and long term averages from net tows (Motoda & Minoda 1974) were similar, acoustic measurements can detect dense zooplankton layers which may be present or absent in various years, depending on oceanographic conditions. Since these layers vary in size and frequency, they may have little impact on the overall average biomass, but may substantially influence predator populations which depend on zooplankton for forage. Comparison of the distribution of foraging least auklets to that of zooplankton biomass in the upper 15 m, which is the maximum foraging depth of least auklets, has clearly indicated the profound influence that patch distribu-

tions can have on the foraging ecology of apex predators (Hunt et al. 1998).

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### Literature Cited

- Brodeur, R. D. & D. M. Ware 1992. Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. *Fish. Oceanogr.* 1: 32–38.
- Clarke, K. R. & R. M. Warwick 1994. *Changes in Marine Communities: an Approach to Statistical Analysis and Interpretation*. Bourne Press Limited, Bournemouth.
- Coyle, K. O. 1998. Acoustic assessment of *Neocalanus* scattering layers near the western Aleutian Islands. *J. Plankton Res.* 20: 1189–1202.
- Coyle, K. O., T. J. Weingartner & G. L. Hunt, Jr. 1998. The distribution of acoustically determined biomass and major zooplankton taxa in the upper mixed layer relative to water masses in the western Aleutian Islands. *Mar. Ecol. Prog. Ser.* 165: 95–108.
- Coyle, K. O., V. G. Chavtur & A. I. Pinchuk 1996. Zooplankton of

- the Bering Sea, p. 97–133. In *Ecology of the Bering Sea: a Review of the Russian Literature* (eds. Mathisen O. A. & K. O. Coyle). Univ. Alaska Fairbanks.
- Damkaer, D. M. 1977. Initial zooplankton investigations in Prince William Sound, Gulf of Alaska, and Lower Cook Inlet, p. 137–274. In *Environmental Assessment of the Alaska Continental Shelf*. US Dept. Commerce, National Oceanic and Atmospheric Administration, Boulder Colorado.
- Fulton, J. 1983. Seasonal and annual variations of net zooplankton at Ocean Station P, 1966–1980. *Can. Data Rep. Fish. Aquatic Sci.* No. 374.
- Hunt, G. L. Jr., R. W. Russell, K. O. Coyle & T. Weingartner 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Mar. Ecol. Prog. Ser.* **167**: 241–259.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**: 187–211.
- Incze, L. S., D. W. Siefert & J. M. Napp 1997. Mesozooplankton of the Shelikof Strait, Alaska: abundance and community composition. *Cont. Shelf. Res.* **17**: 287–305.
- Isaaks, E. H. & R. M. Srivastava 1989. *An Introduction to Applied Geostatistics*. Oxford University Press, New York., 561 pp.
- Motoda, S. & T. Minoda 1974. Plankton of the Bering Sea, p. 207–241. In *Oceanography of the Bering Sea with Emphasis on Renewable Resources* (eds. Hood, D. W. & E. J. Kelley). Univ. Alaska Fairbanks.
- Parsons, T. R., Y. Maita & C. M. Lalli 1984. *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, Oxford, 173 pp.
- Pavlov, V. K. & P. V. Pavlov 1996. Oceanographic description of the Bering Sea, p. 1–95. In *Ecology of the Bering Sea: A Review of the Russian Literature* (eds. Mathisen, O. A. & K. O. Coyle). Univ. Alaska Fairbanks.
- Reed, R. K. & P. J. Stabeno 1994. Flow along and across the Aleutian Ridge. *J. Mar. Res.* **52**: 639–648.
- Reed, R. K. & P. J. Stabeno 1993. The recent return of the Alaska Stream to Near Strait. *J. Mar. Res.* **51**: 515–527.
- Reed, R. K. 1984. Flow of the Alaska Stream and its variations. *Deep-Sea Res.* **31**: 369–389.
- Stabeno, P. J. & R. K. Reed 1994. Circulation in the Bering Sea basin observed by satellite-tracked drifters: 1986–1993. *J. Phys. Oceanogr.* **24**: 848–854.
- Stabeno, P. J. & R. K. Reed 1992. A major circulation anomaly in the western Bering Sea. *Geophys. Res. Lett.* **19**: 1671–1674.
- Vidal, J. & S. L. Smith 1986. Biomass, growth and development of populations of herbivorous zooplankton in the southeastern Bering Sea during spring. *Deep-Sea Res.* **33**: 523–556.
- Wiebe, P. H. 1988. Functional regression equations for zooplankton displacement volume, wet weight, dry weight and carbon: a correction. *Fish. Bull.* **86**: 833–835.