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The abundance and distribution of euphausiids and zero-age pollock on the inner shelf of the southeast Bering Sea near the Inner Front in 1997–1999

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Abstract

Acoustic data and net samples were collected during late spring and early fall 1997–1999 to assess zooplankton and micronekton abundance and distribution relative to the Inner Front at three sampling grids (Port Moller, Cape Newenham and Nunivak Island) on the inner shelf of the southeast Bering Sea. Epibenthic scattering layers were observed during May–June and August–September in all three years. Acoustic data were scaled to euphausiid biomass using target strength models. Mean euphausiid biomass determined acoustically for each transect line was $0.7\text{--}21\text{ g m}^{-2}$, with most values below 5 g m^{-2} . There was no consistent relationship between the distribution and biomass of euphausiids and the location of the Inner Front. Zero age pollock were observed on the inner shelf in August–September during all years, but were confined primarily to the stratified side of the Inner Front and to the frontal regime. The acoustic data for pollock were scaled to biomass using laboratory measurements of gas bladder dimensions and target strength models. Acoustic determinations of mean transect biomass for euphausiids did not differ from literature values for the inner shelf of the southeast Bering Sea, and pollock biomass on the inner shelf did not differ from that around the Pribilof Islands. Despite recent anomalies in climate and oceanographic conditions on the inner shelf, and high mortality of shorttail shearwaters during 1997, we found no evidence of significant interannual differences in the biomass of euphausiids or zero-age pollock on the inner shelf of the southeast Bering Sea.

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1. Introduction

The eastern Bering Sea sustains one of the most productive fisheries in the world (NRC, 1996). In addition to the commercial fisheries, the region also supports immense populations of marine mammals and seabirds (Nasu, 1974; Schneider and Shuntov, 1993). Among the wildlife resources are millions of short-tailed shearwaters (*Puffinus*

tenuirostris), which migrate annually from their breeding grounds in the south polar sea to forage on plankton on the continental shelf in the southeast Bering Sea (Hunt et al., 1981), where they consume primarily euphausiids (Ogi et al., 1980; Schneider et al., 1986). Since foraging on the shelf was thought to be concentrated at the Inner Front (Schneider and Shuntov, 1993; Hunt et al., 1996), we hypothesized that frontal mechanisms enhanced the concentration or availability of euphausiid prey in the frontal region. The continental shelf of the southeast Bering Sea is divided into three major domains (middle, inner and outer)

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separated by physical fronts or transition zones (Coachman and Charnell, 1979; Coachman, 1986; Schumacher and Stabeno, 1998). The Inner Front forms the transition between the unstratified water in the inner domain and the seasonally stratified water in the middle domain. In most years, the Inner Front is about 25 km wide and is centered over the 50 m isobath (Stabeno et al., 2001).

In 1997 El Nino-related climate anomalies resulted in a number of unusual physical and biological events in the southeast Bering Sea (Vance et al., 1998; Hunt et al., 1999; Overland et al., 2001). Unusually warm calm weather resulted in elevated surface temperatures, a very intense pycnocline (Stabeno et al., 2001), nutrient depletion below the pycnocline as well as above, and an intense coccolithophorid bloom over much of the southeastern Bering Sea (Stockwell et al., 2001; Sukhanova and Flint, 1998). The above anomalous conditions were accompanied by unusually high mortality of shearwaters (Baduini et al., 2001). A low condition index and lack of evidence of disease indicated that the mortality was due to starvation. Birds with unusually low condition index also were observed in 1998 (Baduini et al., 2001). If starvation was the cause of the mortality, the birds starved either because their prey densities were substantially lower than normal or because the birds could not locate their prey. The abnormal conditions cited above, as well as the mass mortality of shearwaters, constituted substantial evidence of an ecological shift altering the concentration of the euphausiid prey. A test of the above hypotheses required information on the horizontal and vertical distribution of the euphausiid prey both in and outside the frontal region.

While net tows could provide information on the mean concentrations and species composition of the zooplankton taxa, they could not provide the detailed information on the spatial distribution, required to address the hypotheses. Acoustic measures of zooplankton density in conjunction with net tows provided additional spatial coverage to improve estimates of the abundance and distribution of the prey species. Although care must be exercised in the quantitative interpretation of acoustic data (Coyle, 2000; Stanton et al., 1994a; Smith et al., 1992), acoustics has proved

useful in documenting the distribution of zooplankton and micronekton in a number of predator–prey studies (Coyle et al., 1992; Macaulay et al., 1995; Coyle et al., 1998; Coyle and Hunt, 2000; Swartzman et al., 1999). In this paper we examined the interannual distribution and abundance of euphausiids and zero-age pollock both within and outside the frontal region using acoustics and net tow data. The resulting information was used to look for significant differences in the distribution and average biomass of euphausiids and pollock on the inner shelf between years and seasons.

2. Methods

Sampling was done during 1997–1999 on six cruises to the southeast Bering Sea (Table 1). Spring samples were collected in May and June, summer–fall samples were collected in late July, August and September. Samples on the inner shelf were collected at three sampling grids: Port Moller, Cape Newenham and Nunivak Island (Fig. 1). The sampling grids consisted of three to five transect lines running orthogonal to the bathymetry from near-shore to beyond the 50-m depth contour. Acoustic data were collected consistently along the central line in the grids (the C line, Fig. 1). Supplemental data were occasionally taken on parallel lines on either side of the C line (lines A and E).

Conductivity–temperature–depth (CTD) measurements were made with a Seabird CTD at stations along the C line. Additional CTD samples

Table 1
Year and dates of each cruise at the Inner Front of the southeastern Bering Sea

Year	Cruise	Dates
1997	HX196	June 1–27
1997	HX200	Aug 30–Sept 11
1998	HX209	May 26–June 19
1998	HX213	Aug 20–Sept 5
1999	HX220	May 20–June 14
1999	HX222	July 21–Aug 18

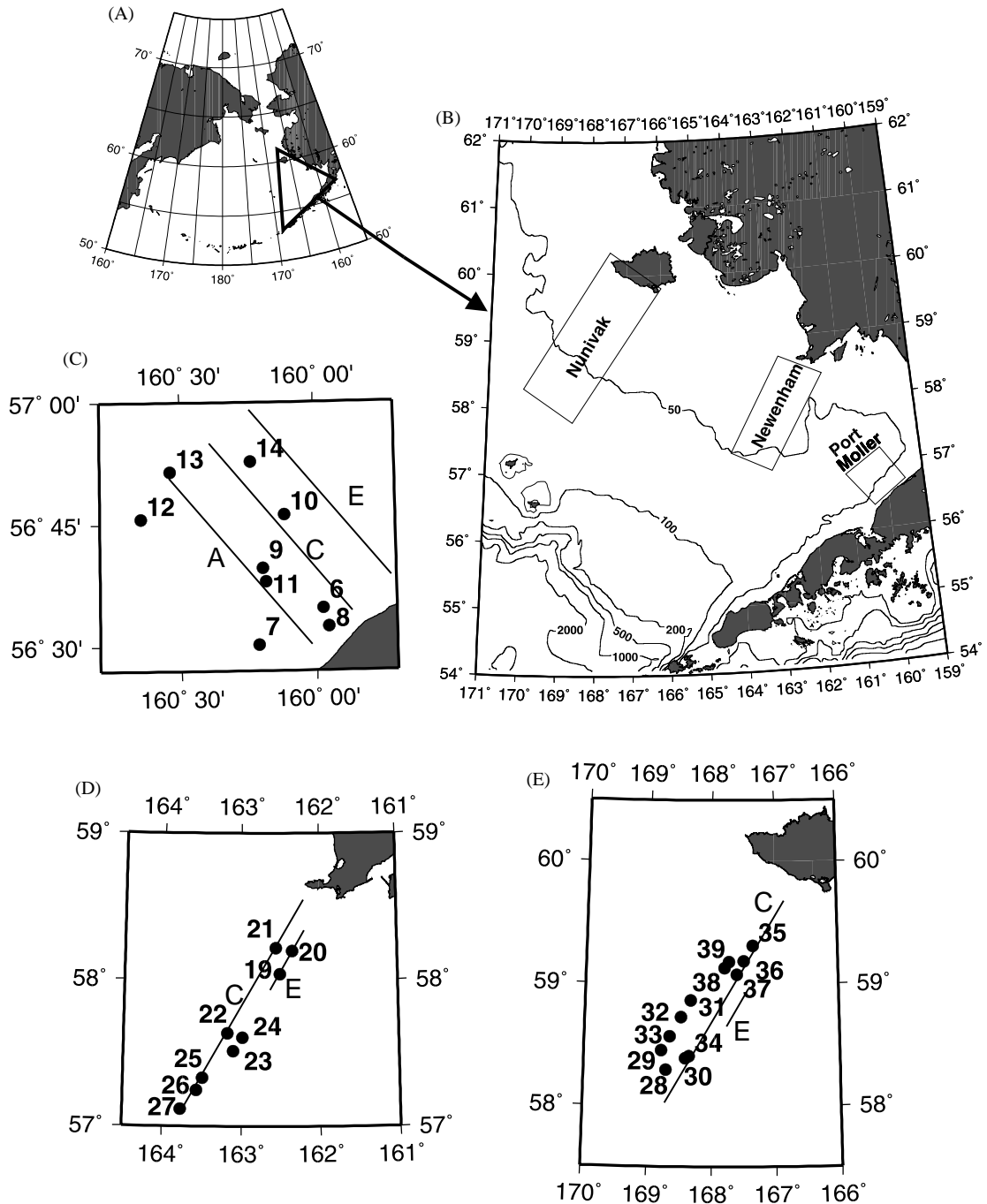


Fig. 1. Location of study region (A, B), Port Moller Grid (C), Cape Newenham Grid (D), Nunivak Island Grid (E). MOCNESS tow locations for the cruise in May–June 1998 (solid dots); main transect is labeled C and supplemental transects are labeled A and E (solid lines).

were taken along part or all of the A and E lines in the grid. Euphausiid eggs and larvae were sampled with a quarter-meter CalVET (CalCOFI vertical egg tow, Smith et al., 1985) equipped with 150- μm mesh nets and General Oceanics flowmeters. The nets were towed vertically from the bottom to the surface at stations along the C line. The large zooplankton were sampled with a 1-m MOCNESS (Wiebe et al., 1976) with 500 μm mesh nets. Seven to 12 MOCNESS tows were taken at night in each grid during each cruise. Each tow consisted of 4–8 discrete samples taken at 10–20 m depth intervals from the bottom to the surface. The maximum tow depth was 60 m. The MOCNESS was fished primarily at night to minimize net avoidance by micronekton. The MOCNESS system was equipped with nine nets and simultaneously collected data on salinity, temperature, fluorescence, depth, net angle, volume sampled, Greenwich Meridian Time (GMT) and global positioning system (GPS) position. Large gelatinous zooplankton were removed from the samples, their volume was measured, and they were discarded. The rest of the material was preserved in 10% formalin and returned to the laboratory for processing. Zooplankton in the samples were identified to the lowest taxonomic category possible, they were staged, enumerated and the wet weight was measured. The data were uploaded to an INGRES data base, and analysis was done with FORTRAN calls to IMSL statistics routines.

Acoustic transects were taken along the A, C and E lines at Port Moller, and along portions of the C and E lines at Cape Newenham and Nunivak Island (Fig. 1). Acoustic data were collected using a Hydroacoustic Technology Inc. (HTI) model 244 split-beam digital system. Data used in this presentation were collected with 43 kHz 7° split beam and 120 kHz 6° split-beam transducers. The transducers were towed beside the vessel at about 3 m s⁻¹ in a dead-weight tow body about 4 m from the hull and 2 m below the surface. Sampling was done during the day and was restricted to calm conditions when noise due to surface bubbles and waves were not observed in the data. The system collected simultaneous 40 log *R* data for target strength and 20 log *R* data for echo integration. The data were integrated at 1-min intervals during

1997 and 15-s time intervals during 1998 and 1999, and at 1-m depth intervals. The sample interval distances during transecting thus consisted of about 180 m during 1997 and 45 m during 1998 and 1999. System calibrations were applied before writing the averaged voltages to computer files. Differential GPS position and GMT from the ship's navigation system were appended to each record before writing the data to disk.

Noise was observed in the upper 19 m in the 43 kHz volume scattering data. A noise threshold was computed for the 43 kHz volume scattering (S_v) data as follows: a portion of the Nunivak C line with minimal scattering at other frequencies in the upper 20 m was identified. The 43 kHz S_v at each depth interval and integration interval was converted to the arithmetic equivalent and the mean S_v , the assumed noise level, was computed for each depth interval. Only signals above the mean noise level were considered valid. Since the noise threshold was below the target strength of the fish, and euphausiids are generally transparent to the 43 kHz system, the noise probably had minimal effect on estimates of euphausiid and fish densities.

Volume scattering at 43 and 120 kHz was scaled to biomass using sound-scattering models. The bent cylinder model (Stanton et al., 1994b) was used to estimate S_v due to euphausiids. The length, width and weight of 200 euphausiids were measured. A weight–length regression was used to estimate the average euphausiid length from wet weight biomass in each tow. The width of each length category was determined from the average length–width ratio. Post-larval pollock (*Theragra chalcogramma*) were modeled using the prolate spheroid high pass model for gas filled objects (Stanton, 1989; Stanton et al., 1994b). The length and width of the gas bladder in 100 specimens were measured to estimate its dimensions. A regression was run to fit the total length of the fish to the gas bladder dimensions. Sound scattering was assumed to result from the gas bladder alone. The target strength was corrected for depth using Boyle's Law (Mukai and Iida, 1996).

Statistical analyses were run to look for differences in mean acoustically determined euphausiid and fish biomass on each transect. Due to the close proximity of adjacent measurements in

Table 2
Reference points for distance calculations for each transect line

Grid and transect	Latitude	Longitude
Port Moller A	56.56	159.78
Port Moller C	56.49	159.94
Port Moller E	56.43	160.09
Cape Newenham C	58.63	162.15
Cape Newenham E	58.67	162.27
Nunivak Island C	59.94	166.93
Nunivak Island E	59.89	166.79

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 and Srivastava, 1989; Kern and Coyle, 2000) were used to predict the mean and 95% confidence intervals of acoustically determined biomass (ADB) for each transect. The ADB between the bottom and surface was integrated to produce biomass estimates in g m^{-2} . The position coordinates were converted to distance (km) along the transect from a consistent starting position for each transect (Table 2). The distances between all transect data points were computed, bin averaged, and the variance with respect to distance was modeled using standard transitive, spherical or exponential geostatistical models (Isaaks and Srivastava, 1989). A block kriging algorithm was used to generate mean ADB estimates with the upper and lower 95% confidence intervals. Analysis was done only on those portions of the transects that overlapped between years. The above procedure permitted direct comparison of ADB on individual transects between years. All kriging analyses were done on data converted from volume scattering to biomass using target strength models.

3. Results

3.1. Euphausiids, spring data

Target strength estimates for the euphausiids were computed to convert volume scattering to

estimates of euphausiid biomass. The bent cylinder model estimate of euphausiid target strength for 120 kHz was $-77.8 \text{ dB animal}^{-1}$. The values for h (speed of sound contrast between the animal and the medium) and g (density contrast) were taken from Kogeler et al. (1987): $h = 1.026$, $g = 1.058$, which produced an R (reflection coefficient) of 0.041, somewhat below that of Stanton et al. (1994b) for shrimp-like targets (0.058). With the R value of Stanton et al. (1994b), the target strength was -74.8 dB . Wiebe et al. (1990) measured the target strength of euphausiids at -75.8 to -78.9 dB at 420 kHz. We chose the value $-77.8 \text{ dB animal}^{-1}$ computed for euphausiids of 18.2 mm total length, 3.6 mm width and 40.2 mg animal^{-1} , average values for euphausiids from the HX196 MOCNESS catches. The target strength at 43 kHz was $-87.7 \text{ dB animal}^{-1}$. When the target strength per animal at 120 kHz (-77.8 dB) was converted to target strength per gram wet weight, the result was -63.85 dB g^{-1} . The latter value was used to convert S_v at 120 kHz to acoustically determined biomass of euphausiids.

Model prediction of euphausiid target strength at 43 and 120 kHz was -87.7 and -77.8 dB respectively, a difference of 9.9 dB. Since fish with gas bladders scatter sound at roughly equal intensities at both frequencies, it was assumed that scattering in any records having differences in the S_v at 43 and 120 kHz of less than 8.8 dB were due to fish. In addition, records where the difference in S_v at 43 and 120 kHz was greater than 18.8 dB were considered artifact. Records with differences in S_v between 8.8 and 18.8 dB were assumed to be due to scattering from euphausiids and scaled to euphausiid biomass using the 120 kHz S_v data and a target strength of -63.85 dB g^{-1} . All other records were assumed to be due to scattering from sources other than euphausiids and scaled to zero. Acoustically determined biomass consistently overestimated biomass from net samples (Table 3).

The acoustic data fit to transitive, exponential and spherical geostatistical models with r^2 values consistently above 0.88 (Table 4). The range of influence was 2.5 to 20 km, indicating substantial spatial correlations in the data set. Mean ADB per transect computed using kriging on overlapping

Table 3

Mean euphausiid biomass (mg m^{-3}) as computed using target strength models at 120 kHz (ADB) for S_v measurements and MOCNESS net samples taken during spring 1997 (HX196), 1998 (HX209) and 1999 (HX220)

Grid and transect	HX196		HX209		HX220	
	ADB	Net	ADB	Net	ADB	Net
Port Moller A line	—	10	18.0	5	230	58
Port Moller C line	107		6.4		208	
Port Moller E line	137		15		67	
Cape Newenham C line	174	8	95	43	66	14
Cape Newenham E line	10		164		95	
Nunivak Island C line	74	19	53	11	135	41
Nunivak Island E line	77		51		125	

Table 4

Statistical results comparing acoustically determined euphausiid biomass during spring cruises at the Port Moller (PM), Cape Newenham (CN) and Nunivak Island (NI) sampling grids

Transect	June 1997 (HX196)			June 1998 (HX209)			June 1999 (HX220)		
	Nugget	Range	Model	Nugget	Range	Model	Nugget	Range	Model
PMA	0.422	20	Exp 0.941	0.834	4	Exp 0.911	0.694	2.5	Tran 0.988
PMC	0.631	18	Exp 0.894	0.612	3	Tran 0.995	0.494	9.6	Exp 0.887
PME	—	—		0.761	19	Exp 0.981	0.409	14	Tran 0.995
CNC	0.537	15	Exp 0.934	0.615	12	Tran 0.992	0.710	9	Tran 0.920
CNE	0.918	4	Tran 0.932	0.641	5	Tran 0.997	—	—	—
NIC	0.273	9	Sph 0.989	0.564	12	Tran 0.987	0.677	19	Exp 0.920
NIE	0.192	9	Tran 0.978	0.703	6	Exp 0.962	0.416	8	Tran 0.987

Nugget = nugget effect (fraction of variance); Range = range of influence (km); Models: Exp = exponential, Tran = transitive, Sph = spherical, number next to the model is the r^2 value for the data fit to the model.

transect segments fall into three categories. Exceptionally high values ($15\text{--}20 \text{ g m}^{-2}$) were observed on transects A and C at Port Moller in June 1999 (Table 5). Moderately high values ($5\text{--}7 \text{ g m}^{-2}$) were observed at Port Moller E line in 1999, Cape Newenham in 1998, and Nunivak Island in 1999 (Table 5). Biomass in the third category ranged from 0.2 to 3 g m^{-2} . Confidence intervals between the three categories did not overlap, suggesting significantly different mean biomass between the categories. The overall impression is one of biomass averaging $0.1\text{--}7 \text{ g m}^{-2}$, with isolated regions where mean biomass was roughly 2 to 4 times higher. The above biomass would be equivalent to $2\text{--}175 \text{ animals m}^{-2}$ with values of $375\text{--}500 \text{ animals m}^{-2}$ in regions of elevated biomass.

When euphausiid biomass was elevated, most of the scattering occurred as a dense layer within

about 10 m of the bottom (Fig. 2). Moderately high euphausiid biomass on the Cape Newenham E line was observed during June 1998 between km 40 and 80, where thermal stratification was absent and temperatures were $3\text{--}4^\circ\text{C}$. In contrast, the elevated scattering at Port Moller during June 1999 occurred on the outer part of the line, outside the thermal discontinuity at km 25–30 where water temperatures were -1°C to 1°C . The low water temperatures observed at Port Moller were also a common feature at all other grids during June 1999. When euphausiid densities were low, scattering was generally confined to small patches near the bottom (Fig. 3). Isolated patches also were observed in the water column. The bottom patches were commonly observed in regions of horizontal temperature discontinuities (Fig. 3C, D). Patches of elevated euphausiid biomass were observed near the bottom on the Cape Newenham C line during

Table 5

Statistical results comparing acoustically determined euphausiid biomass during spring cruises at the Port Moller (PM), Cape Newenham (CN) and Nunivak Island (NI) sampling grids

Location		June 1997 (HX196)		June 1998 (HX209)		June 1999 (HX220)	
Transect name	Range (km)	Mean (g m ⁻²)	Upper and lower CI	Mean (g m ⁻²)	Upper and lower CI	Mean (g m ⁻²)	Upper and lower CI
PMA	5–55	2.258	1.945–2.571	0.765	0.538–0.992	17.270	13.274–21.267
PMC	5–55	2.982	2.358–3.608	0.345	0.249–0.438	15.760	14.602–17.460
PME	5–55	—	—	0.726	0.617–0.834	5.288	4.298–5.649
CNC	123–170	1.910	1.138–2.683	5.497	5.261–5.734	2.754	1.595–3.913
CNE	35–85	0.154	0.120–0.188	5.465	4.706–6.224	—	—
NIC	75–200	1.578	1.461–1.697	2.377	2.262–2.493	6.818	5.906–7.718
NIE	85–180	1.245	1.129–1.362	1.933	1.623–2.194	5.456	4.895–6.019

Ordinary Kriging with no rotation, orientation 0, search radius 4, models were the spherical, transitive or exponential. CI refers to the 95% confidence intervals.

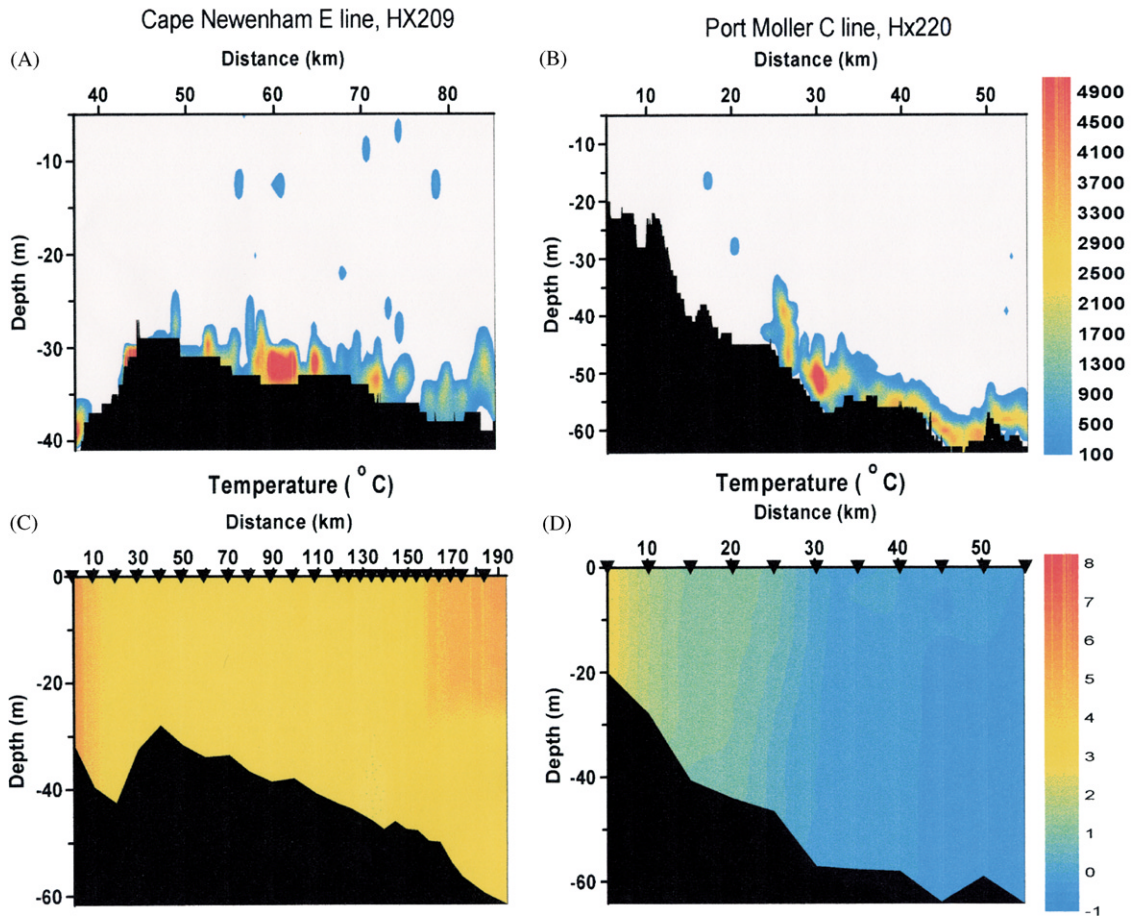


Fig. 2. Acoustically determined euphausiid biomass (ADB) and temperature profiles along the Cape Newenham E line in June 1998 (HX209) and the Port Moller C line in June 1999 (HX220). Acoustically determined biomass (mg m⁻³) (A, B), temperature profiles (C, D). Triangles above temperature profiles indicate CTD locations.

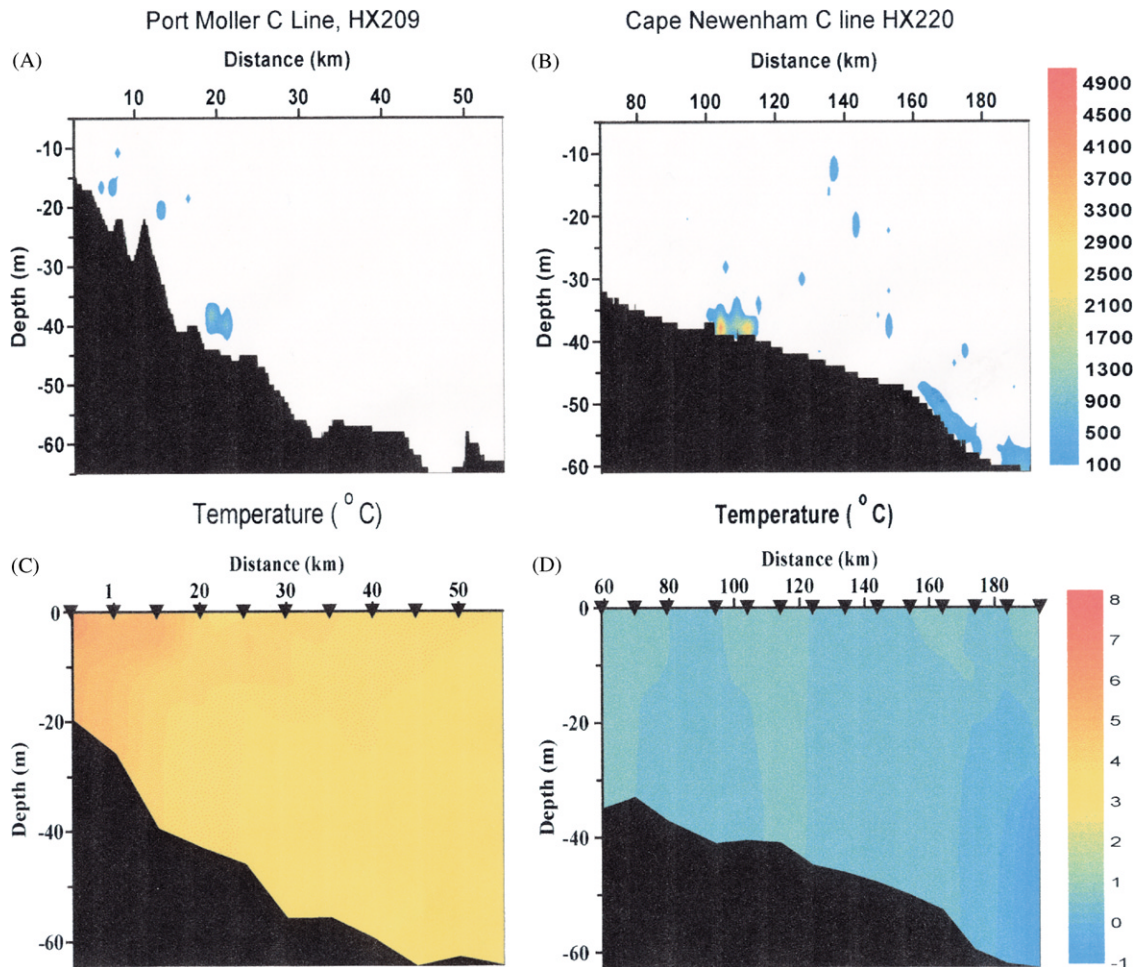


Fig. 3. Acoustically determined euphausiid biomass and temperature profiles along the Port Moller C line in June 1998 (HX209) and Cape Newenham C line in June 1999 (HX220). Acoustically determined biomass (mg m^{-3}) (A, B), temperature profiles (C, D). Triangles above temperature profiles indicate CTD locations.

June 1997 (Fig. 4A). Most of the biomass was observed between km 70 and 160, where temperature below the pycnocline was $2\text{--}5^\circ\text{C}$ (Fig. 4C). The intense pycnocline observed between km 80 and 160 was typical of conditions during the June 1997 cruise. Patches of elevated euphausiid biomass were consistently observed on the inner end of the Nunivak Island C transect between km 80 and 120 (Fig. 4B). Elevated biomass was occasionally observed at the Inner Front near the 50 m contour at km 160–200 (Fig. 4B, D). Biomass in the bottom layers often exceed 1 g m^{-3} , with values sometimes as high as 5 g m^{-3} , equivalent to densities of up to $125 \text{ animals m}^{-3}$.

The euphausiids in the MOCNESS tows consisted primarily of *Thysanoessa raschii*. The tows during the spring cruises were dominated by adult males and females between 17 and 26 mm length (tip of rostrum to tip of telson) (Fig. 5). Although fall tows had juveniles between 7 and 15 mm length, adults dominated the biomass because of their larger size. Mysids were usually a minor component of the catches but occasionally dominated (Fig. 6). Since euphausiids and mysids cannot be distinguished acoustically, some of the scattering, particularly on the inner part of the Port Moller grid and the outer part of the Nunivak grid, is undoubtedly due to mysids. *Thysanoessa*

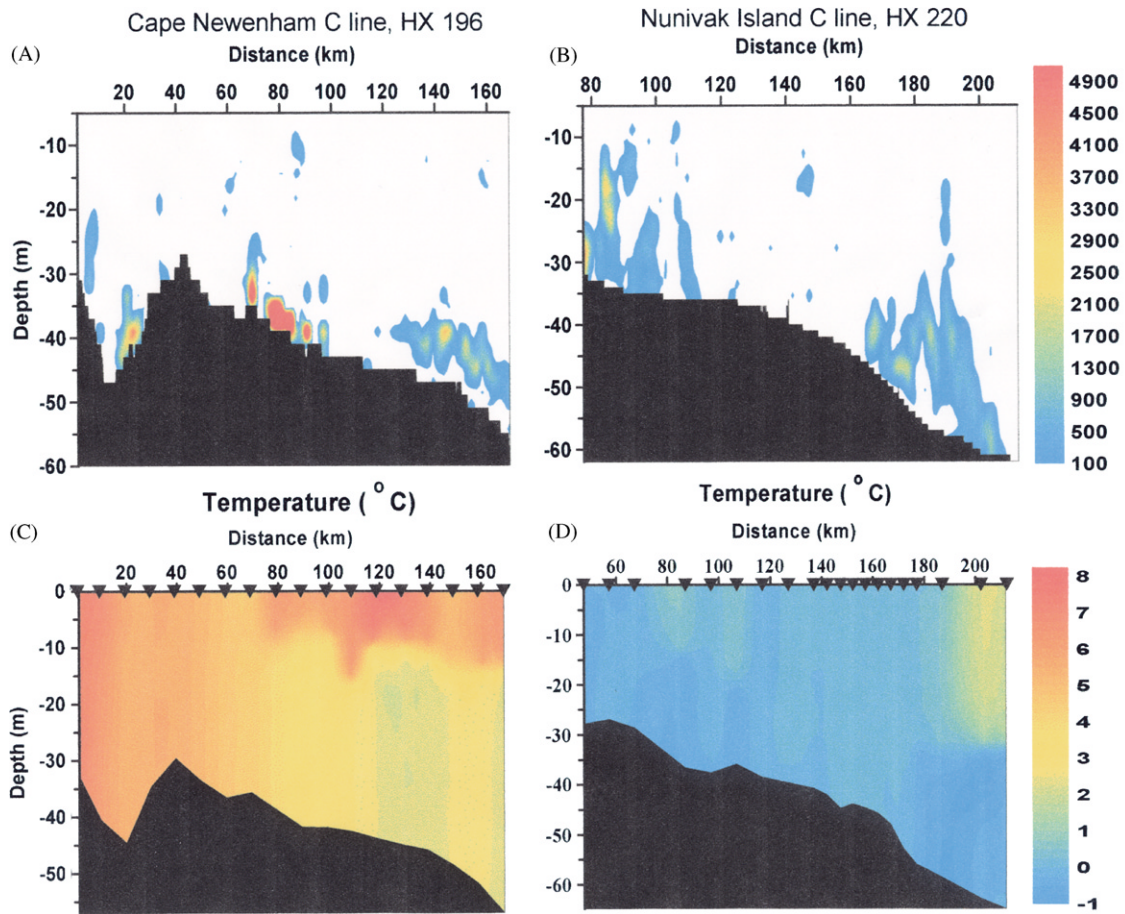


Fig. 4. Acoustically determined euphausiid biomass and temperature profiles along the Cape Newenham C line during June 1997 (HX196) and the Nunivak Island C line in June 1999 (HX220). Acoustically determined biomass (mg m^{-3}) (A, B), temperature profiles (C, D). Triangles above temperature profiles indicate CTD locations.

inermis were a minor constituent of the tows except at the outer end of the Nunivak line in 1998, when they dominated in several of the tows (Fig. 6B). When present, *T. inermis* consisted primarily of juveniles. They occurred in combination with *Neocalanus flemingeri* and *Metridia pacifica*, both common species on the outer shelf and in the oceanic regime during spring. *T. inermis* was a minor component of the euphausiid complement in samples from Cape Newenham and Port Moller. Euphausiid eggs and nauplii were more abundant during spring and summer cruises than during fall cruises (Table 6, ANOVA $p < 0.05$). Euphausiid eggs and nauplii were more

abundant during spring and furciliid stages were more abundant in fall of 1999 than during the two previous years (MANOVA $p < 0.05$).

3.2. Euphausiid and pollock biomass, fall cruises

Pollock dominated in the acoustic data during fall. Pollock from cruises in August–September 1998 and July–August 1999 varied in length from 11 to 70 mm, and wet weight per individual varied from 9 to 2066 mg. Regression analysis produced a good fit for data relating pollock wet weight to the total length of the fish, the swim bladder length, and the swim bladder width (Table 7). The average

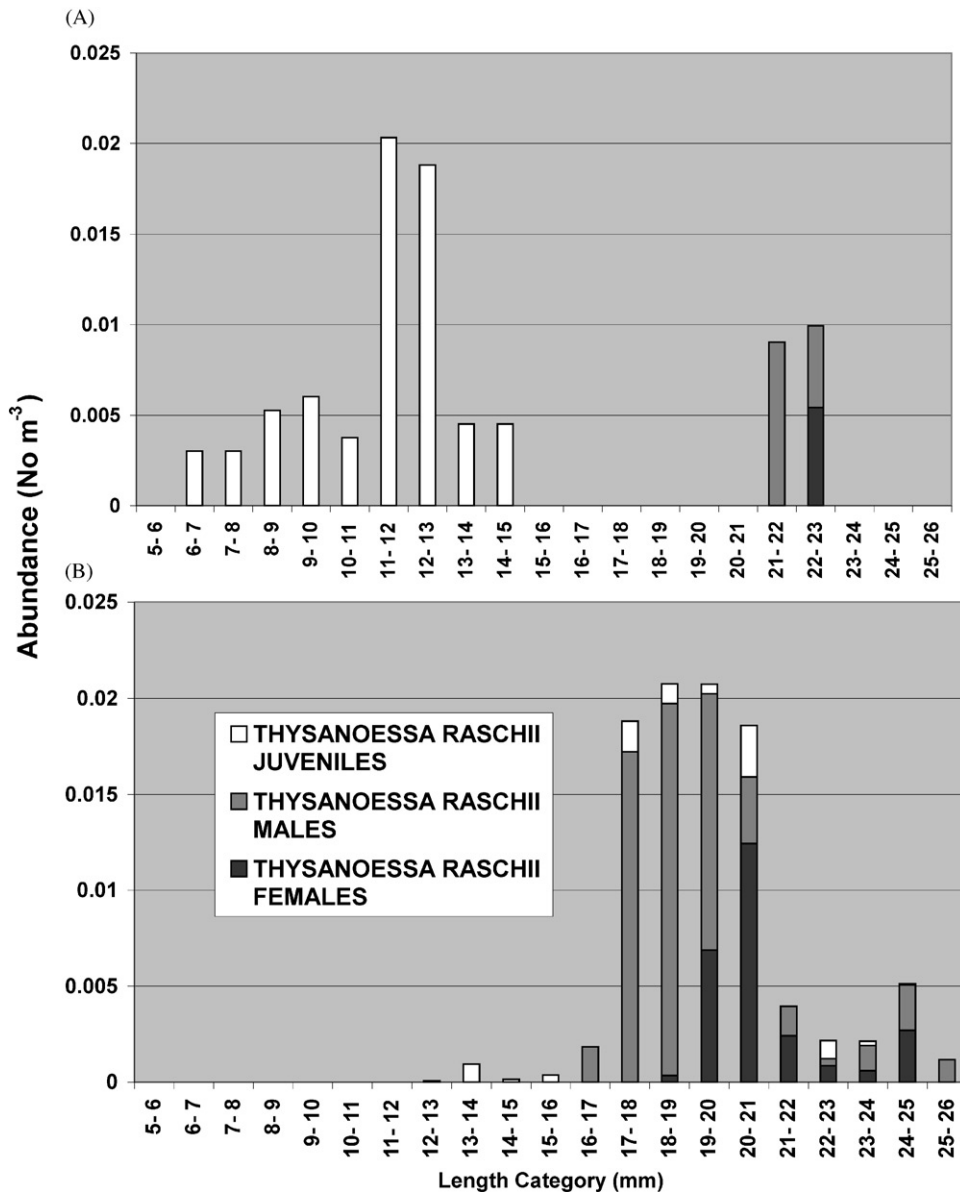


Fig. 5. Length distribution of euphausiids in MOCNESS tows from Cape Newenham in fall 1998 (A) and spring 1997 (B).

total length of pollock from the net catches at Cape Newenham and Nunivak Island in August–September 1998 was 48 and 53 mm, respectively, with mean weight per fish of 591 and 892 mg, respectively. Target strength computed for fish of the above lengths using the prolate spheroid model (Stanton, 1989) was -54.06 and -52.36 dB for

Cape Newenham and Nunivak Island, respectively. The F coefficient for the model was computed using the equation in Stanton et al. (1994b) for animals with gas-filled inclusions. The spherical model (Stanton et al., 1994b) and the empirical model (Foote and Traynor, 1988) produced target strength values at 43 and

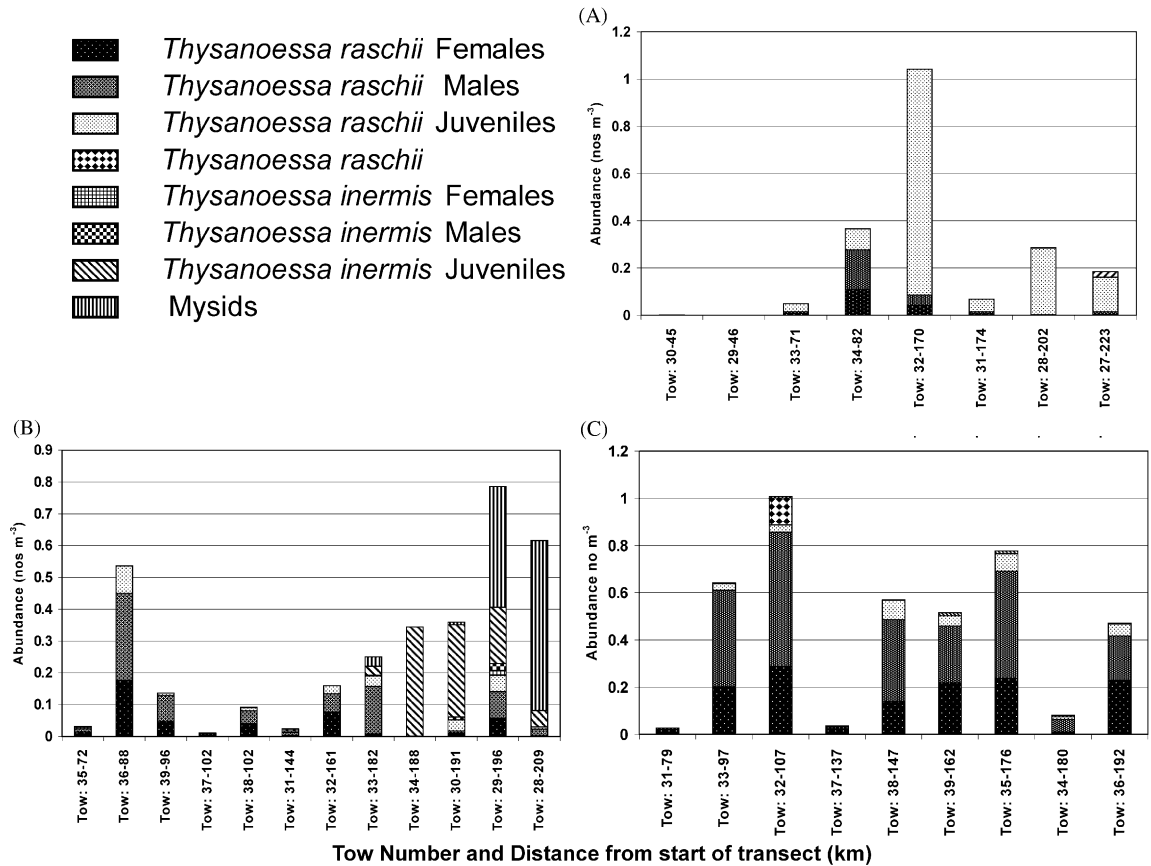


Fig. 6. Abundance of major euphausiid taxa in the Nunivak grid during spring 1997–1999: (A) 1997 (Cruise HX196); (B) 1998 (Cruise HX209); (C) 1999 (Cruise HX220).

Table 6
Abundance (no m⁻³) of euphausiid larvae from CalVET net samples taken in the southeast Bering Sea

Stage	1997		1998		1999	
	Spring–Summer	Fall	Spring–Summer	Fall	Spring–Summer	Fall
Eggs	40	0	74	6	144	0.5
Nauplii	16	0.16	59	5	162	3
Calytopis	2.1	0	2.6	0.5	1.0	0.6
Furcildid	0.20	0	0.008	0.008	0.037	0.9

120 kHz of about 8 dB below and 6 dB above the target strength estimates from the prolate spheroid model. The simple linear relationship between total length and gas bladder length resulted in overestimation of target strength predictions by

the prolate spheroid model relative to the empirical model as total length of the fish increased above about 60 mm. The model results tended to converge above a standard length of about 200 mm if an exponent of 0.88 was added to the

Table 7

Results from regressions on total length (mm)—wet weight (mg), total length—swim bladder length (mm), and swim bladder length—swim bladder width (mm) for pollock of length 11–70 mm from the southeast Bering Sea in August–September 1998 and July–August 1999

Dependent	Independent	Slope	Intercept	r^2
log (length)	log (weight)	0.235	0.777	0.988
Length	Bladder length	0.1975	−0.938	0.914
Bladder length	Bladder width	0.9154	−0.5105	0.889

independent variable of the regression relating swim bladder length to total length (Fig. 7). The prolate spheroid model should not necessarily be extended to fish over 70 mm length and under 200 mm length because empirical data (Traynor, 1996) suggest that they have higher target strengths than the model prediction.

The mean weight of pollock juveniles during July–August 1999 was 96 mg, equivalent to 26 mm length. The target strength for 43 and 120 kHz was estimated at −58.17 and −60.36 dB, respectively when the prolate spheroid model was used. The above target strength estimates were used to compute biomass for transects run at Cape Newenham and Nunivak Island for 1999. Pollock biomass estimates on the Cape Newenham and Nunivak Island C lines exceeded the net estimate of pollock biomass by 2–30 times (Table 8). Assuming that scattering in any records having differences in the S_v at 43 and 120 kHz of less than 8.8 dB were due to fish, as outlined above for earlier cruises, records with euphausiid biomass estimates in excess of 90 g m^{-3} were still observed in the transect data. Records with exaggerated euphausiid biomass estimates had elevated target strength values at 120 kHz, indicating the presence of large fish, with target strengths as high as −32 dB. Therefore, all records with mean target strength estimates over −70 dB and volume scattering over −55 dB at 120 kHz were assumed to be fish and deleted from the euphausiid biomass estimates. The resulting mean euphausiid biomass estimates determined acoustically were lower than net values at Nunivak Island and Cape Newenham in fall 1997 and 1998 (Table 8). The lower acoustic estimates relative to net estimates resulted from the inability of the acoustic data to discriminate euphausiids from fish where their distributions

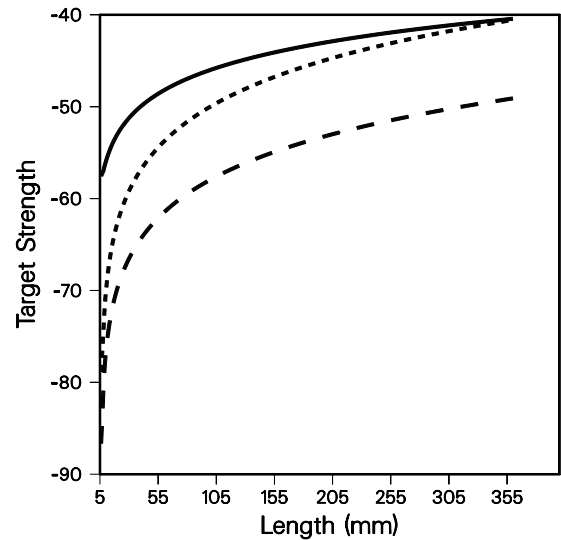


Fig. 7. The target strength of larval and juvenile pollock as computed from the empirical model of Foote and Traynor (1988) (solid line), the high-pass spherical model for gas-filled objects (Stanton et al., 1994a) (dashed line) and the prolate spheroid model for gas-filled objects (Stanton, 1989) (dotted line) plotted against total length (mm).

overlapped. Euphausiid ADB was about three times higher than the net estimate at Cape Newenham and about equal to net estimates at Nunivak Island in summer–fall 1999 (Table 8).

The Inner Front, expressed as a horizontal temperature discontinuity, was observed off Nunivak Island between km 140 and 180 in the August–September data sets for all years (Fig. 8E, F). Most of the ADB from pollock occurred on the outer portion of the line, at or in the thermocline and frontal region (Fig. 8C, D). Acoustically determined biomass from euphausiids was limited primarily to the outer end of the line in 1997, but epibenthic euphausiid aggregates

Table 8

Mean biomass (mg m^{-3}) per transect for euphausiids and pollock as computed using target strength models at 120 kHz for euphausiids and 43 kHz for pollock (ADB) and from MOCNESS net samples (Net) taken during fall 1997 (HX200), 1998 (HX213) and 1999 (HX222)

Transect	Taxa	HX200		HX213		HX222	
		ADB	Net	ADB	Net	ADB	Net
Nunivak C Line	Euph	29	44	40	206	76	77
	Fish	116	3.3	19	3	23	10
Cape Newenham C Line	Euph	—	—	31	66	50	16
	Fish	—	—	121	11	55	8

also were observed in the unstratified regions between km 40 and 80 during 1998 (Fig. 8A, B) and 1999. The Inner Front was also well developed in the Cape Newenham region in August–September 1998 and 1999 (Fig. 9E, F). Detectable thermal stratification was observed clear in to km 80 in 1998. Pollock were observed along the transect clear in to km 80 during 1998, but were confined to the outer half of the transect in 1999 (Fig. 9C, D). Scattering attributed to euphausiids was observed in the upper 20 m along the entire line in August–September 1998 (Fig. 9A), but was confined to the outer end of the line in August 1999, with highest concentrations in an epibenthic layer between km 150 and 200 (Fig. 9B).

The only time during the study that euphausiid populations were clearly associated with the chlorophyll maximum at the front occurred off Cape Newenham during August 1999. The chlorophyll maximum was observed on the stratified side of the front between km 150 and 200 (Fig. 10E, F). *Thysanoessa raschii* also was observed near the chlorophyll maximum between km 150 and 200 (Fig. 10C). *T. inermis* was present but made up less than 10% of the euphausiid biomass. Pollock were observed with both acoustics and net tows from km 120 outward to the end of the line at km 300 (Fig. 10A). Pollock in the daytime acoustic data were at the base of the euphotic zone, in the thermocline or below it (Fig. 9D). The net data indicate that the pollock were migrating into the euphotic zone at night (Fig. 10A). Mysids were confined to the inner most stations, inside km 50 (Fig. 10D).

The acoustic data for fish and euphausiids fit the transitive and exponential geostatistical models

(Table 9). The mean ADB attributed to euphausiids during the summer–fall cruises on the Nunivak Island C line showed an increasing trend between 1997 and 1999 (Table 10). ADB of pollock at Nunivak Island showed the opposite trend, with mean ADB significantly higher in 1997 than in 1998 and 1999. The mean euphausiid ADB at Cape Newenham was not significantly different between 1998 and 1999 (Table 10); however, the mean pollock density was about five times higher in 1998 than in 1999.

4. Discussion

Fronts divide the Bering Sea shelf into distinct regions, the inner, outer and middle domains (Coachman, 1986; Smith and Vidal, 1986; Cooney and Coyle, 1982). The outer domain has an oceanic zooplankton species assemblage, while the middle and inner domains contain more neritic species (Smith and Vidal, 1986; Cooney and Coyle, 1982). The distribution of euphausiid species across the shelf also is associated with the domains. *Thysanoessa inermis* tends to dominate on the outer shelf, while *T. raschii* is more dominant in the middle and inner domains (Smith, 1991). As expected from the above distribution pattern, euphausiids on the inner shelf consisted almost entirely of *T. raschii* during the warm-calm summer of 1997. However, *T. inermis* was a major constituent of the euphausiid community on the stratified side of the Inner Front near Nunivak Island during the stormier summer of 1998. Substantial numbers of the oceanic copepod species *Neocalanus flemingeri*

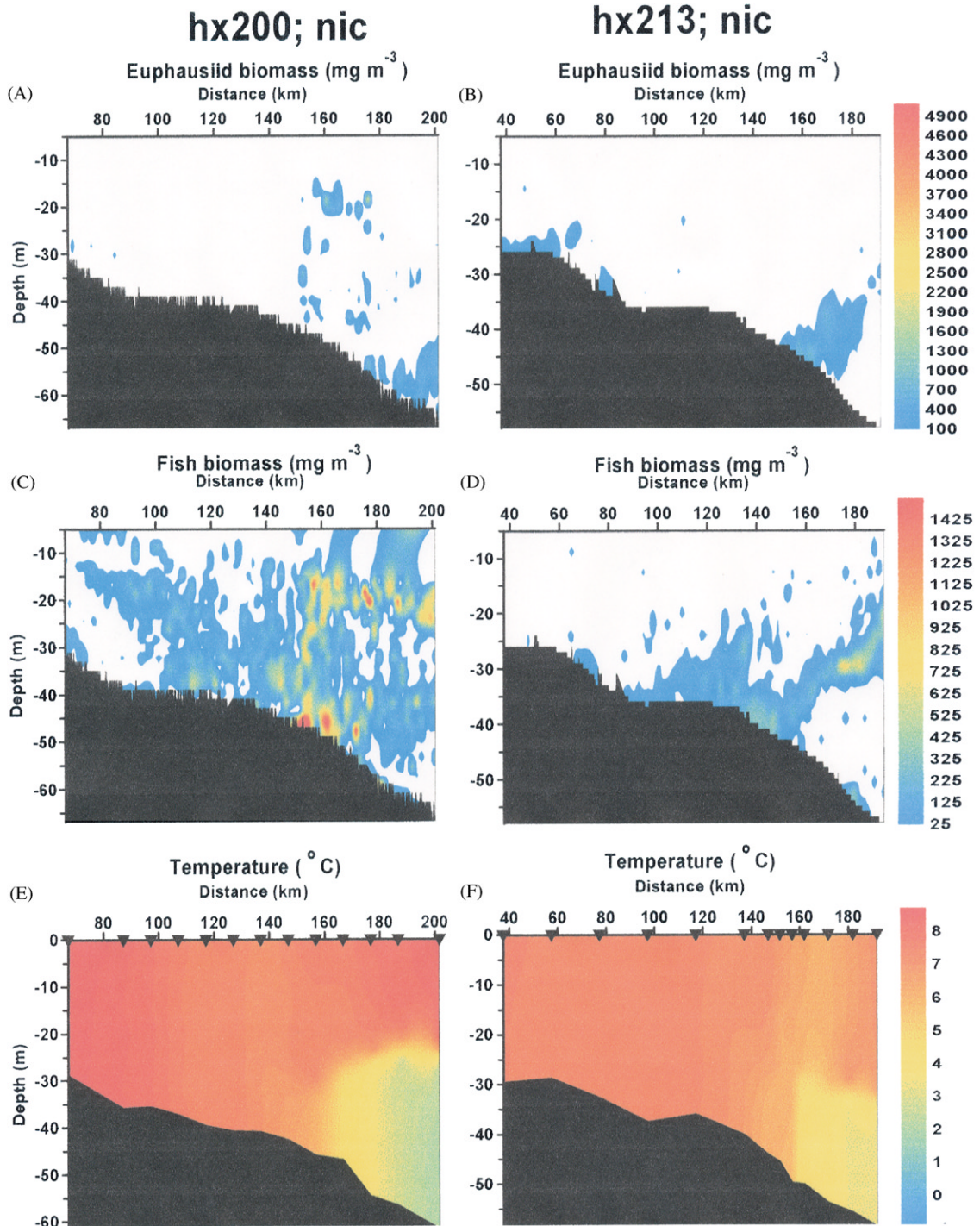


Fig. 8. Acoustically determined biomass (mg m^{-3}) and temperature profiles along the Nunivak Island C line during August–September 1997 (HX200) and 1998 (HX213). Euphausiid biomass (A, B), biomass of zero-age pollock (C, D), temperature profiles (E, F).

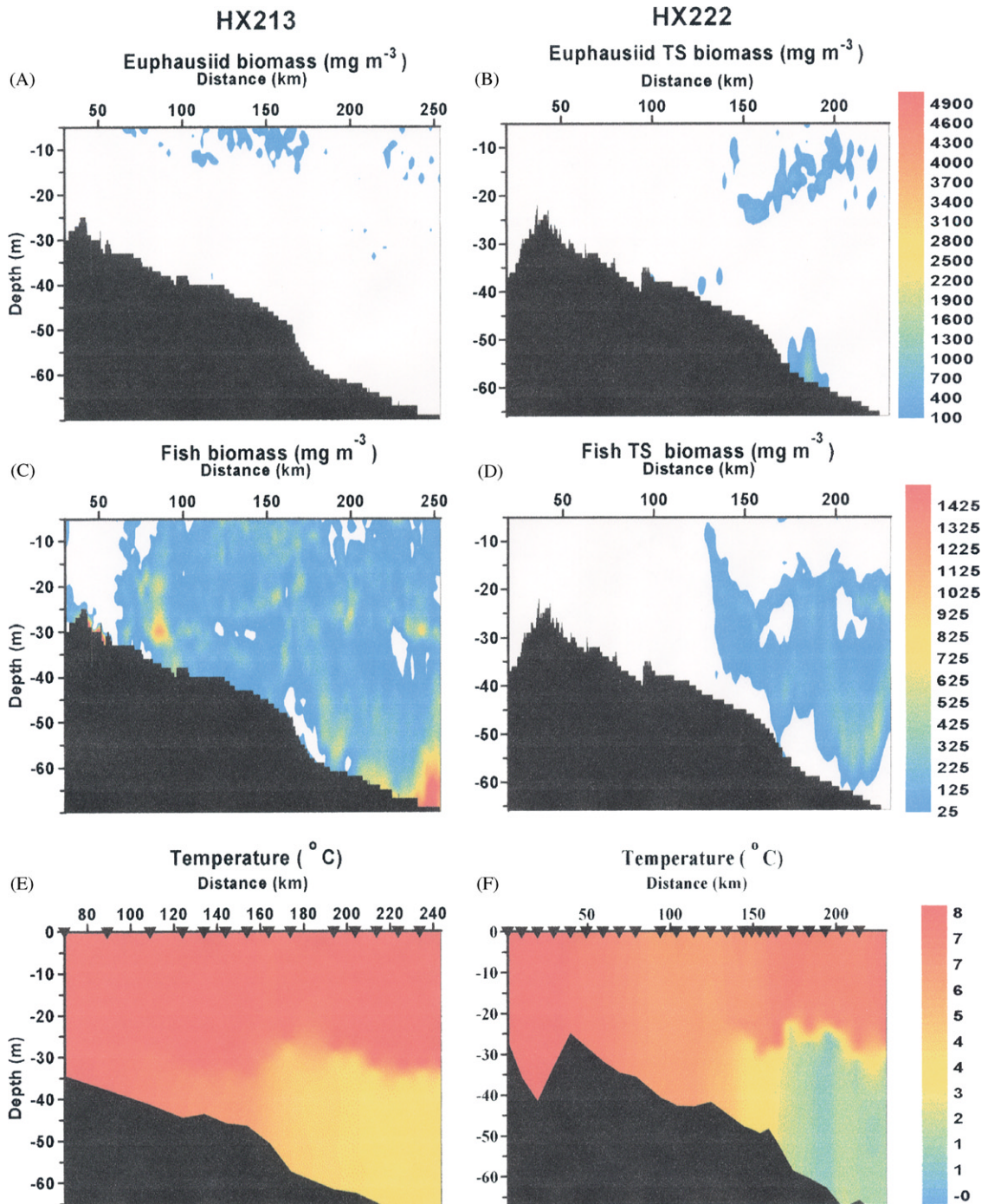


Fig. 9. Acoustically determined biomass (mg m^{-3}) and temperature profiles along the Cape Newenham C line during August–September 1998 (HX213) and July–August 1999 (HX222). Euphausiid biomass (A, B), biomass of zero-age pollock (C, D), temperature profiles (E, F).

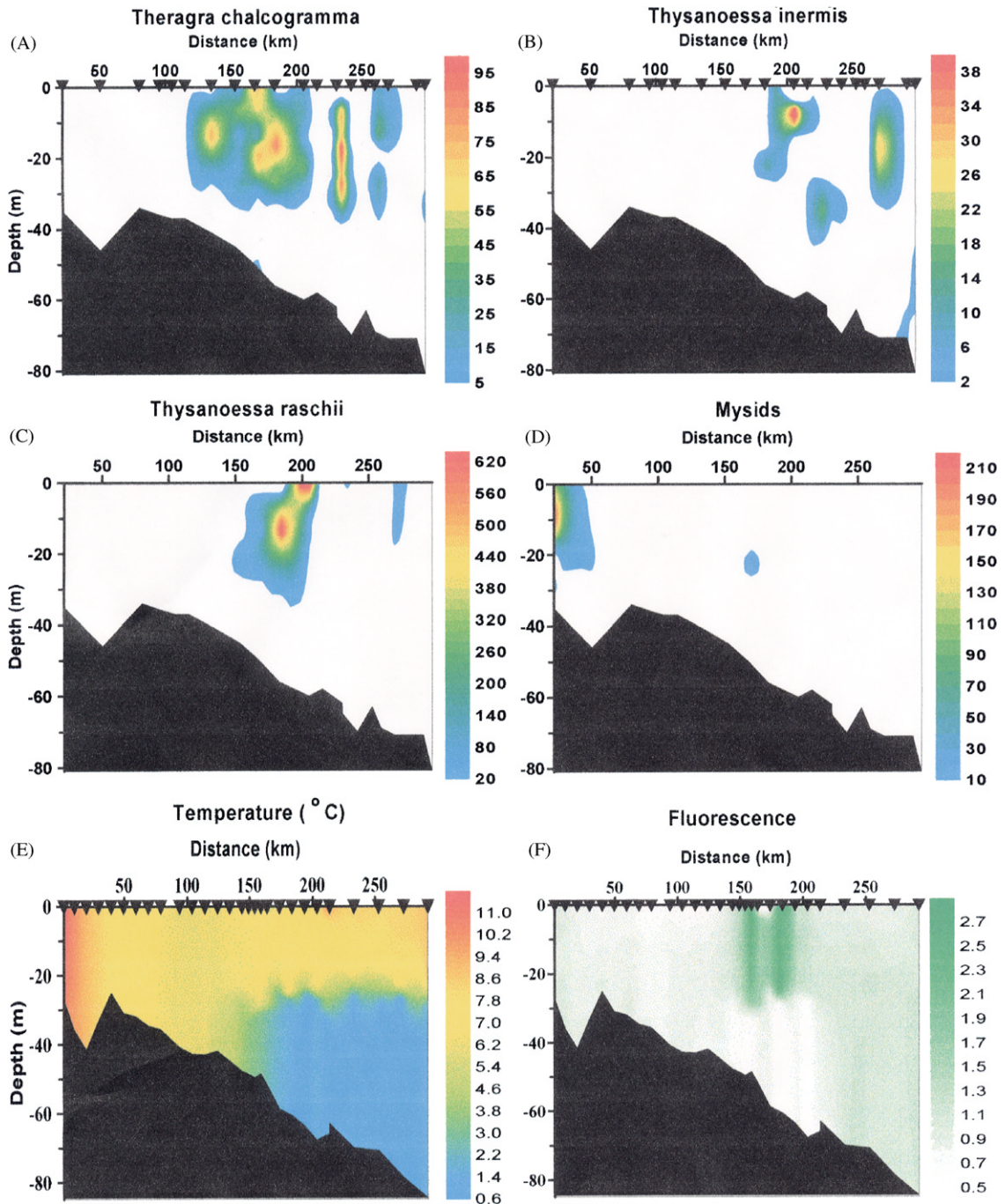


Fig. 10. Distribution of temperature and fluorescence (volts) from CTD casts, and micronekton biomass (mg m⁻³) from MOCNESS tows taken along the Cape Newenham C line during August–September 1999. Pollock (A), *Thysanoessa inermis* (B), *Thysanoessa raschii* (C), Mysids (D), temperature (E) fluorescence (F). Triangles above plots indicate the locations of MOCNESS tows and CTD stations.

Table 9

Statistical results comparing acoustically determined euphausiid (Eups) and fish biomass during summer–fall cruises on the Cape Newenham (Cpnhm) and Nunivak Island C lines

Transect	Aug–Sept 1997 (HX200)			Aug–Sept 1998 (HX213)			July–Aug 1999 (HX222)		
	Nugget	Range	Model	Nugget	Range	Model	Nugget	Range	Model
Nunivak Eups	0.745	51	Tran 0.951	0.359	25	Tran 0.996	0.883	87	Exp 0.875
Nunivak Fish	0.521	57	Exp 0.981	0.066	35	Tran 0.991	0.235	68	Tran 0.901
Cpnhm Eups	—	—	—	0.851	30.5	Tran 0.985	0.686	58.7	Exp 0.991
Cpnhm Fish	—	—	—	0.382	88	Exp 0.901	0.010	81	Tran 0.956

Nugget = nugget effect (fraction of variance); Range = range of influence (km); Models: Exp = exponential, Tran = transitive, number next to the model is the r^2 value for the data fit to the model

Table 10

Statistical results comparing acoustically determined euphausiid (Eups) and fish biomass during spring cruises at the Cape Newenham (CN) and Nunivak Island (NI) sampling grids

Location		Aug–Sept 1997 (HX200)			Aug–Sept 1998 (HX213)		Aug–Sept 1999 (HX222)	
Transect name	Taxa	Range (km)	Mean (g m^{-2})	Upper and lower CI	Mean (g m^{-2})	Upper and lower CI	Mean (g m^{-2})	Upper and lower CI
NIC	Eups	75–200	0.512	0.417–0.606	0.763	0.548–0.979	2.037	1.704–2.370
NIC	Fish	75–200	2.142	1.88–2.40	0.379	0.320–0.436	0.440	0.327–0.552
CNC	Eups	70–170	—	—	1.757	1.651–1.863	1.455	1.056–1.854
CNC	Fish	70–170	—	—	5.146	4.970–5.322	1.140	0.816–1.464

Ordinary Kriging with no rotation, orientation 0, search radius 4, models were the spherical, transitive or exponential, whichever gave the best fit. CI refers to the 95% confidence intervals.

and *Metridia pacifica* also were observed along with the *T. inermis*.

The occurrence of shelf-break species at the 50-m depth contour off Nunivak Island in 1998 implies cross shelf movement of the shelf-break water mass shoreward to the Inner Front. Shoreward movement of the shelf-break water mass is a common occurrence along the shelf, especially near the Pribilof Islands, but the exact mechanism generating on-shore flow is not understood (Stabeno et al., 1999). Cross-shelf advection of nutrient-rich water from the shelf break to the Inner Front may be a critical component to the frontal circulation patterns generating prolonged primary production at the Inner Front following the spring bloom (Kachel et al., 2002). Elevated euphausiid densities associated with the chlorophyll maximum at the Inner Front were observed once during this study, at Cape Newenham in July–August 1999. The absence of euphausiid patches at the chlorophyll maximum during other

cruises may have been related to the timing of the cruises. During spring of 1998 and 1999, the seasonal development of frontal structure at the Inner Front was just beginning (Kachel et al., 2002). Intense stratification across the shelf and nutrient depletion from the bottom water limited production at the Inner Front during 1997 (Stockwell et al., 2001; Kachel et al., 2002). Thus, while frontal conditions can produce elevated production and euphausiid densities at the Inner Front, such conditions are not necessarily the norm. Both epibenthic and water-column euphausiid aggregates were commonly observed outside the frontal regions in both the inner and middle domains.

Euphausiid abundance is difficult to assess because they avoid plankton gear, particularly during the day (Smith, 1991; Cochrane et al., 1991; Sugisaki et al., 1998). Comparison of net-caught abundance estimates with concurrently collected acoustic data indicate that the MOCNESS is

probably catching about 30% of the euphausiids, even during the night (Coyle, 2000). The above observation accounts for the consistently higher euphausiid abundance estimates obtained by the acoustic measurements relative to the net samples during the spring cruises. During the late summer–fall sampling period, zero-class pollock dominated the acoustic record over much of the study area. The target strength of pollock is so much higher than that of euphausiids, that, when present in substantial numbers, they completely mask the euphausiid acoustic signal. Therefore, when the distribution of euphausiids and pollock overlapped, the euphausiids were not detected, causing an overall underestimation of euphausiid densities in the acoustic record during the fall cruises. The euphausiid biomass estimates for the fall are therefore minimal values.

The mean euphausiid biomass and confidence intervals reported here and from the PROBES study (Stockwell et al., 2001) fall within the range of values reported for the southeast Bering Sea shelf in summer of 1969 (Fukuchi, 1977) and July 1995 and 1996 (Sugisaki et al., 1998). We therefore conclude that there is no evidence of significant changes in euphausiid densities related to the anomalous weather conditions of 1997 and 1998. Examination of other zooplankton data sets also failed to reveal any significant differences in the biomass of major zooplankton species in the southeast Bering Sea during 1997 and 1998 relative to earlier studies (Napp et al., 2002). While patches with euphausiid biomass of more than 5 g m^{-3} (equivalent to about 125 individuals m^{-3}) were commonly observed, euphausiids are thought to form patches of 3000–10,000 individual m^{-3} with the smallest (less than 3 m diameter) densest patches having numbers as high as 3.0×10^5 to 5.0×10^5 individuals m^{-3} (Dolphin, 1987). Since the acoustic data integrated about 45 m of water, some of the patches in this study may have had densities on the order of thousands m^{-3} .

Previous data on shearwater diets indicated that they consume primarily *Thysanoessa raschii* on the inner shelf of the southeast Bering Sea (Ogi et al., 1980). The most obvious explanation for the observed starvation of the shearwaters in 1997 would be a marked decline in euphausiid densities

on the inner shelf. Detailed surveys to assess euphausiid densities in the southeast Bering Sea have not been done before. Nevertheless, they are common constituents of the plankton in the southeast Bering Sea (Vidal and Smith, 1986; Smith, 1991; Cooney, 1981). Smith (1991) reported average densities of adult *Thysanoessa raschii* in 1980 of 131 and 88 adults m^{-2} . These values are one to two orders of magnitude above the densities measured in this study. However, closer inspection of the original data revealed that the high average values in 1980 were due primarily to samples taken in March and April (Stockwell et al., 2001). By May and June of 1980 and 1981, euphausiid densities measured on the inner shelf off Cape Newenham were not different from values we measured in 1997–1999. Smith (1991) observed a trend toward increasing euphausiid densities in July 1981. While we collected very few samples in July, samples from August and September did not reveal elevated euphausiid abundances relative to spring abundance estimates on the inner shelf. Note however, that *T. inermis* juveniles were significantly more abundant near the shelf break in the fall than in the spring in 1997 (Stockwell et al., 2001).

Euphausiid are well known to be diurnal vertical migrators, rising into the euphotic zone at night and descending out of the euphotic zone during the day. Therefore, the observation of shearwaters feeding on surface swarms of euphausiids during the day is not necessarily expected. Previous data on *Thysanoessa* species suggest that they form aggregates near the surface when spawning (Hanamura et al., 1989; Smith and Adams, 1988). Although we observed adult *T. raschii* on the inner shelf throughout the summer, most of the spawning in the southeast Bering Sea apparently occurs in May and early June (Smith, 1991). The elevated abundances of larval stages observed during this study in May–June of 1997–1999 conform to the early spring spawning pattern. Eggs and nauplii were present during late summer–fall 1997–1999, but their abundance was very low. The significantly higher densities of eggs and larvae in the water during the cold year (1999) may indicate prolonged spawning relative to warmer years. The elevated larval abundance in 1999 also may

have been due to the earlier timing of the 1999 cruise relative to the 1997 and 1998 cruises (late July–early August as opposed to late August–early September, respectively). Although warm and cold years were observed during 1980 and 1981, differences in the abundance of larvae on the inner shelf were not observed (Smith, 1991).

The general distribution of euphausiids over the shelf suggests an overall low abundance with isolated regions of very high density. The shearwater foraging behavior is apparently adapted to exploit prey distributed in isolated patches (Lovvorn et al., 2001). They forage by flying great distances within a few meters of the sea surface, and when prey swarms are detected they either dive directly from the air into the water or land on the water and then dive for the prey (Ogi et al., 1980; Hunt et al., 1996). Energetic models indicate that the shearwaters were preying on small dense euphausiid swarms by filter feeding (Lovvorn et al., 2001). The birds must encounter a minimum number of swarms within their foraging range to survive, probably at least several per day (Lovvorn et al., 2001). Given that euphausiid densities were not significantly different between years, the most obvious difference in 1997 relative to earlier years is the appearance of the coccolithophorid bloom (Sukhanova and Flint, 1998; Vance et al., 1998; Stockwell et al., 2001). One possible explanation for the mass starvation is that the coccolithophorids clouded the water, thus interfering with the ability of shearwaters to locate euphausiid aggregates over a large portion of their foraging range in the southeast Bering Sea (Lovvorn et al., 2001). In addition, the unusually warm conditions in the surface in 1997 may have inhibited euphausiids from producing breeding swarms in surface waters, or may have advanced their breeding cycle to earlier in the year (Stockwell et al., 2000). In the absence of prey in the surface waters, birds habituated to foraging on euphausiids in the region apparently starved, while those able to shift to more available prey survived. Examination of the diet of shearwaters between 1997 and 1999 indicated a substantial shift from a diet dominated by euphausiids to a dominance of sandlance or zero-age pollock in the diets (Hunt et al., 2002). The occasional massive die-offs of shearwaters

suggest that they have rather strict foraging requirements that can sometimes be disrupted by environmental perturbations such as the coccolithophorid bloom (Oka and Maruyama, 1986; Oka et al., 1987; Lovvorn et al., 2001).

The presence of pollock eggs and larvae along the north shore of the Alaska Peninsula is apparently fairly common (Bailey et al., 1999). Prevailing currents are northward, along the eastern shore of Bristol Bay (Napp et al., 2000). The eggs and larvae from the Alaska Peninsula region are apparently transported northward by the current and by August–September the zero-class juveniles are observed off Cape Newenham and Nunivak Island (Bailey et al., 1999; this study). The acoustic and net records from the Inner Front area indicated that the zero-class pollock were undergoing diurnal vertical migrations. Apparently, the older zero-class pollock are observed to undergo migrations through the pycnocline (Schabetsberger et al., 2000). Juvenile pollock in the St. Paul Island region in the fall of 1994 and 1995 ranged in densities from 13 to 202 individuals 1000 m^{-3} as assessed by an anchovy trawl (Brodeur et al., 1997). The average density of juvenile pollock during 1994 through 1997 was 4 to 132 1000 m^{-3} (Brodeur et al., 2002). The mean transect ADB for fish reported here for the fall cruises ranged from 23 to 116 mg m^{-3} (Table 8). Given a mean fish wet weight of roughly $900\text{ mg individual}^{-1}$ from the MOCNESS tows in 1997 and 1998, the above biomass estimates are equivalent to 25–129 fish 1000 m^{-3} , completely within the range of values recorded for the frontal region near St. Paul Island during the same season in 1994–1997. The lower overall average biomass of Pollock in MOCNESS net samples relative to acoustic estimates is expected, since the MOCNESS is a plankton sampler that fish generally avoid. Consistent interannual trends in pollock biomass were not observed. Declines in pollock abundance after 1997 at Nunivak Island were followed by substantially higher biomass estimates at Cape Newenham in 1998.

Given the climate anomalies in the southeastern Bering Sea during 1997 and 1998, it is tempting to assume that the shearwater die off was the result of climate related impacts on the zooplankton

community itself. Nevertheless, close scrutiny of the available data do not support such a contention. We found no evidence of consistent differences in the biomass of euphausiids (this paper) and other major zooplankton species (Napp et al., 2002) during 1997 and 1998 relative to earlier estimates. While there is evidence of higher calanoid biomass in 1994–1998 relative to earlier periods, the differences were not necessarily related to the 1997–1998 climate anomalies (Napp et al., 2002; Stockwell et al., 2001). Nevertheless, marked interannual differences in zooplankton biomass were observed on the inner shelf of the southeastern Bering Sea during June of 1997–1999. These biomass differences will be addressed in a subsequent paper.

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