



Climate-related variability in abundance and reproduction of euphausiids in the northern Gulf of Alaska in 1998–2003 [☆]

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ARTICLE INFO

Available online 1 April 2008

Keywords:

Interannual variability
Climatic changes
Life history
Pelagic environment
Population density
Euphausiids
North Pacific
Gulf of Alaska

ABSTRACT

Interannual variability in abundance of the dominant euphausiids *Thysanoessa inermis*, *Thysanoessa spinifera* and *Euphausia pacifica* was studied in the northern Gulf of Alaska during the production season from 1998 to 2003. *T. inermis* abundance increased significantly over the shelf from 1998 to 2002, the abundance of *T. spinifera* (which also inhabits the shelf) did not change, while the abundance of *E. pacifica* (usually common on the outer shelf) declined in 2001. Based on the incidence of spermatophores on the females, reproduction of *T. inermis* occurred during April in all years, and was extended through May in 2000–2002. The major spawning of *T. spinifera* and *E. pacifica* occurred from April through July, and from late May through August, respectively. The spawning of *T. inermis* and *T. spinifera* appeared to be closely related to the spring diatom bloom on the inner shelf, while the spawning of *E. pacifica* occurred later in season, when the temperature of the mixed layer increased. A strong increase in abundance of *T. inermis*, associated with the extended colder phase in the North Pacific, indicates that progressive cooling in 1999–2002 may have resulted in greater reproductive success of the early spawning *T. inermis* on the inner shelf.

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1. Introduction

The Gulf of Alaska (GOA) continental shelf supports a rich and diverse marine ecosystem which includes the most important commercial fisheries in the United States EEZ such as crustacean, salmon, pollock, halibut and sablefish (Weingartner et al., 2002) in addition to seabird and marine mammal populations. There is substantial variability on both interannual and longer time scales in harvest and recruitment success to major GOA fisheries including shrimp (*Pandalus* spp.) (e.g. Albers and Anderson, 1985), king crab (*Paralithodes* spp.) (Blau, 1986), walleye pollock (*Theragra chalcogramma*) (Hollowed et al., 1994), Pacific cod (*Gadus macrocephalus*) (Thompson and Zenger, 1994) and salmon (*Oncorhynchus* spp.) (e.g. Mantua et al., 1997), which appears to be related to North Pacific basin-scale climate changes (Francis and Hare, 1994; Trenberth and Hurrell, 1994; Anderson and Piatt, 1999). Climate perturbations could affect this variability in several ways. For example, climate-induced changes in the timing and magnitude of the spring phytoplankton bloom would likely propagate through the food web, influencing the composition, abundance and condi-

tion of zooplankton, with consequences for feeding success, growth and survival of planktivorous fish and their predators.

Euphausiids are a major prey for many of the commercially harvested fishes in the GOA, including all species of salmon (e.g. Armstrong et al., 2005); pollock (Brodeur, 1998); herring (Hart, 1973) and sablefish (Sigler et al., 2001) as well as seabirds and baleen whales (Mauchline, 1980). They feed on a variety of phyto- and microzooplankton, as well as suspended organic matter including “marine snow”, consequently serving as an important link between primary producers and top predators in the GOA shelf ecosystem (Ponomareva, 1966; Dilling et al., 1998; Bargu et al., 2003; Nakagawa et al., 2001, 2004). In addition, they undergo extensive diel migrations thus contributing to the vertical carbon flux. Therefore, a more comprehensive knowledge of the mechanisms affecting euphausiid population dynamics is important for understanding the GOA ecosystem.

The shelf in the study area, offshore the central GOA coast, is about 200 km wide and bottom depths exceed 150 m across the whole shelf. The bottom topography includes submarine canyons, ridges and the offshore extension of fjords. GOA shelf waters are characterized by two major currents, the Alaskan Stream, which flows westward at or near the shelf break, and the Alaska Coastal Current (ACC), a buoyancy driven current flowing westward within 20–50 km of the shore (Royer, 1998; Weingartner et al., 2005). These currents may interact with the complex coast and bathymetry to generate eddies and meanders, which may enhance

[☆] This paper was presented at the PICES/GLOBEC Symposium on “Climate Variability and Ecosystem Impacts on the North Pacific: A Basin-scale Synthesis” held during April 19–21, 2006, in Honolulu, USA.

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cross-shelf transport of water masses, influencing the species composition and distribution of euphausiids along the shelf.

The euphausiid fauna of the northern GOA comprises seven species of which three predominate: *Thysanoessa inermis*, *Thysanoessa spinifera* and *Euphausia pacifica* (Coyle and Pinchuk, 2003). Population surveys during 1998–2001 indicated that the species prefer different environments, with *T. inermis* and *T. spinifera* occurring primarily over the shelf up to the shelf break, and *E. pacifica* most common near and beyond the shelf break, but also occurring on the innermost shelf in the end of summer (Coyle and Pinchuk, 2005). Here we undertake a more detailed analysis, over a longer time period, with the objective of relating krill spatial and temporal variability to climate fluctuations that may impact krill life histories. We describe the cross-shelf distribution and interannual differences in abundance and timing and magnitude of spawning of the major euphausiid species in relation to temperature and chlorophyll-*a* distribution during the production season in the northern Gulf of Alaska from 1998 to 2003.

2. Methods

Zooplankton samples, conductivity–temperature–depth (CTD) and fluorescence profiles were taken on main stations along the Seward Line in the northern GOA during US GLOBEC LTOP cruises from 1998 to 2003 (Fig. 1, Table 1). CTD profiles were taken both on main and intermediate stations with a Seabird model 911 Plus with dual conductivity and temperature sensors. Water samples for fluorometric estimation of chlorophyll-*a* concentrations were collected on all stations with Niskin bottles and the chlorophyll concentration was averaged over the upper 50 m of the water column (D.A. Stockwell and T.E. Whitledge, unpublished data). Euphausiids were collected using a 1-m² MOCNESS fitted with 500 μ m mesh black nets and equipped with a flowmeter, conductivity and temperature probes. The net was fished at night and five oblique samples were collected in 20 m increments from 100 m depth to the surface. Typically 150–200 m³ of water were fished in each layer. The samples were preserved in a 10% formalin seawater solution for later analysis.

Sub-samples taken using a Folsom splitter were examined to identify and enumerate euphausiids by species and stage as follows: adult males were individuals with fully developed petasmae; adult females were individuals with spermatophores attached to fully developed thelycum, indicating mating since her last molt (Mauchline, 1980); and juveniles were individuals with all luminescent organs, five pairs of setose pleopods, spines on telson equivalent in numbers to adults, but with reproductive organs and characteristics not fully developed. The proportion of the total sample in the sub-sample varied according to the abundance of zooplankton.

The data were uploaded to a Microsoft Access database, and analysis was performed using STATISTICA 6 software. Physical properties influencing euphausiid distribution were analyzed in the upper 100 m as follows. The depths of the thermocline and pycnocline were computed for each station by locating the depth where dT/dZ or $d\sigma_t/dZ$ were maximum (T = temperature, °C; σ_t = sigma-t; Z = depth, m). The mean water-column temperature above and below the thermocline, and the mean salinity above and below the pycnocline were then computed. In addition, the stratification parameter expressed as the energy required to redistribute the water-column mass by complete vertical mixing ($J m^{-3}$) was computed (Fiedler et al., 1998; Simpson et al., 1977). The magnitude of seasonal dense ($\sigma_t > 26$) water renewal on the inner shelf was estimated from cross-shelf vertical profiles (surface to 300 m or bottom depth) for each cruise as an area under the 26 isopycnal between 0 km and 90 km from the coast. Krill analysis included a

total of 2826 MOCNESS samples. MOCNESS samples from the same tow are autocorrelated and cannot be treated as independent when running statistical analyses. Therefore an integrated estimate of abundance or biomass for each station was computed as follows. The abundance and biomass of each taxon was computed for each net as numbers m⁻³ or g m⁻³. The data were integrated through the depth interval for each net to estimate abundance or biomass m⁻² for each net sample. The values m⁻² were summed to estimate values per m⁻² for the whole water column sampled by the tow. If net depths overlapped, the mean of the overlapping portion for each net was computed for each depth interval before summing. Since nets were fished in an oblique manner from 100 m to the surface, little overlap was observed. The value m⁻³ for each station was determined by dividing the numbers m⁻² by the total depth interval (m) sampled by the tow.

Due to uneven spatial distribution of euphausiids, the abundance data were log-transformed to stabilize the variance. If the data failed normality assumption, the abundance was reported as median rather than mean for each species to describe central tendency. Identical approach was used to analyze environmental data. Analysis of variance (ANOVA) was used to test for significant effects of location, season and year on physical and biological variables, and the distribution of residuals was analyzed. When the residuals satisfied the normality assumption (in practice always after log-transformation of the raw data) and ANOVA results indicated significant effects, Tukey post-hoc test was applied to identify significant differences ($p < 0.05$). If the residuals distribution failed to meet the normality assumption, non-parametric Mann-Whitney or Kruskal-Wallis tests were used on non-transformed data.

3. Results

3.1. Physical/biological oceanographic conditions

The mean temperature was ~ 5 °C throughout the water column from March through May (Fig. 2A). The upper layer (0–25 m) warmed to ~ 12 °C in July–August, then decreased to ~ 10 °C by October, while the layer below the thermocline remained cool (between 5 and 7 °C) throughout the year. The mean water column salinity remained between 32.0 and 32.5 psu from March through May (Fig. 2B). The upper layer salinity decreased to 31.2 psu by August as a result of freshwater runoff. The temperature and salinity changes resulted in strong stratification of the water column by July (Fig. 2C). The mean water column chlorophyll-*a* content was lowest (< 0.5 mg m⁻³) in March gradually increasing through April with maximum (~ 2 mg m⁻³) in May, indicating the development of the spring phytoplankton bloom (Fig. 2C). As stratification increased, chlorophyll-*a* content decreased to ~ 0.7 mg m⁻³ in July (Fig. 2C), and in December it was < 0.5 mg m⁻³. Based on the seasonal temperature, salinity and stratification parameter curves we define time period from March through May as spring, and that from July through October as summer/fall.

The cross-shelf salinity gradient, which results from interactions of the less saline ACC and the oceanic Alaska Current, was strongest in spring and early summer, and it was often observable as a shelf-break salinity front located ~ 120 km offshore (Fig. 3A). As the ACC and its associated frontal zone expanded and mixed across the shelf during summer, the shelf-break front became undetectable (Fig. 3B). Another seasonal feature was the annual summertime renewal of dense ($\sigma_t > 26$), saline water on the inner shelf less than 100 km offshore (Fig. 4), which was significantly greater in summer than in spring (Tukey test, $p = 0.0001$). Based on these differences we divide the study area into shelf (stations GAK1–GAK7) and shelf-break/slope (stations GAK8–GAK13) regions.

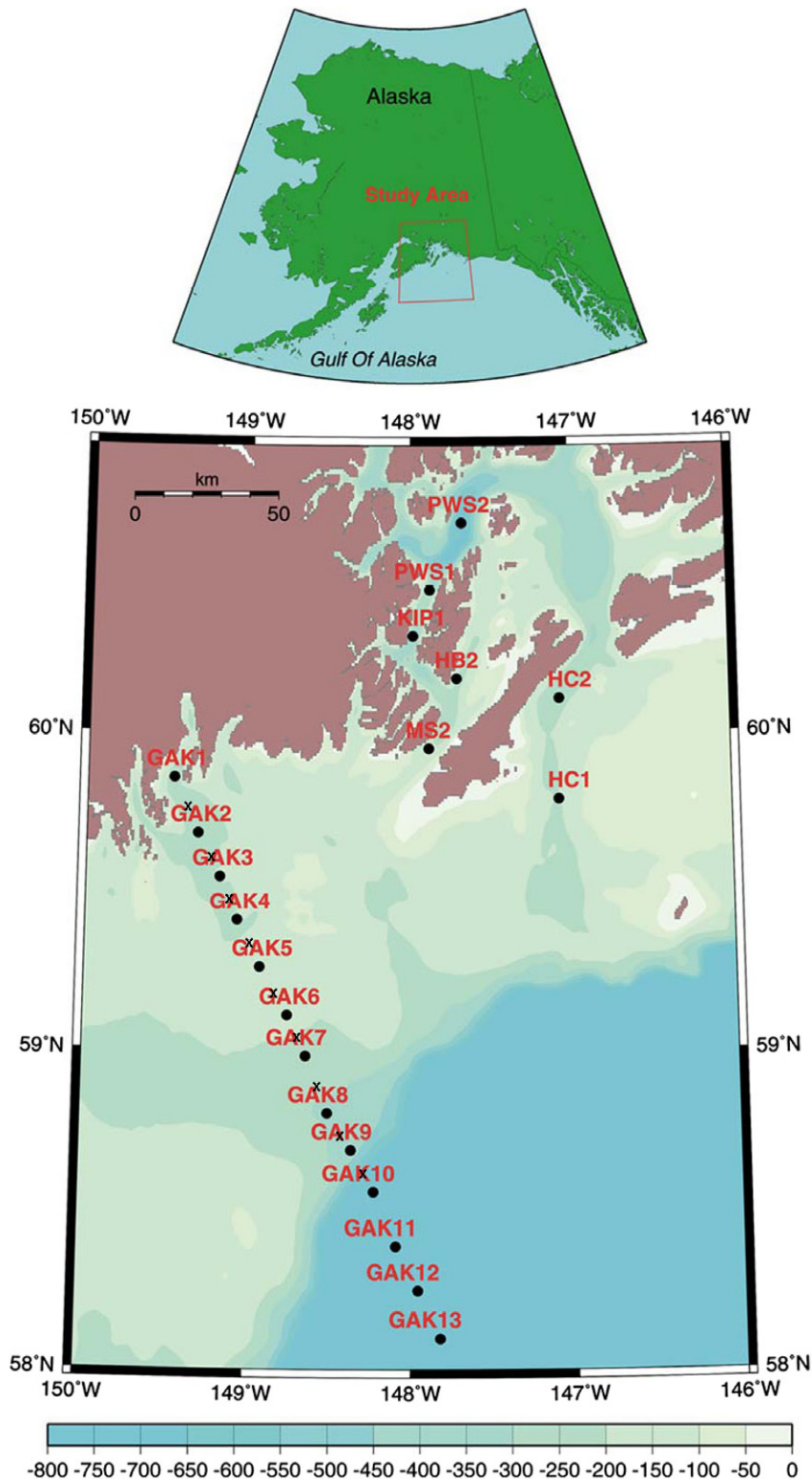


Fig. 1. Map of sampling locations in the northern Gulf of Alaska (● – main stations (GAK), x – intermediate stations).

The average temperature of the upper 100 m in spring was significantly warmer ($>6\text{ }^{\circ}\text{C}$) in 1998 and 2003 than in 1999–2002 (Tukey test, $p < 0.05$), both on the shelf and beyond the shelf-break, with the coldest temperatures ($<5\text{ }^{\circ}\text{C}$) observed on the shelf in 1999 and 2002. The trend was consistent with interannual changes in Pacific Decadal Oscillation (PDO) index (Fig. 5A, upper panel). In contrast, the mean summer/fall temperature showed little interan-

nual variability over the study area and remained around $9\text{ }^{\circ}\text{C}$ (Fig. 5B). The mean salinity during spring was significantly less on shelf in 1998 and 2003 than in any other year (Tukey test, $p < 0.05$), and the same trend was observed in summer/fall with exception of 1999, which did not differ from 1998 or 2003 (Fig. 6). Similarly, the salinity beyond the shelf-break was different in 1998 and 2003 from that in 1999–2002 (Tukey test, $p < 0.05$),

Table 1
Summary of GLOBEC LTOP cruises in the northern Gulf of Alaska

Year	Month					
	March	April	May	July	August	October
1998	×	×	×	×		×
1999	×	×	×		×	×
2000	×	×	×		×	×
2001	×	×	×	×	×	×
2002	×	×	×	×	×	×
2003	×	×	×	×	×	×

but there were no significant differences in summer/fall. There was no clear pattern in interannual changes of stratification parameter

values for each region in any season, which indicates the importance of other environmental factors contribution (e.g. winds). Our dataset was too small to test for interannual differences in the amount of dense water inflow on the shelf in spring ($n = 3$ for each year). However, it is worth noting that the dense water was absent from the inner shelf in all spring months of 1998 and 2003, while, in the other years, it was observed as early as in April (Fig. 4).

During the warm springs the chlorophyll-*a* concentrations in the upper 50 m were slightly higher in March and substantially lower in May compared to the cold years, indicating earlier and weaker spring blooms in 1998 and 2003 (Table 2). The highest median chlorophyll-*a* concentrations (1.336 mg m^{-3}) were

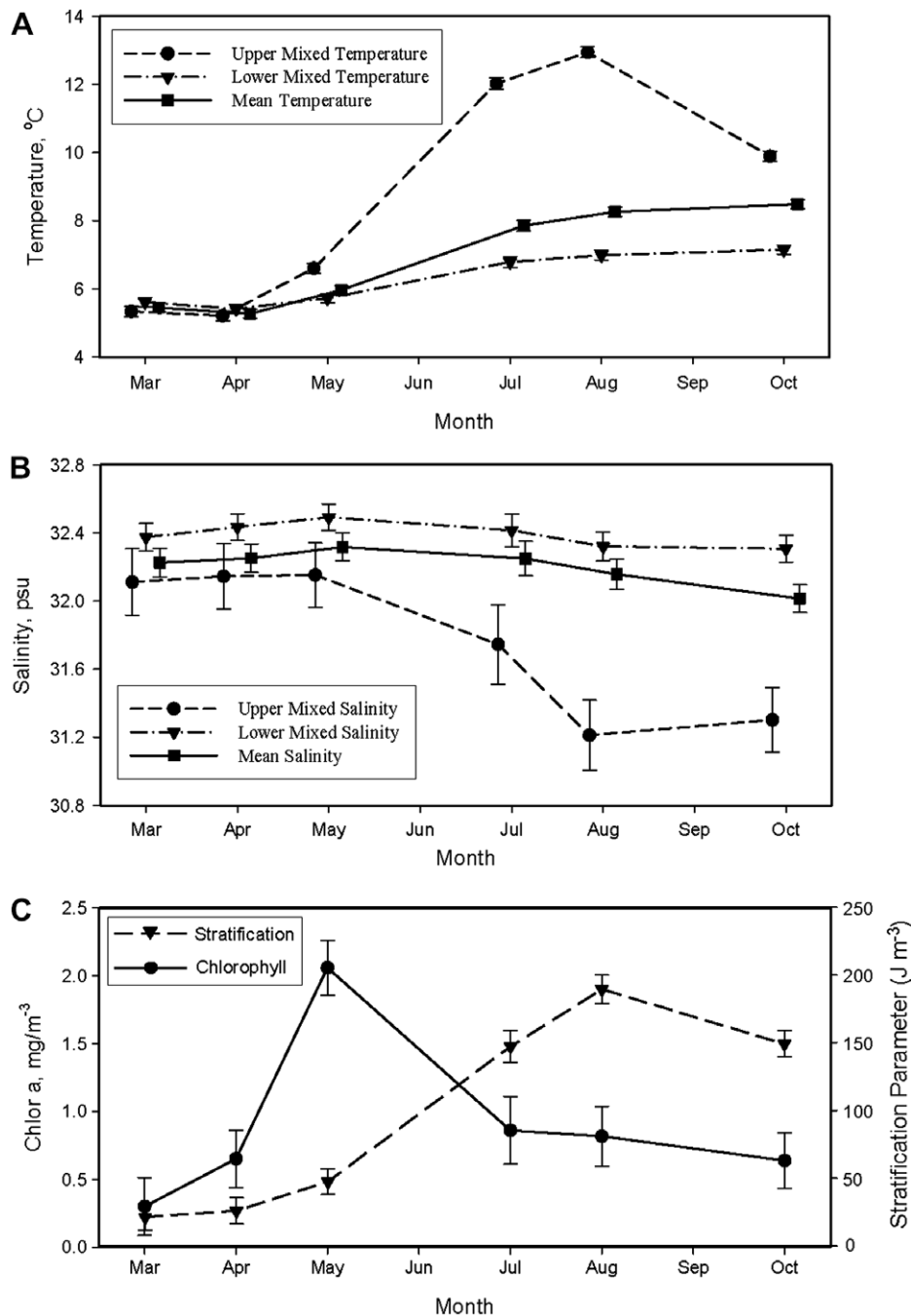


Fig. 2. Seasonal changes in temperature (A) and salinity (B) above and below the pycnocline, and through the entire mixed layer (0–100 m); and chlorophyll-*a* concentrations and stratification parameter (C), along the Seward line in the northern Gulf of Alaska in 1998–2003.

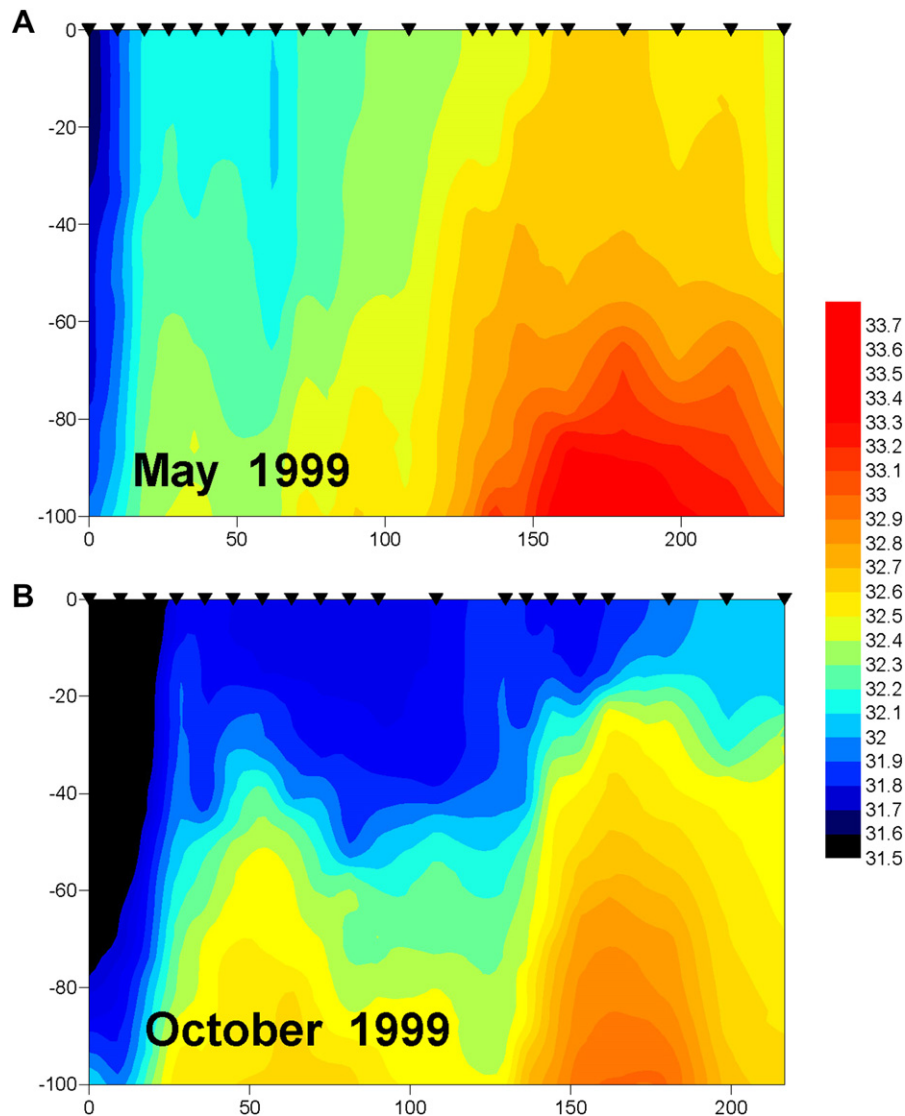


Fig. 3. Seasonal changes in development of the salinity shelf-break front along the Seward Line in May and October 1999. Inverted triangles indicate locations of stations.

observed during the cold years in May. There were no significant differences in chlorophyll-*a* content during the summer months (Table 2).

3.2. Euphausiid cross-shelf distribution

There were significant differences in cross-shelf euphausiid abundance distribution (Table 3). *T. inermis* was usually abundant on the shelf within 100–120 km of shore, but sharply declined at the shelf-break, and *T. spinifera* generally mirrored the distribution of *T. inermis* (Fig. 7). In contrast, in the shelf break and slope region, *E. pacifica* was most abundant beyond 120 km from shore (Fig. 7). There were no significant differences in the cross-shelf distribution of *Thysanoessa* species between seasons (Table 3). In contrast, the cross-shelf distribution of *E. pacifica* showed substantial seasonal variability (Table 3). In spring (March–May) it was scarce on the shelf, but was abundant over the slope, while by the end of the summer it appeared on the shelf in quantities not significantly different from those beyond the shelf break (Table 3).

3.3. Euphausiid interannual variability

The interannual variability in euphausiid abundance on the northern GOA shelf during 1998–2003 showed a distinctive pat-

tern over the years (Fig. 8A). ANOVA revealed significant effects of year on *T. inermis* and *E. pacifica* abundance ($F = 25.92$, $p < 0.0001$ and $F = 5.367$, $p < 0.0001$, respectively), but no effect on *T. spinifera*. The abundance of *T. inermis* was steadily increasing from 1998 through 2002 followed by a sharp decline in 2003. In contrast, the abundance of *E. pacifica* declined slightly from 1998 to 2001 and increased slightly from 2001 to 2003, showing significant effect of year both in spring ($F = 9.03$, $p < 0.0001$) and summer/fall ($F = 3.7$, $p = 0.004$). These changes resulted in a shift of dominant species on the shelf: the euphausiid community was dominated by *T. spinifera* in 1998–2000 and in 2003, while in 2001 and 2002 *T. inermis* prevailed (Fig. 8A). There were no significant interannual changes in *E. pacifica* abundance beyond the shelfbreak, except for exceptionally low numbers in 1998, which probably resulted from undersampling the outer end of Seward Line due to weather conditions in the spring (Fig. 8B).

The longevity and magnitude of spawning events reflected by abundance of adult females carrying spermatophores showed substantial interspecific and interannual variability (Fig. 9A–C). Female *T. inermis* with spermatophores occurred only in April–May (except for March 1999, when the sampling occurred late). The abundance of fertilized *T. inermis* females was an order of magnitude higher in 2002 than in other years (Tukey test, $p < 0.05$). In addition, the abundance of fertilized females in 1998, 1999 and

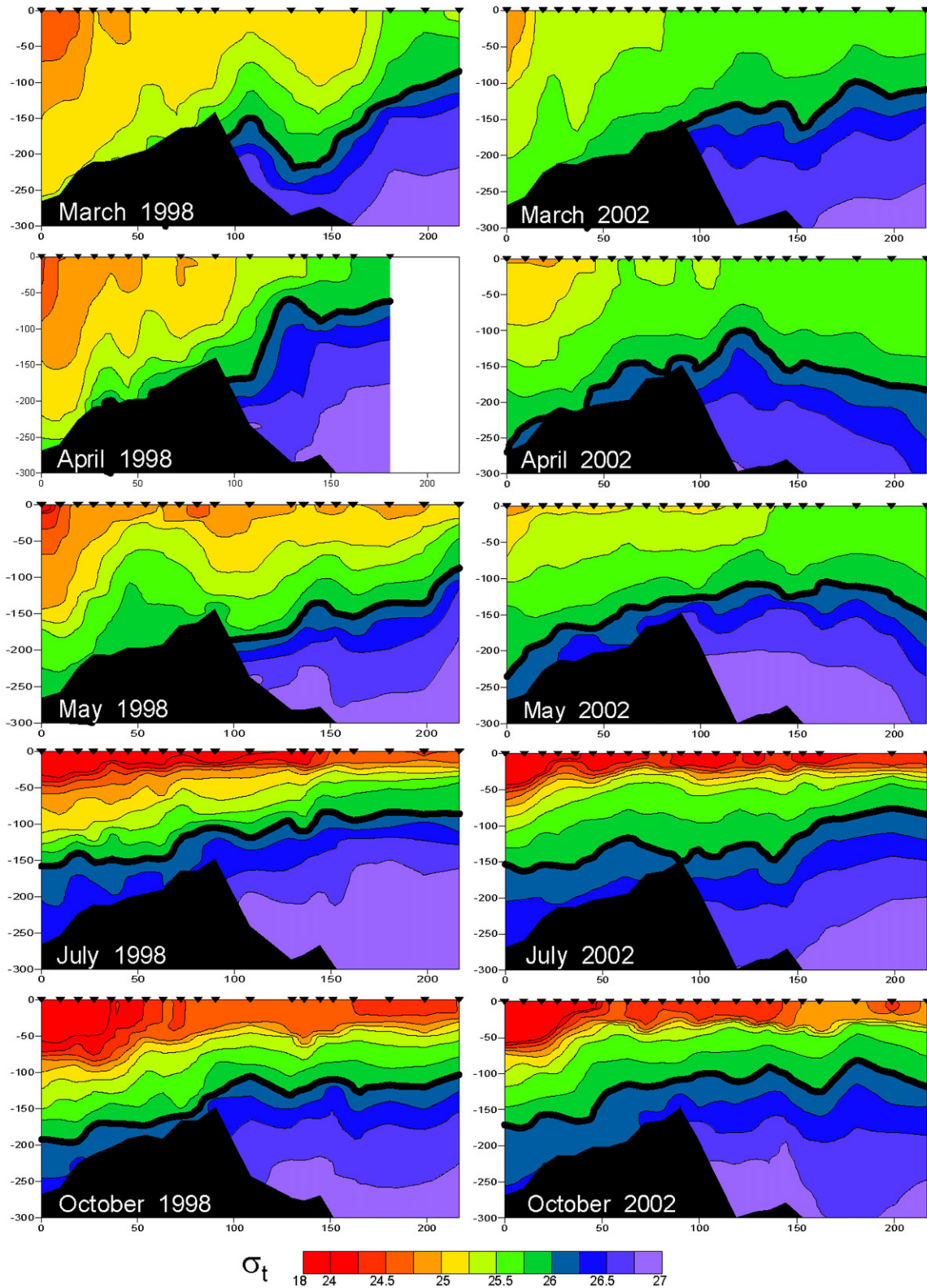


Fig. 4. Seasonal changes in renewal of dense water on the Gulf of Alaska shelf in 1998 and 2002. Inverted triangles indicate locations of stations.

2003 was significantly greater in April than in May (Tukey test, $p < 0.05$), indicating a shift in peak spawning activity. However, the proportion of fertilized *T. inermis* females was not statistically different between months or years (Fig. 9A). Fertilized females of *T. spinifera* occurred from March through August, but were most abundant in April and May (Tukey test, $p < 0.05$) (Fig. 9B). Gravid

T. spinifera with blue colored ovaries and attached spermatophores were occasionally found as late as October. The total number of spawning *T. spinifera* females did not significantly differ between the years (ANOVA). The proportion of fertilized females was higher in April and May (Tukey test, $p < 0.05$) indicating the onset of the spawning season. Similarly, fertilized female *E. pacifica* were pres-

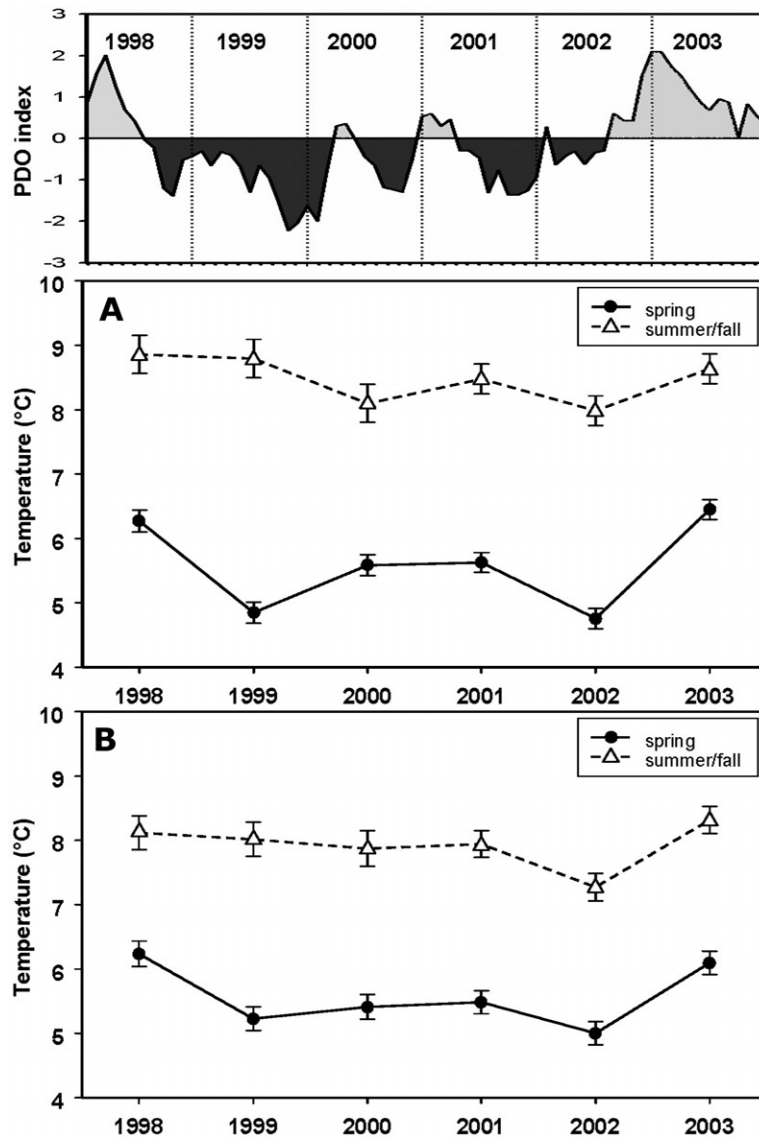


Fig. 5. Interannual variability in the upper 100 m layer temperature in the northern Gulf of Alaska averaged for spring and summer/fall over the shelf (A) for GAK1–GAK7 and beyond the shelf break (B) for GAK8–GAK13 (error bars – 95% confidence intervals) with PDO index (from <http://jisao.washington.edu/pdo/>) on the upper panel.

ent from May through August (Fig. 9C) with few individuals observed in October, and their abundance was not different between the years (ANOVA). There were no significant seasonal differences in percentage of fertilized *E. pacifica* females (ANOVA). The peak abundance of spawning females of *E. pacifica* was consistently lower than that of the other euphausiid species (Fig. 9A–C).

4. Discussion

4.1. Cross-shelf distribution

The inter-specific differences in euphausiid cross-shelf distribution found in this study generally confirm our earlier findings (Coyle and Pinchuk, 2005). Based on four years of observations it was concluded that distribution of the major zooplankton species, including euphausiids, was influenced by cross-shelf water mass distribution and movement (Coyle and Pinchuk, 2005). The northern Gulf of Alaska is divided into three domains: an inner shelf dominated by the colder and fresher buoyancy-driven Alaska Coastal Current (ACC), a shelf break and beyond influenced by the warmer and saline oceanic Alaska Current, and a broad transi-

tion zone between, often crossed by mesoscale eddies branching from the meandering main currents (Weingartner, 2005). Seasonal deep (>100 m) onshore flow develops in the summer during the relaxation of alongshore winds, and is thought to be responsible for advecting nutrients and oceanic organisms onto the shelf (Weingartner et al., 2005; Coyle and Pinchuk, 2005), while the onshore movement of water due to Ekman transport persists through most of the year (Livingstone and Royer, 1980).

Thysanoessa inermis and *T. spinifera* were numerous in the ACC and transition zone, and *E. pacifica* apparently originated from the oceanic Alaska Current (Coyle and Pinchuk, 2005, this study). Our analysis of multiyear data suggests that the actual boundary separating the shelf *Thysanoessa* species from the oceanic domain lies along the shelf break 120–130 km offshore, although the exact position and structure of the shelf break front is often altered by wind forcing and the passage of large mesoscale eddies (Musgrave et al., 1992; Okkonen et al., 2003). Similar distribution of *T. spinifera* and *E. pacifica* is well known from the Pacific northwest (e.g. Lu et al., 2003), while *T. inermis* is usually common over deeper (>50 m) parts of the continental shelf in the North Atlantic, Arctic and Bering Sea (Smith, 1991; Dalpadado and Skjoldal, 1996;

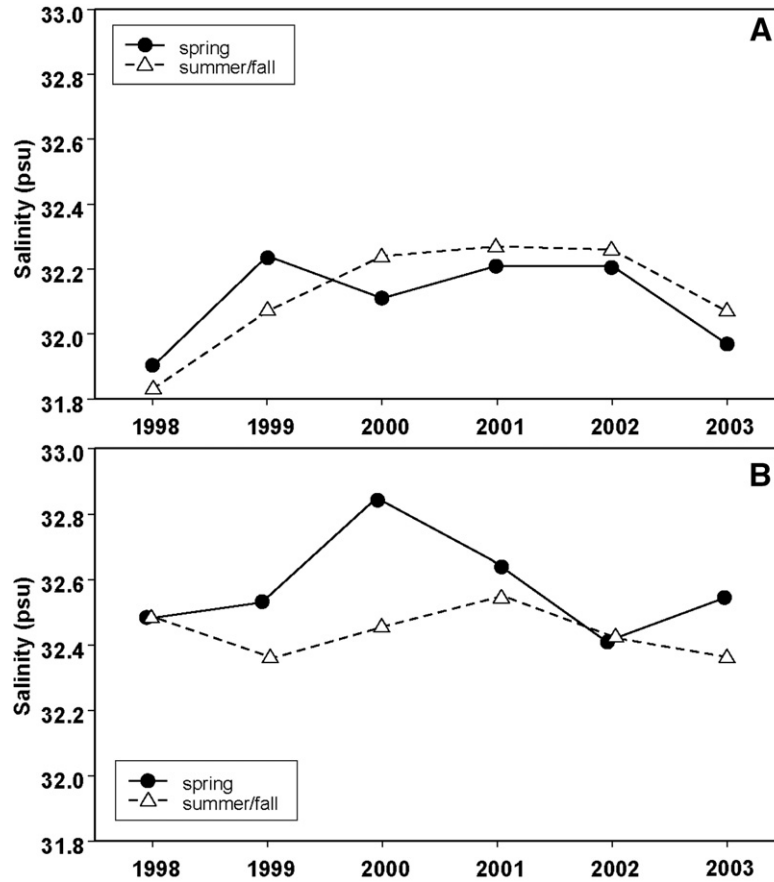


Fig. 6. Interannual variability in the upper 100 m layer salinity in the northern Gulf of Alaska averaged for spring and summer/fall over the shelf (A) for GAK1–GAK7 and beyond the shelf break (B) for GAK8–GAK13.

Table 2
Differences in chlorophyll-*a* concentrations (median, range) in the upper 50 m during spring and summer months between warm and cold years (ANOVA) in the northern Gulf of Alaska

Month	Chlorophyll- <i>a</i> (mg m^{-3})		ANOVA
	Warm (1998, 2003)	Cold (1999–2002)	
March	0.387 (0.204–0.568), $n = 31$	0.279 (0.010–0.692), $n = 83$	$F = 10.36, p = 0.002$
April	0.436 (0.065–0.922), $n = 38$	0.592 (0.001–5.788), $n = 76$	$F = 0.0002, p = 0.99$
May	0.681 (0.199–2.274), $n = 42$	1.336 (0.250–14.07), $n = 84$	$F = 19.7, p = 0.00002$
July/August	0.847 (0.288–2.210), $n = 65$	0.734 (0.365–2.770), $n = 127$	$F = 1.74, p = 0.189$

Table 3
Effects of location (SH – shelf, SL – slope) and season on euphausiid abundance (median, range) along the Seward Line in the northern Gulf of Alaska

Species	Effect of location								
	All season ^a			Spring ^b			Summer ^b		
	SH	SL	Tukey	SH	SL	Tukey	SH	SL	Tukey
<i>T. inermis</i>	156, 0–10223	5, 0–2931	SH > SL	171, 0–10222	18, 0–1857	SH > SL	115, 0–7961	2, 0–2931	SH > SL
<i>T. spinifera</i>	159, 0–6301	55, 0–6556	SH > SL	96, 0–6301	35, 0–2104	SH > SL	336, 0–4527	129, 0–6556	SH > SL
<i>E. pacifica</i>	59, 0–6556	349, 0–7998	SH < SL	14, 0–2084	255, 0–7998	SH < SL	196, 0–6555	423, 0–7168	SH = SL
N	226	186		122	97		104	89	

^a ANOVA, Wilks lambda = 0.58375, $F(3, 408) = 96.978, p < 0.001$.

^b ANOVA, Wilks lambda = 0.90247, $F(3, 406) = 14.625, p < 0.001$.

Astthorsson and Gislason, 1997; Coyle and Pinchuk, 2002) The shelf break fronts mark the transition from the colder and fresher shelf water to the warmer and more saline slope water along the outer continental shelf. Such fronts are known to mark ecological boundaries between oceanic and neritic communities in many

areas of the world ocean (e.g. Longhurst, 1998), albeit physical barriers to cross-frontal exchange of water and organisms are often variable in their location and effectiveness (Mackas and Coyle, 2005). Typically, these fronts are well developed in winter, when the shelf water is well mixed, and the offshore water is mildly

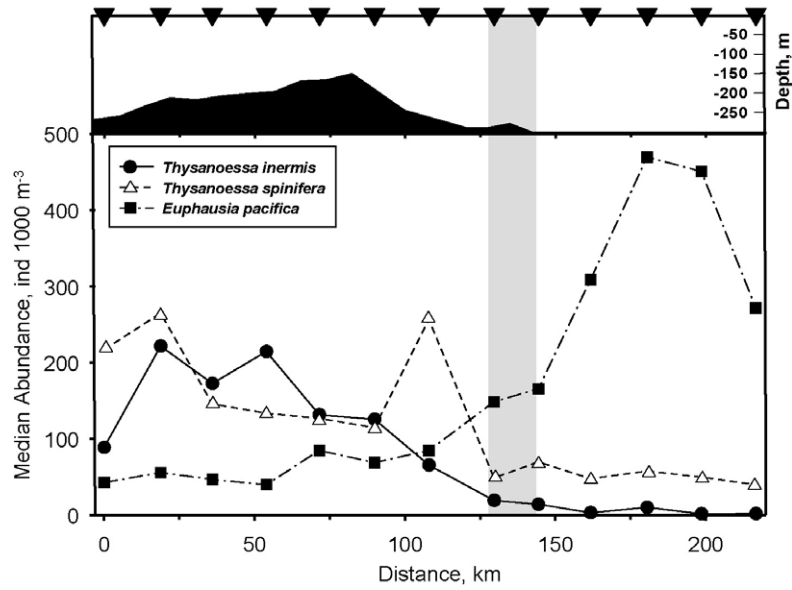


Fig. 7. Cross-shelf (from the coast to offshore) distribution of median abundance of dominant euphausiid species (lower panel) in relation to the bottom topography (upper panel) in the northern Gulf of Alaska. Inverted triangles indicate locations of stations. Shaded is approximate position of the shelf-break salinity front when present. Symbols offset slightly to improve presentation.

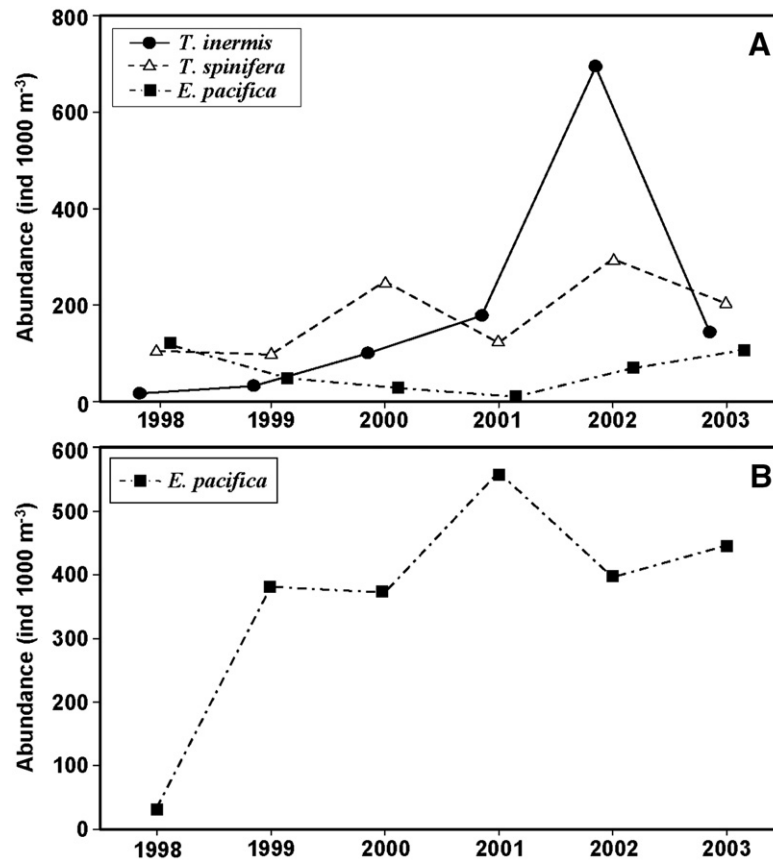


Fig. 8. Interannual changes in median abundance of dominant euphausiid species in the northern Gulf of Alaska on the shelf (A), and beyond the shelf-break (B).

stratified, while in summer the shelf becomes stratified and the fronts weaken (e.g. Mann and Lazier, 1991). The shelf-break front in the northern GOA is often poorly developed in the upper layer due to Ekman transport; however, it can be detected on cross-shelf density profiles in winter and early spring from the base of mixed

layer down to the bottom (e.g. Weingartner et al., 2005). Onshore Ekman transport and the subsurface frontal boundary likely favor retention of the euphausiids on the shelf in winter.

In summer the bottom-attached part of the front separating buoyant shelf water from homogeneous offshore water migrates

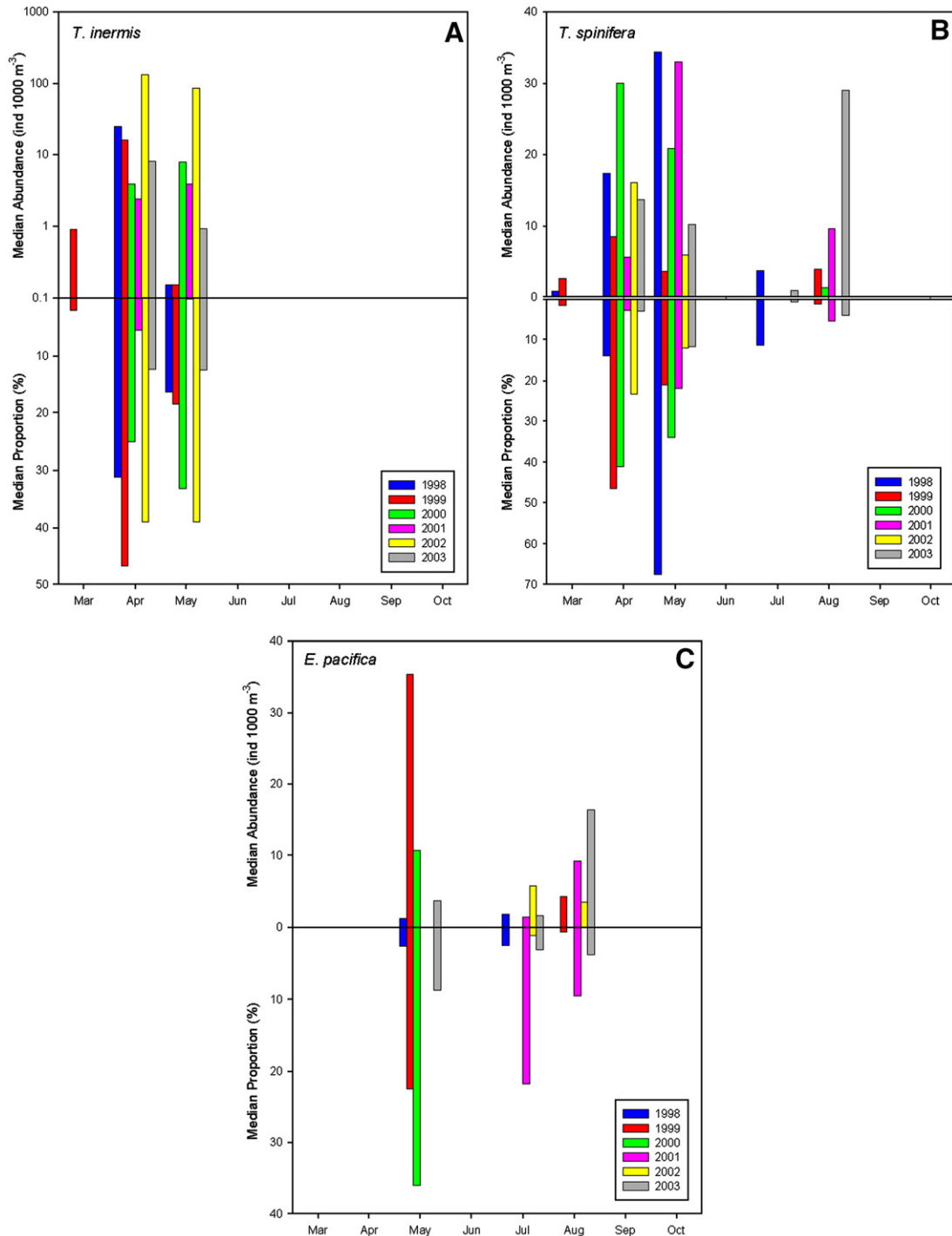


Fig. 9. Interannual abundance of adult female *T. inermis* (A), *T. spinifera* (B) and *E. pacifica* (C) with attached spermatophores and their relative proportion to population size in the northern Gulf of Alaska.

onshore until it reaches an equilibrium isobath (Weingartner et al., 2005). Since GOA shelf depths usually drop to ~150 m within a few kilometers of the coast, the shoaling of the equilibrium isobath allows the saline waters to move inshore along the bottom. Effectively, this not only traps euphausiids originating from the shelf, but provides a mechanism whereby offshore species can be moved onto the shelf. Substantial amounts of *E. pacifica* usually occur on the shelf in the summer and coincide with the development of the deep onshore flow. Since *E. pacifica* undergo extensive diel vertical migrations, spending most of the daytime below 100 m depth

(Lu et al., 2003), the shoreward migration of bottom water during summer is probably an important conduit for *E. pacifica* from offshore to onshore. Other mechanisms might include flow up canyons intersecting the shelfbreak (e.g. Allen, 2000), topographically induced upwelling (Freeland and Denman, 1982), and shelf break eddies and flow meanders forming primarily in years of anomalously strong cyclonic winds (Bower, 1991; Meyers and Basu, 1999; Crawford and Whitney, 1999; Okkonen et al., 2003). Analysis of seasonal changes in pollock diet from the northern GOA inner shelf showed an increasing role of *E. pacifica* as a prey item in

August (Adams et al., 2007), indicating that the summer influx of *E. pacifica* on the shelf might have important consequences for shelf biota.

4.2. Interannual variability

We found distinctive pattern of interannual variability in abundance of *T. inermis* (steady increase of an order of magnitude from 1999 through 2002), less evident pattern for *E. pacifica* (slight decline from 1998 through 2001 and subsequent increase through 2003), and no pattern for *T. spinifera* on the northern GOA shelf. The gradual increase in *T. inermis* abundance coincided with a few consequent years of colder temperatures and higher chlorophyll-*a* concentrations observed over the shelf in spring, while in years of warmer spring temperatures and lower chlorophyll-*a* content, *T. inermis* population declined. In contrast, *E. pacifica* were slightly more abundant during warmer years marked with earlier and less intense spring phytoplankton blooms.

The observed differences in abundance might result from changes in physical transport, changes in reproductive success, environmental changes affecting growth (bottom-up) and/or increased mortality due to predation/parasites (top-down). Since there are little data on krill mortality due to predation or on relative abundance and demands of predators from the northern GOA, the predation mortality cannot be examined. Food deficiencies (bottom up) would result in interannual variability in euphausiid growth rates, with slower or negative growth potentially resulting in years of lower euphausiid abundance, and faster growth in years of higher abundance. Food limitation is not generally supported by field measurements of euphausiid instantaneous growth rates in the northern GOA; strong seasonal pattern occurs, but no significant interannual differences have been observed (Pinchuk and Hopcroft, 2007). Since we did not detect much interannual variability in temperature and chlorophyll-*a* concentration in summer and fall, but observed significant differences in spring, it is reasonable to suggest that spring conditions may have influenced the changes in euphausiid populations.

We assume the euphausiid spawning to be concurrent with the presence of adult females with spermatophores attached (Brinton, 1976). The accuracy of our timing of the spawning events is largely limited by sampling frequency, because the molt duration of euphausiids from the northern GOA is relatively short (6–10 days, depending on temperature) (Pinchuk and Hopcroft, 2007). Additionally, the spermatophore technique provides no information on interannual variability in individual brood sizes. Nevertheless, our data provide evidence that the timing and magnitude of euphausiid spawning events in the GOA may undergo substantial interannual variability, with earlier and shorter spawning of *T. inermis* in warm years, but no clear interannual spawning pattern in *T. spinifera* and *E. pacifica*. The intensity of spawning of *T. inermis* and *T. spinifera* on the GOA shelf appeared to be closely related to the spring bloom of large diatoms in April and May with spawning lasting about two months, while the spawning of *E. pacifica* occurred later in the season, when the temperature of the mixed layer had increased. Similar spawning times are known for *E. pacifica* and *T. spinifera* off the Oregon and British Columbia coasts (Smiles and Pearcy, 1971; Tanasichuk, 1998a, 1998b), and for *T. inermis* from other regions of subarctic Atlantic and Pacific (Kulka and Corey, 1978; Astthorson, 1990; Smith, 1991; Dalpadado and Skjoldal, 1991; Timofeev, 1996).

T. inermis is assumed to release eggs only once per spawning season (though release might last over a few days) and they may breed in two or more successive years (Dalpadado and Skjoldal, 1996; Timofeev, 1996; Pinchuk and Hopcroft, 2006). The data on seasonal dynamics of fatty acids composition for *T. inermis* from Arctic waters suggest that the species is herbivorous and heavily

dependent on spring and summer phytoplankton blooms for accumulating neutral lipids and achieving quick somatic growth (Falk-Petersen, 1981; Falk-Petersen et al., 1981, 2000). During winter only minor food intake occurs, and the lipid stores are mobilized to sustain the animals and to fuel reproductive efforts the following spring (Falk-Petersen et al., 2000). Since euphausiids can quickly adjust their growth rates to food concentrations (e.g. Atkinson et al., 2006), the usage of lipids in winter would result in a zero or negative growth. This is consistent with observations of *T. inermis* growth rates in the northern GOA, where maximum growth (>0.12 mm day⁻¹) occurred in May during the spring bloom, while growth was consistently negative before the onset of the spring bloom (Pinchuk and Hopcroft, 2007). In addition, the brood size of *T. inermis* in the northern GOA does not depend on ambient chlorophyll-*a* concentrations, which also indicates their reliance on lipid reserves or other type of food (Pinchuk and Hopcroft, 2006).

In contrast, *E. pacifica* is known to be omnivorous, utilizing various food sources such as small copepods, microzoo- and phytoplankton cells, and marine snow (Dilling et al., 1998; Bargu et al., 2003; Nakagawa et al., 2001, 2004). It can effectively capture prey items >5 μ m (Suh and Choi, 1998), giving it an advantage in consumption of small diatoms, flagellates and ciliates abundant in the oceanic North Pacific throughout most of the year (Booth, 1988; Miller et al., 1991a, 1991b; Weingartner et al., 2002). *E. pacifica* produces multiple broods throughout the season, sizes of which are strongly dependent on ambient chlorophyll-*a* concentrations (Pinchuk and Hopcroft, 2006). Unlike *T. inermis*, *E. pacifica* did not show significant seasonal variations in growth, maintaining averages of 0.01–0.02 mm day⁻¹ throughout the most of the year (Pinchuk and Hopcroft, 2007).

T. spinifera releases large numbers of eggs with an unknown frequency (Pinchuk and Hopcroft, 2006). Its food habits are largely unknown, but there are indications that they can consume not only phyto- and microzooplankton but also small copepods (A. Pinchuk, pers. observations). While there are no data on seasonal lipid dynamics in the GOA, the extended spawning cycle with a strong peak in April–May indicates that they may rely on ambient food during the production season, similar to *E. pacifica*. In addition, *T. spinifera* growth rates are maximal in July, well after the spring bloom when the abundance of small phyto- and zooplankton is greatest, but are negative in March, when their abundance is lowest.

The success of the strategy employed by *T. inermis* would largely depend on the condition of euphausiids at the start of the production season and the amount of food to replenish the energetic demands immediately after the spawning. Larger lipid reserves might ensure greater success in terms of number of eggs released. However, warmer temperature during winter and early spring would increase metabolic rates, leading to faster expenditure of the lipid stores. Seasonal cooling in the northern GOA starts in September and the mixed layer temperature gradually decreases to its lowest values in March (Weingartner et al., 2005), reflecting the entire winter thermal conditions except for the years re-adjustment occurred after an El-Nino (i.e. winters of 1998/1999 and 2003/2004). Thus euphausiids may experience substantially different thermal regimes in different years over periods of several months. Even a 1 °C difference in ambient temperature would influence individual energy expenditures over a period of several months due to increased metabolic rates, assuming that the euphausiids occur in the mixed layer in winter. *T. inermis* undergo vertical migrations year-around in the southeastern Barents Sea (Zelicman et al., 1979), and, in the GOA, they were commonly caught inshore in the upper 100 m layer using smaller CalVET nets in December 2001–2004 (Hopcroft, unpublished data).

The potential impact of warmer winter conditions can be estimated using data on carbon energy budgets for *T. inermis* (Sameoto, 1976) and *E. pacifica* (Iguchi and Ikeda, 1995). The weight-specific respiration rate at 4 °C for *T. inermis* ranging from 6.2 to 35 mg dry weight (DW) from the Gulf of St. Lawrence was $1.41 \mu\text{l O}_2 \text{ h}^{-1} \text{ mg DW}^{-1}$ (Sameoto, 1976), while at the same temperature for *E. pacifica* of comparable DW range from the southern Japan Sea, it was similar, $1.39 \mu\text{l O}_2 \text{ h}^{-1} \text{ mg DW}^{-1}$ (Iguchi and Ikeda, 1995). The weight-specific respiration rates of *E. pacifica* and *T. inermis* calculated using the respiration/temperature relationship (Iguchi and Ikeda, 1995), $1.503 \mu\text{l O}_2 \text{ h}^{-1} \text{ mg DW}^{-1}$ and $1.629 \mu\text{l O}_2 \text{ h}^{-1} \text{ mg DW}^{-1}$ for 5 °C and 6 °C, respectively, can be converted to daily carbon-specific rates (e.g. Ikeda et al., 2000) using a respiratory quotient of 0.97 (Gneiger, 1983) and a carbon content of 43% of DW (Iguchi and Ikeda, 1995). The resulting carbon-specific rates are 0.044 d^{-1} at 5 °C and 0.047 d^{-1} at 6 °C. Applying these rates to the winter thermal regime, conservatively estimated to be 5 months long, reveals that the difference in weight-specific energy expenditure of *T. inermis* is 0.45, which means that an individual animal may spend extra 45% of its body weight on metabolic activity during warmer relative to colder winters.

Therefore, after a warmer winter, *T. inermis* females are likely to have less internal reserves for spawning, leading to less egg production or, possibly, to lower quality of eggs with lesser lipid content. Moreover, the weak bloom in warmer years might lead to poor survival of spent animals, as well as less successful lipid accumulation for the next winter. In addition, short lived blooms in warmer years may impact first-feeding *T. inermis* calyptopis larvae. While the non-feeding naupliar larval stages of *Thysanoessa* spp. and *Euphausia* spp. rely on internal energy reserves and their growth and developmental rates are primarily controlled by environmental temperature (e.g. Pinchuk and Hopcroft, 2006), by the time of molting into the first calyptopis stage, a functional digestive system is formed, the lipid stores are resorbed, and the larvae must feed to survive (Zimmer and Gruner, 1956). From this moment the quantity and quality of diet determine krill growth and development in addition to temperature (Huntley and Boyd, 1984). Depending on available food, larval development and growth may progress, be delayed or terminated (Ross et al., 1988; Huntley and Brinton, 1991). In the cold Southern Ocean the first-feeding calyptopis larvae of Antarctic krill *Euphausia superba* must find adequate food within 10–14 days of hatching to survive (Ross and Quetin, 1989). It takes about 10 days for *T. inermis* to reach the calyptopis 1 stage at 5 °C in the GOA (Pinchuk and Hopcroft, 2006). Therefore, a shorter and weaker bloom during warm years may substantially impact larval survival of *T. inermis*. The survival success of the calyptopis cohort will influence euphausiid population dynamics by determining the recruitment of the post-larval euphausiid population in a particular year. The annual recruitment success of the larvae also markedly affects the reproductive potential of the successive season, since there are fewer individuals of other year classes available to contribute to the spawning effect.

Given that the *T. inermis* life span is over 3 years (Falk-Petersen et al., 2000; A. Pinchuk, personal observations), the combined effect may be cumulative, decreasing or increasing population abundance depending on which climatic phase is occurring. The progressive increase in abundance of *T. inermis* during the recent cold phase from 1999 through 2002, observed in our study supports this suggestion. In contrast, the strategy employed by *E. pacifica* and *T. spinifera* would succeed in environments with consistent amounts of available food throughout the season. In conjunction with an ability to ingest a wide range of food, this robust growth and reproductive strategy of the latter two species is likely to help them to maintain relatively constant abundance in the northern GOA.

The Pacific Decadal Oscillation (PDO), which is characterized by the PDO index derived from spatial pattern of sea surface temperature anomalies in the North Pacific, and associated phenomena appear to be major sources of oceanographic and biological variability (Mantua et al., 1997). The most prominent feature of the climate in the GOA is the Aleutian Low (AL), for which the average geographic location changes periodically during the winter (Mundy and Olsson, 2005). The location and intensity of the AL affects storm tracks, air temperatures, wind velocities, ocean currents, and other key physical factors in the GOA and adjacent areas. In years of positive PDOs, an intense low pressure is centered over the Alaska Peninsula, resulting in stronger winds, bringing warm moisture air to the coast with greater precipitation. These conditions strengthen the Alaska Coastal Current and produce wind-driven transport of surface marine waters, bringing water onshore (Ekman transport) causing downwelling (Mundy and Olsson, 2005). In years of negative PDOs, a weaker low pressure facilitates reversed temperature and wind patterns leading to relaxed downwelling, reduced along-shore transport, stronger deep onshore flow and colder sea surface temperatures.

The fluctuations of natural physical forces have a profound effect on biological productivity of the northern GOA. The warm and windy conditions (positive PDOs) may result in earlier spring melt or increased winter rainfall (as opposed to increased snow accumulation) and runoff, thus setting up earlier and possibly greater nearshore stratification (Weingartner et al., 2005). If at the same time the greater winds cannot overcome the stratification during the growing season, but do inhibit the relaxation of downwelling, fewer nutrients are supplied to the inshore regime from the annual transport of deepwater onto the shelf, leading to earlier and less intense phytoplankton bloom on the shelf and lower biological production afterwards (Mundy and Spies, 2005). During cold and less windy years (negative PDOs) a reverse situation occurs when stratification develops later allowing the phytoplankton bloom to use more nutrients for a longer period of time, which leads to elevated production on the shelf. The opposite pattern seems to occur beyond the shelf break (Mundy and Spies, 2005). It is important to note that the described differences seem to be well developed during the winter and spring, while by the end of summer they are obscured by seasonal variability. Therefore, climatic changes may greatly influence the onset of the productive season controlling the timing, span and magnitude of the spring bloom, thereby affecting the structure and recruitment success of zooplankton communities. If such changes occur, it may create a response that propagates through multiple trophic levels of the shelf ecosystem.

With respect to euphausiids, a weak AL is likely to promote overall euphausiid production on the northern GOA shelf facilitating better overwintering survival and reproduction success of *T. inermis*. In contrast, a strong AL will diminish the *T. inermis* population, but the on-shore flow might compensate a decrease in *T. inermis* by advecting *E. pacifica* onto the shelf from offshore. It appears that *T. spinifera* is the most versatile in terms of feeding and reproductive strategies, which may lead to its long-term success on the shelf. The interplay of these factors will ultimately determine the abundance and composition of euphausiids on the shelf, and hence the availability of food for predators such as salmon and pollock.

Acknowledgements

This research was conducted on the RV *Alpha Helix* and RV *Wecoma* with technical support from the captains, crews and ships technicians. The research was multidisciplinary, involving the cooperation of a number of researchers and institutions. We thank all the scientists who participated in the cruises for assistance in

the field, and the staff at the Seward Marine Center (University of Alaska Fairbanks) for providing a supportive work environment. Aid in sample processing and data entry was provided by Chris Stark, Janet Ballek and Elizabeth Stockmar. We thank Dr. E.A. Pakhomov, Dr. H.P. Batchelder and three anonymous reviewers for valuable discussions and comments on the manuscript. This research was a part of the Long Term Observation Program funded by US GLOBEC Award No. NA67RJ0147AMD7, with additional support from the Alliance for Coastal Technologies (ACT), a NOAA-funded program. This is GLOBEC Contribution No. 591.

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