DISTRIBUTION, GROWTH AND EGG PRODUCTION OF EUPHAUSIIDS IN THE NORTHERN GULF OF ALASKA

A

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ABSTRACT

The euphausiids *Thysanoessa inermis*, *Thysanoessa spinifera* and *Euphausia pacifica* are key pelagic grazers and important prey for many vertebrates in the Gulf of Alaska (GOA). This thesis provides the first account of distribution, egg production, growth, development, and temporal variability in abundance of the euphausiids in relation to environmental variations in the northern GOA. *T. inermis* and *T. spinifera* were abundant on the shelf within 120-130 km from the coast, while *E. pacifica* originated from offshore and was advected onto the shelf during summer. *E. pacifica* produced multiple broods with brood size strongly related to ambient chlorophyll *a* concentrations. In contrast, *T. inermis* released eggs once in the season and its brood size did not depend on chlorophyll content. Early development of these species showed a remarkably similar response to changes in temperature. The highest molting increments were observed during the spring phytoplankton bloom for *T. inermis,* and in summer for *T. spinifera* and *E. pacifica*, suggesting coupling with food availability. The molting rates were strongly influenced by temperature. Growth rates depended on euphausiid size, and were close to 0 in early spring, reaching maximum values in May (0.123 mm d^{-1} or 0.023 d^{-1} for *T. inermis*) and July (0.091 mm d^{-1} or 0.031 d^{-1} for *T. spinifera*). The growth rates for *E. pacifica* remained below 0.07 mm d^{-1} (0.016 d^{-1}) throughout the season. The relationship between *T. inermis* weight specific growth rate (adjusted to 5°C) and ambient chlorophyll-*a* concentration fit a Michaelis-Menten curve (r^2=0.48), but such relationships were not significant for *T. spinifera* or *E. pacifica.* Reproduction of *T. inermis* occurred during April in 1998 and 2003, and was extended through May in 1999-2002. The spawning of *T. inermis* and *T. spinifera* was related to the spring diatom bloom on the inner shelf, while the spawning of *E. pacifica* occurred later in season, when the water temperature 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 early spawning *T. inermis* on the inner shelf.

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INTRODUCTION

The Gulf of Alaska (GOA) continental shelf supports a rich and diverse marine ecosystem including the most important commercial fisheries in the United States EEZ such as crustacean, salmon, pollock, halibut and sablefish (Weingartner et al. 2002) as well as sea bird and marine mammal populations. 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, Wilson et al. 2006); herring (Hart 1973); and sablefish (Sigler 2001) as well as seabirds and baleen whales (Mauchline 1980). *Euphausia pacifica, Thysanoessa spinifera* and *Thysanoessa inermis* are the common euphausiid species during all seasons in the GOA along with less abundant *Thysanoessa longipes*, *Thysanoessa raschii, Thysanoessa inspinata,* and *Thessarobrachion oculatus.* Euphausiids feed on a variety of phyto- and microzooplankton, as well as suspended organic matter including "marine snow" and serve 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 fuller knowledge of the mechanisms affecting euphausiid population dynamics is important for understanding the GOA ecosystem. Growth dynamics of euphausiids and factors influencing growth are crucial for understanding and quantifying the role of euphausiids in ecosystem production cycles and energy transfer to apex predators. Among others, a problem to be addressed is: how does climate variability affect the recruitment, vital rates, and other measures of population dynamics of euphausiids.

Egg production and growth are key parameters characterizing the rates at which euphausiids process material, and are related to euphausiid's potential to supply energy and matter to higher trophic levels. Egg production also determines the potential rate of recruitment to a population, thus representing an important parameter in demographic studies. Egg production is dependent on the resources available to adult females, and consequently may be food-limited, while egg hatching and postembryonic development times show strong temperature dependence in a wide range of animal groups, including zooplankton (Peterson 2001; Gillooly et al. 2002).

The growth of oceanic zooplankton, including euphausiids, is governed primarily by temperature and food (e.g. Huntley and Boyd 1984; Clarke and Peck 1991; Hirst et al. 2003). Both factors undergo substantial seasonal variability in high latitudes. Euphausiids may respond to changes in these factors in two ways: by altering the duration of the intermolt period, and by changing the growth increment (Buchholz 1991; Iguchi and Ikeda 1995). The intermolt period is thought to be affected mainly by temperature (e.g. Kawaguchi et al. 2006, Tarling et al. 2006) and to a smaller degree by individual size (Fowler et al. 1971; Iguchi and Ikeda 1995). In contrast, the growth increment appears to be strongly influenced by quantity and quality of food (Iguchi and Ikeda 1995; Ross et al. 2000) and may become negative under unfavorable conditions leading to body shrinkage (Nicol et al. 1992; Marinovic and Mangel 1999).

The life history pattern of euphausiids is known to vary geographically. For example, *Euphausia pacifica* breed from February through May in the southern Japan Sea (Iguchi et al. 1993), in June in the Okhotsk Sea (Ponomareva 1966), June through September off Oregon (Smiles and Pearcy 1971) and in all seasons in southern California (Brinton 1976). The life span of *Euphausia pacifica* ranges from 8-12 months off southern California to 2 years in the Okhotsk Sea and waters around the southern Aleutian Islands (Ponomareva 1966). Because of such plasticity, a comparison of physiological parameters of euphausiids inhabiting different geographical locations is important for understanding the biology of these species. There have been attempts to estimate *Euphausia pacifica* growth in the laboratory (Lasker 1966; Fowler et al. 1971; Ross 1981; Ross et al. 1982, Iguchi and Ikeda 1995) as well as from field data (Brinton, 1976; Smiles and Pearcy, 1971; Iguchi et al. 1993, Iguchi and Ikeda 1999). The growth of adult *Thysanoessa spinifera* off the Pacific coast of Canada has been estimated by Tanasichuk (1998b). The only experimental study of growth and development for *Thysanoessa spinifera* from Barkely Sound was done by Summers (1993). Most studies of *Thysanoessa inermis* population biology have been done in the North Atlantic and

Barents Sea, although this species is common in the North Pacific, Bering and Okhotsk seas as well. It has been found that at its southern distribution limits *T. inermis* attain a maximum age of 1 year, while in temperate waters around Scotland, Iceland and Nova Scotia part of the population survives for another year, and in the Barents Sea, off Greenland and near the eastern Aleutians they reach a maximum age of just over 3 years (Siegel, 2000). However, there is no such information on these species in the GOA.

Studies of *Thysanoessa spinifera* and *Euphausia pacifica* population biology in British Columbia coastal waters (Tanasichuk, 1998a, 1998b) showed that their production varied considerably between years. The production of *Thysanoessa spinifera* dramatically decreased during the 1992 ENSO event. In contrast, *Euphausia pacifica* production increased during stronger upwelling in 1992. However, these changes could not be explained by temperature differences alone, suggesting that physical transport, food and predation played an important role (Tanasichuk, 1998a, 1998b).

This thesis is a component of a larger study, the U.S. Global Ocean Ecosystem Dynamics (GLOBEC) Northeast Pacific Program (NEP), which endeavors to increase the understanding of the physical and biological interactions linking the Gulf of Alaska ecosystem to climate change (Weingartner *et al.*, 2002). Recent observations in the GOA showed that physical forces result in an extremely dynamic environment. Moreover, the phytoplankton assemblage appears to be different in the inner and outer shelf regions. On the inner shelf large diatoms dominate the community, while on the outer shelf smaller phytoplankton cells are common during the production season. This probably results in altered pathways of energy flow through the trophic chain and ultimately will influence euphausiid biology.

One of the aims of GLOBEC NEP is to determine the development and growth of dominant euphausiid species within the GOA. This thesis will evaluate seasonal and interannual variability in spatial distribution, population structure, growth rates and production as well as quantify effects of temperature and food on the growth and egg production of dominant euphausiid species. The study will lead to better understanding of the seasonal cycle, interannual variability and production of euphausiid populations in the

GOA and the resulting data will be crucial for building a numerical model able to predict climate related variations in euphausiid abundance, age structure, growth and production.

The main objective of this research was to study seasonal and interannual variations in abundance, age structure, growth, and production of *Thysanoessa inermis*, *Thysanoessa spinifera* and *Euphausia pacifica* in the GOA relative to the physical environment and food availability. Specific objectives were as follows:

1. Describe the spatial distribution and inter-annual differences in abundance, timing and magnitude of spawning of the major euphausiid species in relationship to temperature, salinity and chlorophyll-*a* distribution during the production season
2. Document field and laboratory observations on egg production and hatching as well as on early larval development in relation to temperature and food concentrations;
3. Describe seasonal variability in growth rates of the major euphausiid species from the northern GOA, and examine factors controlling euphausiid growth throughout the productive season.
4. Relate krill spatial and temporal variability to climate fluctuations that may impact krill life histories.

Chapters 1, 2 and 3 directly address the above objectives. Appendices A and B deal with seasonal dynamics of the northern GOA zooplankton community as a whole, including euphausiids, and are included to give a broader prospective on the role of euphausiids in the ecosystem. The chapters have been prepared as manuscripts for publication. They are written as stand-alone papers with appropriate sections. The author's contribution for the papers in the appendices included field collection of the zooplankton samples, identification, staging, enumeration and weighing of the specimens, parts of in statistical analyses and participation in the preparation of the manuscripts.

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CHAPTER 1

Egg production and early development of *Thysanoessa inermis* and *Euphausia pacifica* (Crustacea: Euphausiacea) in the northern Gulf of Alaska[1]

1.1 Abstract

Early life history patterns were studied in the dominant euphausiids from the northern Gulf of Alaska (GOA) in 2001-2004. Gravid females of *Thysanoessa inermis* were observed in April and May. Brood size varied from 10 to 1021 eggs with an average of 138±19 (95% CI) eggs female^{-1}. Most gravid females started to release eggs within the first 2 days of incubation. The average number of eggs released per female was similar in incubation Day 1 and 2, but significantly smaller on Day 3 and 4. About 25% of the females were continuously releasing eggs over 3 days rather than producing a single distinctive brood. In contrast, gravid females of *Euphausia pacifica* were observed from early July through October. Most gravid females released eggs on the first day of observation, while only 2% of females produced eggs repeatedly. Brood size varied from 20 to 246 eggs with an average of 102±12 (95% CI) eggs female^{-1}. The relationship between *E. pacifica* brood size and ambient chlorophyll-*a* concentration was sigmoidal ($r^2 = 0.73$), with food saturated brood size of 144±14(SE, p<0.001) eggs , and half-saturation occurring at 0.46±0.02(SE, p<0.001) mg chlorophyll-*a* m^{-3}. The average interbrood interval of *E. pacifica* reared at 12°C and satiated food conditions in the laboratory was ~8 days, suggesting their potential individual fecundity in the GOA was 1148 – 1530 eggs per spawning season. Hatching and early development (from egg to furcilia stage) was studied under 5°C, 8°C and 12°C. Hatching was nearly synchronous and lasted 3-6 hours, depending on incubation temperature. Development times from egg to the first furcilia stage ranged between 20 and 33 days for *T. inermis*, and 15 and 45 days for *E. pacifica* at 12°C and 5°C, respectively.

---

[1] Pinchuk AI, Hopcroft RR (2006) Egg production and early development of *Thysanoessa inermis* and *Euphausia pacifica* (Crustacea: Euphausiacea) in the northern Gulf of Alaska. J Exp Mar Biol Ecol 332: 206-215.

1.2 Introduction

Thysanoessa inermis, Euphausia pacifica and *Thysanoessa spinifera* are the dominant euphausiid species found in the Gulf of Alaska (GOA) frequently occurring in high numbers over the broad, deep shelf characteristic of its northern region (Coyle and Pinchuk, 2003, 2005). The oceanic *E. pacifica* are usually abundant over the outer shelf, while *T. inermis* and *T. spinifera* inhabit the inner shelf (Coyle and Pinchuk 2005). These species are thought to be primarily grazers and predators on variety of phyto- and microzooplankton as well as suspended organic matter (Ponomareva, 1966; Bargu et al., 2003; Nakagawa et al., 2004). They 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 (e.g. Brodeur, 1998); herring (e.g. Hart, 1973); and sablefish (e.g. Sigler, 2001) as well as seabirds and baleen whales (Mauchline, 1980). Thus, euphausiids represent important elements in the transfer of energy from the lower trophic levels through the planktonic food web upwards to apex predators in the northern GOA marine ecosystem.

Egg production and growth are key parameters characterizing the rates at which euphausiids process material, and are related to euphausiid's potential to supply energy and matter to higher trophic levels. Egg production also determines the potential rate of recruitment to a population, thus representing an important parameter in demographic studies. Egg production is dependent on the resources available to adult females, and consequently may be food-limited, while egg hatching and postembryonic development times show strong temperature dependence in a wide range of animal groups, including zooplankton (Peterson, 2001; Gillooly et al., 2002).

Many euphausiid species are capable of releasing eggs more than once during a single spawning season (Ross and Quetin, 2000). Therefore, the information on brood size as well as frequency of brood releases, and duration of the reproduction season, are prerequisites for estimating individual and population fecundity. A traditional method of counting all stages of eggs in the ovary estimates the fecundity of *E. pacifica* from the Japan Sea to be 1200-1700 eggs female^{-1} (Ponomareva, 1966). The same technique applied to *T. inermis* suggests a wide range, from 300-350 eggs female^{-1} in the Barents Sea (Zelikman, 1958) to 1700 eggs female^{-1} in the North Pacific (Ponomareva, 1959). Counting ovarian eggs may, however, lead to an overestimation since not all ovarian eggs are necessarily released (Iguchi and Ikeda, 1994). Broods, obtained during experimental incubations, comprised substantially smaller 12-296 eggs female^{-1} for *E. pacifica* from the Japan Sea (Iguchi and Ikeda, 1994) and 30-110 eggs female^{-1} for *T. inermis* from the Barents Sea (Dalpadado and Ikeda, 1989; Dalpadado and Skjoldal, 1991), however, no multiple spawning events were observed in these studies. Recent work off the Oregon coast has documented repetitive spawning of *E. pacifica* in the laboratory, and estimated potential individual fecundity in excess of 6000 eggs per season (Feinberg et al., 2003). Indirect estimates, derived from observations on proportion of experimental *E. pacifica* females producing eggs over 24 hours, and the duration of the spawning season in Puget Sound, imply individual fecundity of 600-4000 eggs female^{-1} per season (Ross et al., 1982).

Despite their importance as prey for major commercial fisheries in the GOA and the Bering Sea, fundamental information on reproductive and developmental biology of these species is absent from this region, and for the temperature ranges characteristic of it. Nothing is known of fecundity for either *E. pacifica* at the northernmost extreme of its range in the northern GOA or for *T. inermis* in the entire subarctic North Pacific. Similarly, while the general development patterns of *T. inermis* and *E. pacifica* are well documented (Einarsson, 1945; Boden, 1950; Suh et al., 1993), there is little information on development rates of their early larval stages across the broad temperature range characteristic of the North Pacific (Ross, 1981; Iguchi and Ikeda, 1994). The U.S. Northeast Pacific GLOBEC program in the northern Gulf of Alaska seeks to address such deficiencies in our knowledge (Weingartner et al., 2002). In the present study, we document field and laboratory observations on egg production and hatching as well as on early larval development at different temperatures of *T. inermis* and *E. pacifica* from the northern GOA.

1.3 Materials and Methods

1.3.1 Sampling and maintenance of gravid females

All sampling was conducted in the northern Gulf of Alaska from March 2001 through October 2004 (Fig. 1.1, Table 1.1). Water samples were collected with Niskin bottles for fluorometric estimation of chlorophyll-*a* concentration as described in Childers et al. (2005) and the results averaged over the upper 50 m of the water column (D.A. Stockwell and T.E. Whitledge, unpublished data). Night-time euphausiid aggregations were located with an HTI multi-frequency acoustic system and then fished using 1 m^2 MOCNESS equipped with black 100 μm mesh nets at 0.25-0.5 m s^{-1}. The contents were immediately diluted into a 20 l pail to facilitate sorting. Gravid females of *E. pacifica* were identified by a purple band under the pericardial area of the thorax (Ross et al., 1982). Gravid females of *T. inermis* were distinguished by a light blue color of the ovaries (Dalpadado & Ikeda, 1989). They were gently removed from the catch and placed in individual 750 ml tissue flasks filled with seawater collected simultaneously at the site. The animals were maintained at the ambient mixed layer water temperature (i.e. 5°C in April-May and 8-12°C in July and August and 10°C in October) in the dark and were checked every 12 hours for eggs.

When eggs were observed, the female was removed and transferred to a new container filled with fresh seawater. Females were incubated for 4 days to estimate the length of an individual spawning event. At the end of each experiment, all animals were preserved individually. The newly released eggs were counted, then either preserved in 4% formalin, or returned to the incubator. To estimate possible extent of cannibalism during the experiments, known numbers of eggs were added to 14 *E. pacifica* females maintained under the same conditions and recounted after 24 hours. The egg capsule and embryo diameters were measured on preserved eggs. Brood size was calculated as a cumulative number of eggs released by a female during the experiment. Very small amounts of eggs (<10) were found in 7 *T. inermis* and 1 *E. pacifica* flasks, and were excluded because we assumed they represented contamination introduced during sorting.

1.3.2 Rearing of eggs and larvae

Harvested eggs were placed in multiwell trays (15 ml well volume), about 25-50 eggs per well, and were kept at 5±0.5°C, 8±0.5°C and 12±0.5°C until they hatched or became moribund. Nauplii were transferred into multiwell trays with fresh seawater. Since the nauplii and metanauplii do not feed, no food was introduced until they molted into calyptopis. The trays were inspected every 3 –12 hours depending on incubation temperature. After the larvae reached the calyptopis stage, they were individually transferred into single wells and inspected daily. Water and food were changed every 3-5 days. The larvae were fed *ad libitum* a mix of *Thalassiosira* spp., *Isochrisis galbana, Pavlova lutheri* and *Chromonas* spp. Feeding was augmented with *in situ* food (10-150 µm) collected in Resurrection Bay to provide a more nutritionally balanced diet. Cyanobacteria, ciliates, flagellates, diatoms, eggs, small nauplii, and small larvaceans were observed in varying concentrations in these *in situ* samples. The experiments were terminated when larvae reached furcilia stages or died, lasting up to 50 days at 5°C. The euphausiid larvae were staged according to existing descriptions (Lebour, 1926; Einarsson, 1945; Boden, 1950; Suh et al., 1993). The abbreviations used are: N1-N2 = nauplius 1 and 2; MN = metanauplius, C1-C3 = calyptopis 1–3; F1-2 = furcilia 1, 2.

To assess brood size and interbrood interval under food saturated conditions experimentally, a limited number of individual *E. pacifica* larvae hatched during summer 2003 were kept at 12°C in 1000 ml tissue flasks. Water and food were changed every 3-5 days. Chlorophyll-*a* concentrations in the flasks were maintained at ~15 mg m^{-3}. The experiments lasted untill the animals died. When the larvae matured during spring 2004, they were inspected daily for eggs. When egg releases occurred, the eggs where counted and preserved. Only if the consecutive egg releases from a female were separated by more then one day they were considered as separate broods.

1.3.3 Data analysis

All length measurements were made digitally (Roff and Hopcroft, 1986). Carapace length (*CL*, mm) was measured from the tip of rostrum to the posterior dorsal margin of the carapace. The total length (TL, mm) defined as distance from the tip of rostrum to the end of telson was estimated using linear regressions for euphausiids from GOA collected as outlined in Coyle and Pinchuk (2005):

$TL = 2.46CL + 2.99$ for *T. inermis*
$TL = 3.75CL + 0.92$ for *E. pacifica*
$TL = 2.60CL + 2.61$ for *T. spinifera*

All data were uploaded into MS ACCESS database and analyzed using standard STATISTICA routines. Data sets were log-transformed before running statistical tests to satisfy the assumption of normality. The abbreviations used are: CI – confidence interval; SE – standard error, SD – standard deviation.

1.4 Results

1.4.1 Egg production

Gravid females of *T. inermis* were observed only during April and May (Table 1.1). Most females started to release eggs within the first 2 days of incubation (Fig. 1.2a). The size of spawning females ranged from 16.7 mm to 28.3 mm in total length. The average number of released eggs per female was similar in Day 1 and 2, but significantly smaller on Day 3 and 4 (Fig. 1.2a). About 25% of females released eggs over 3 days rather than producing a single distinctive brood, while the number of eggs released per day significantly decreased (Fig. 1.2b). Egg production was arrested during molting. Only a single female produced eggs immediately after molting, and they proved to be non-viable. Brood size varied from 10 to 1021 eggs, and the average brood size was 138±19 (95% CI, n=195) eggs female^{-1}. We suspect the smallest broods represented females that had partially released eggs prior to incubation.

In contrast, gravid females of *E. pacifica* were observed from early July through October (Table 1.1). The total length of spawning females ranged from 17.4 mm to 25.6 mm. Most females released eggs on the first day of observation (Fig. 1.2a) and only 2 females (i.e. 2%) produced eggs repeatedly (Fig. 1.2b). Brood size varied from 20 to 246 eggs female^{-1} and the average brood size was 102±12 (95% CI, n=79) eggs female^{-1}. Female body length explained only a small part of brood size variation (r^2=0.21 and r^2=0.27 for *T. inermis* and *E. pacifica*, respectively). The loss of eggs due to cannibalism in the experimental design was estimated at 11% over 12 hours for *E. pacifica* and was considered negligible. There was no attempt to estimate cannibalism of *T. inermis*.

Occasionally we observed gravid females of *T. spinifera* from April through October. The total length of spawning females ranged from 25.2 mm to 31.5 mm, and brood size varied from 46 to 385 eggs and averaged 153.7±53.8 (95% CI) eggs female^{-1} (n=13). The extremely adhesive eggs were usually found attached to the bottom of the containers and this made further study of the species problematic.

Much of the observed variation in brood size in *E. pacifica,* but not *T. inermis*, could be attributed to ambient chlorophyll-*a* concentrations. While curves fit to Michaelis-Menten form described a large part of the variation (r^2 = 0.56), the data set was described best by the sigmoidal Hill function (r^2 = 0.70) (Fig. 1.3). The relationship indicates that brood size under food saturated conditions ($BS_{\max}$) reaches144±14(SE, p<0.001) eggs female^{-1}, with half-saturation (K_d) occurring at 0.46±0.02(SE, p<0.001) mg chlorophyll-*a* m^{-3}.

Four females of *E. pacifica,* reared in the laboratory under food saturated conditions, produced multiple broods (Fig. 1.4). Since there were no significant differences in brood sizes or interbrood intervals between individual females, the data were pooled. The brood size ranged from 16 to 298 eggs, and averaged 80±23 (95% CI, n=33) eggs female^{-1}; the interbrood interval ranged from 2 to 36 days, averaging ~8 days.

In both species, the variability of egg sizes was generally small within individual broods, but was substantially larger between broods. Comparison of eggs between individual broods revealed significant morphological differences: while embryos in both species did not differ much, the eggs capsules in some broods were significantly larger than in others (Fig. 1.5; Table 1.2) leading to enlarged perivitteline space surrounding the embryos. The difference was especially noticeable in *E. pacifica.* There was no significant relationship between size of females of both species and diameter of the egg capsules they produced.

1.4.2 Hatching and larval development

Hatching and molting of non-feeding stages (from N1 through MN) was nearly synchronous and occurred within a 3-12 hour interval, depending on incubation temperature and stage. Hatching success was generally high (over 90%). However, a few clutches consisted completely of non-viable eggs, which failed to develop. Such clutches were occasionally found throughout the egg production season. Eggs usually hatched into N1 stage. Occasionally we observed delayed hatching of *E. pacifica*, when an embryo developed to the C1 stage within the egg membrane, but the occurrence of such events was very rare. Mean mortality of non-feeding *E. pacifica* larvae, calculated for 10 viable clutches was 40% when they reached the first feeding C1, 61% for C1, 23% for C2 and 11% for C3.

The mean developmental time for *T. inermis* to reach C1 stage from hatching was 10.04±1.55 days (95% CI) at 5°C and 5.36±0.05 days (95% CI) at 12°C; for *E. pacifica* 11.5±0.47 days (95% CI), 5±0.44 days (95% CI) and 4.2±0.11 days (95% CI) at 5°C, 10°C and 12°C, respectively. All stages of both species showed shorter intermolt period (IP) at higher temperatures and appeared to have similar growth patterns (Table 1.3). The IP of non-feeding nauplii (N1 and N2) and metanauplii (MN) were significantly shorter than those of feeding calyptopis stages (C1-C3). The mean IP of *E. pacifica* C1 at 5°C of 13.4 d was probably overestimated, since, during that experiment, incubation temperature dropped down to 2°C for 6-8 hours with surprisingly long-term consequences. Development times from egg to the first furcilia (F1) stage as estimated from stage specific IP ranged between 20 and 33 days for *T. inermis,* and 15 and 45 days for *E. pacifica* at 12°C and 5°C, respectively.

1.5 Discussion

Our findings of breeding *E. pacifica* in the northern GOA from July through October suggest that its spawning season coincides with development of the seasonal stratification, where mixed layer temperature rises from 5-6°C in May, to 12-14°C in July and August, and decreases through late October to ~10°C (Weingartner et al., 2005). This warm layer contains relatively high post-bloom chlorophyll-*a* concentrations (~0.95 mg m^{-3}) in July and August, while in October the chlorophyll-*a* content is generally lower (~0.72 mg m^{-3}), but may substantially vary between years (Childers et al., 2005). Water temperature of 9-16°C and abundant food are thought to facilitate the spawning of *E. pacifica* (Brinton, 1976; Nicol and Endo, 1997; Lu et al., 2003) along the central North American coast. Thus, *E. pacifica* breed year-around with peaks in May-July off southern California (Brinton, 1976), June through September off Oregon (Smiles and Pearcy, 1971), from February through May in the southern Japan Sea (Iguchi et al., 1993) and in June in the colder Okhotsk Sea (Ponomareva, 1966). The *E. pacifica* reproduction in the northern GOA, the northernmost part of its range, also appears to follow local temperature and chlorophyll-*a* seasonal dynamics, resulting in a delayed spawning as compared to the southern areas. In contrast, spawning of *T. inermis* in the northern GOA coincided with the spring bloom of large diatoms in April and May and lasted about two month, similar to the other regions of the subarctic Atlantic and Pacific (Kulka and Corey, 1978; Hanamura et al., 1989; Astthorson, 1990; Smith, 1991; Nicol and Endo, 1997; Dalpadado and Skjoldal, 1991; Timofeev, 1996).

We found brood size poorly correlated to female body size, a trend often observed in pelagic crustaceans, including euphausiids (e.g. Ross et al., 1982; Ross and Quetin, 1983; Harrington and Ikeda, 1986; Iguchi and Ikeda, 1994; Nicol et al., 1995; Thatje et al., 2004). This indicates that the number of eggs released during spawning is influenced by factors other than body size.

The strong functional relationship between brood size and ambient chlorophyll-*a* concentration in *E. pacifica* (Fig. 3) indicates that the reproductive rates in this species are closely coupled with availability of phytoplankton. In contrast, the lack of similar relationship over a broad range of chlorophyll-*a* concentrations (0.35-5.71 mg m^{-3}) in *T. inermis* suggests that either the species relies on substantial lipid reserves for reproduction, or prey items other than phytoplankton are important in their diet. Therefore, the tight coupling of *T. inermis* reproduction with the start of the spring phytoplankton bloom would provide additional advantage, not to spawning adults, but rather to their first feeding larval stages, which would appear in the northern GOA system within 10 days after hatching to find the resources of the bloom available for consumption. Curiously, similar observations were made on *Metridia* copepods from the same area: *M. pacifica* and *M. okhotensis,* which adopt contrasting reproductive strategies analogous to this study's euphausiids. While egg production rates of *M. pacifica*, which spawns throughout the production season from spring till late fall, were closely related to chlorophyll-*a* concentrations, those of *M. okhotensis*, spawning in April and May, were not (Hopcroft et al., 2005).

Our observations show that *E. pacifica* from the GOA is capable of having 11-15 spawning episodes assuming their reproductive season lasting from 3 to 4 months. Applying these (presumably the highest possible) laboratory rates to the natural population in the GOA would yield potential individual fecundity of 1148 – 1530 eggs per season. Our projection is similar to estimates for *E. pacifica* in Puget Sound (Ross et al., 1982) and the Japan Sea (Ponomareva, 1966), but substantially lower than those made off the Oregon coast (Feinberg and Peterson, 2003; Feinberg et al., 2003). In contrast, *T. inermis* are assumed to release eggs only once in a spawning season and they may breed in two or more successive years (e.g. Timofeyev, 1996). Both the mean and maximum brood sizes of *T. inermis* are larger than those of *E. pacifica*, falling well within their reported range (Zelikman, 1958; Ponomareva, 1966; Dalpadado and Ikeda, 1989; Dalpadado and Skjoldal, 1991), but, for the first time, we document that the egg release of *T. inermis* can take up to 3 days.

Euphausiid spawning strategies appear to be linked to the differences in food supply in specific environments. In *Meganyctiphanes norvegica* from the Mediterranean, the ovary appears to continually produce new yoke throughout the season, and oocyte development is progressive, allowing rapid successive production of smaller batches of eggs (Cuzin-Roudy and Buchholz, 1999). Alternatively, in the Antarctic *E. superba,* the yoke develops in successive batches at the start of ovarian maturation, with the possibility of different stages of oocytes occurring simultaneously in the ovary, leading to pulsed oocyte production with larger batches of eggs per individual (Ross and Quetin, 2000). The former strategy is effective when food availability is sufficient during a longer spawning season, while the latter works better when food supply oscillates between brief peaks of excess and long periods of deficiency. The morphology of the *E. pacifica* feeding basket allows effective retention of particles > 5 μm (Suh and Choi, 1998), thus enabling these oceanic animals to feed on smaller diatoms, dinoflagellates and microzooplankton, which are usually abundant throughout the summer in the North Pacific. In contrast, coastal *T. inermis* consume larger diatom cells comprising nearshore spring phytoplankton blooms in northern latitudes (Ponomareva, 1966), and it is also uses accumulated lipid reserves for spring reproduction (Falk-Petersen et al., 1999, cited after Ross and Quetin, 2000). Therefore, the observed differences in timing, frequency, magnitude and factors controlling *E. pacifica* and *T. inermis* reproduction may reflect distinctive spawning strategies they employ to maximize the spawning success in oceanic and coastal habitats.

We found that *E. pacifica* in the northern GOA produced two distinct types of eggs with embryo/egg capsule ratios of 0.52 and 0.78 (Table 1.2). Larger egg capsules with a thicker perivitelline space (embryo/egg capsule ratio of 0.55-0.59) were reported from the western Pacific (Pogodin, 1982; Suh et al., 1993), while those with the greater ratio were observed only in the eastern Pacific (embryo/egg capsule ratio of 0.83) (Brinton et al., 2000). The perivitelline space protects the embryo (Pechenik, 1979; Rass, 1982; Timofeev, 1996) and increases buoyancy of the egg (Timofeev, 1990). The development of perivitelline space is thought to be controlled by environmental conditions (e.g. temperature and salinity), rather than genetics (Marschall, 1983; Timofeev, 1996). It is tempting to suggest that the appearance of larger eggs in the northern GOA results from exposure to the harsh subarctic environment, facilitating better protection and dispersal. However, the occurrence of larger *E. pacifica* eggs in the warm Yellow Sea (Suh et al., 1993) implies that some other factors influence the determination of egg size in this species. The documented occurrence of eggs belonging to the same species but of drastically different proportions indicates that extreme caution must be exercised when identifying the eggs in zooplankton samples based on size proportions.

The general lack of data on rates of early development of the North Pacific euphausiids is probably explained by uncertainties in identification of eggs and larvae collected in the field. Pogodin (1980) reported development times for *Thysanoessa* spp. larvae from egg to C1 as 12-13 days at 7 to 8 °C in the northern Sea of Japan, without discriminating them by species. The alternative incubation of eggs produced in the laboratory at various temperatures was applied to *E. pacifica* from the Puget Sound and the southern sea of Japan (Ross, 1981; Iguchi and Ikeda, 1994). It was concluded that *E. pacifica* early stages can tolerate wide range of temperature (5-20°C), but that these rates required further confirmation from other regions (Iguchi and Ikeda, 1994).

This study confirms that the cumulative duration of non-feeding stages of *E. pacifica* from hatching till molting into C1 was temperature dependent, and allows quantification of this relationship (Fig. 1.6). Other measurements done on *E. pacifica* from other parts of the North Pacific also fit close to the regression line. The available data for *E. pacifica*, therefore, suggest that this species has a consistent temperature – stage duration relationship. Our data for *T. inermis*, and data for other broadcast spawning euphausiid species from the literature, appear to fit the trendline as well, suggesting this relationship may be applied to a variety of euphausiid species inhabiting temperate waters.

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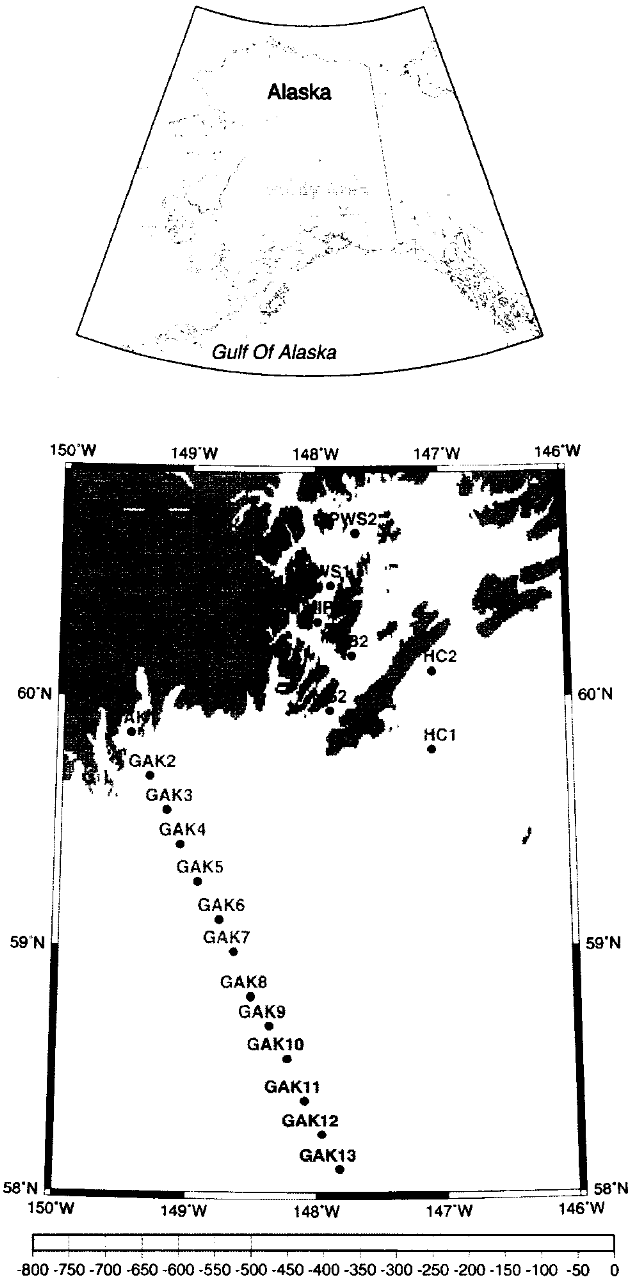

Figure 1.1 Map of sampling locations in the Gulf of Alaska.

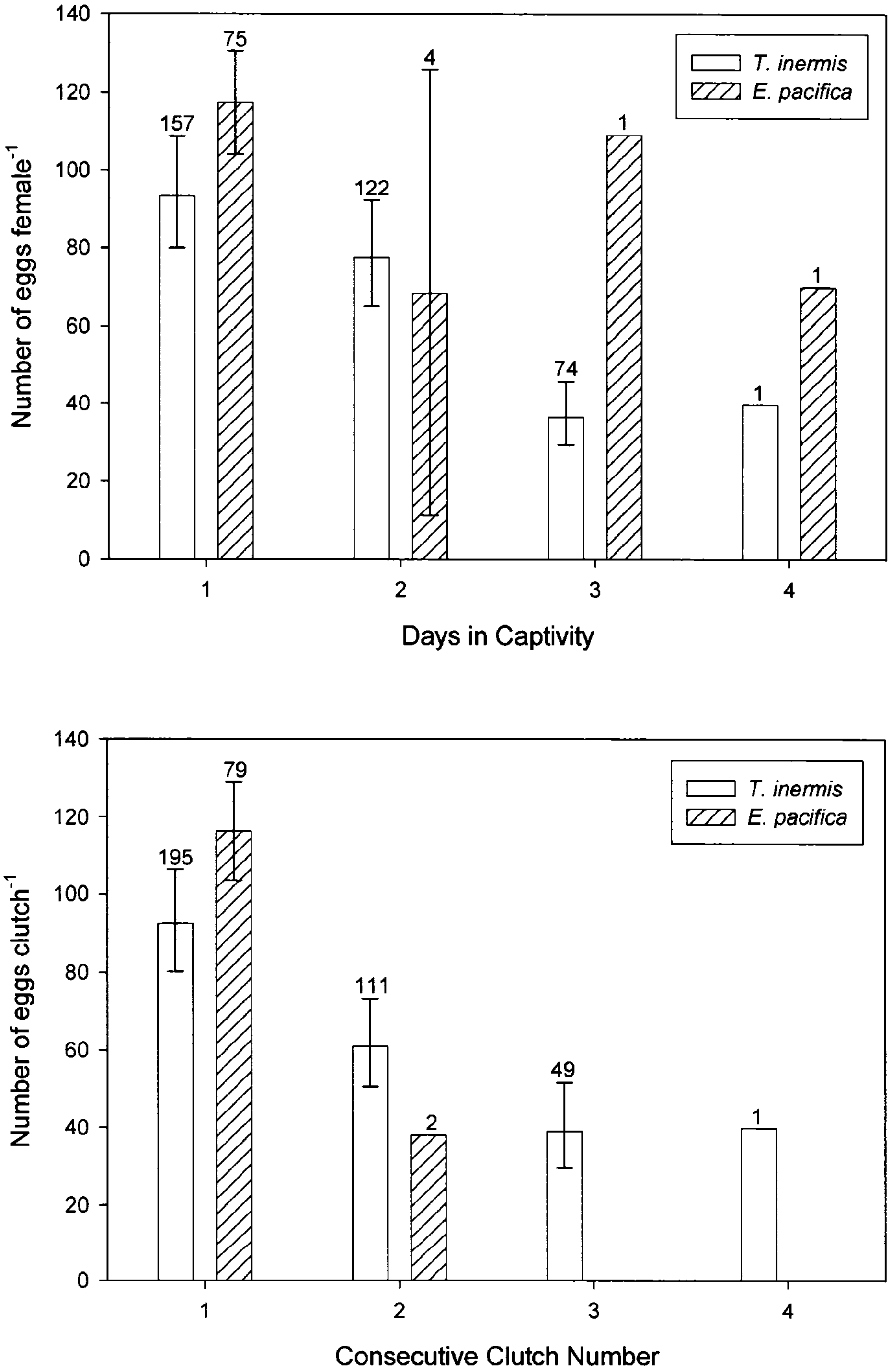

Figure 1.2 Egg release of *Thysanoessa inermis* and *Euphausia pacifica* in the northern Gulf of Alaska. Error bars indicate 95% confidence interval. Numbers above the bars are the number of observations.

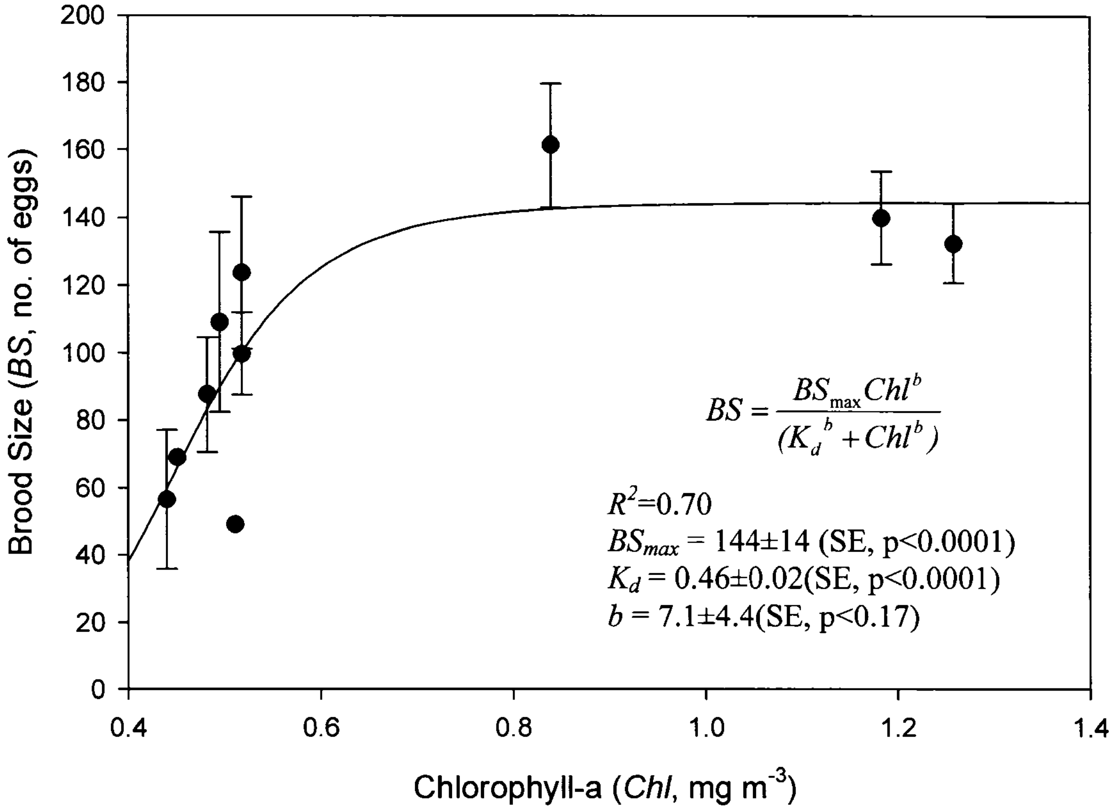

Figure 1.3 Functional relationship between mean brood size of *Euphausia pacifica* and chlorophyll-*a* concentration approximated with the sigmoidal Hill function (vertical bars – SE).

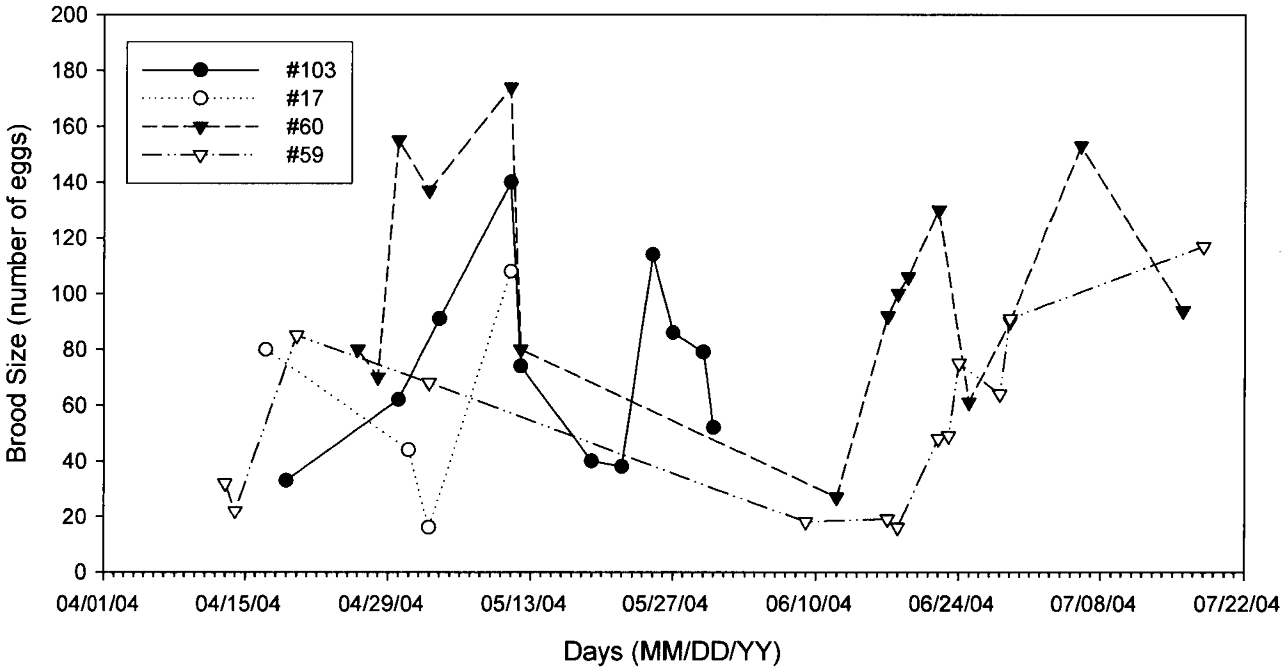

Figure 1.4 Spawning of four laboratory-reared *Euphausia pacifica* females (with numbers assigned).

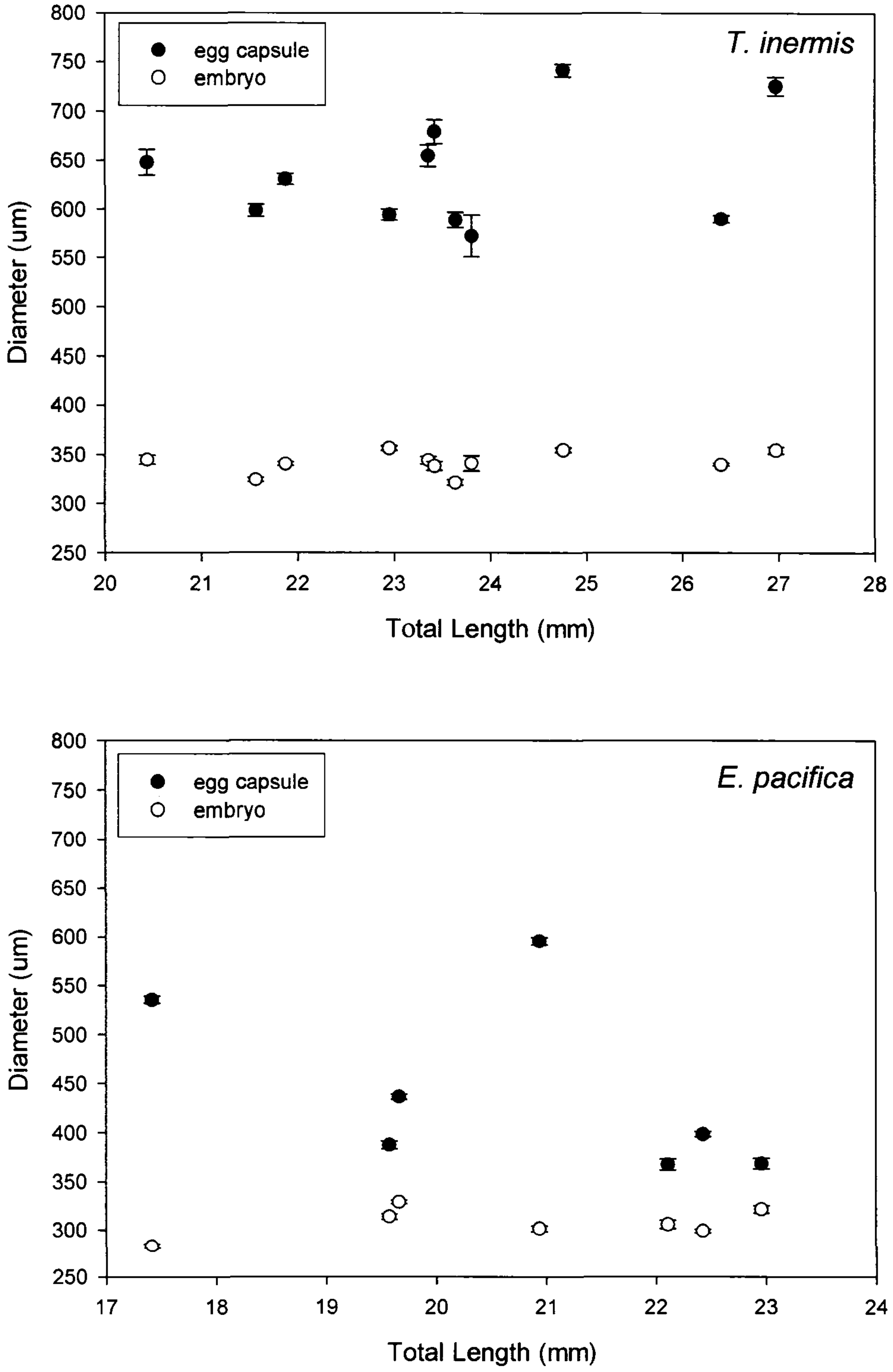

Figure 1.5 Size of egg capsules and embryos vs. carapace length of females in *Thysanoessa inermis* and *Euphausia pacifica* from the northern Gulf of Alaska.

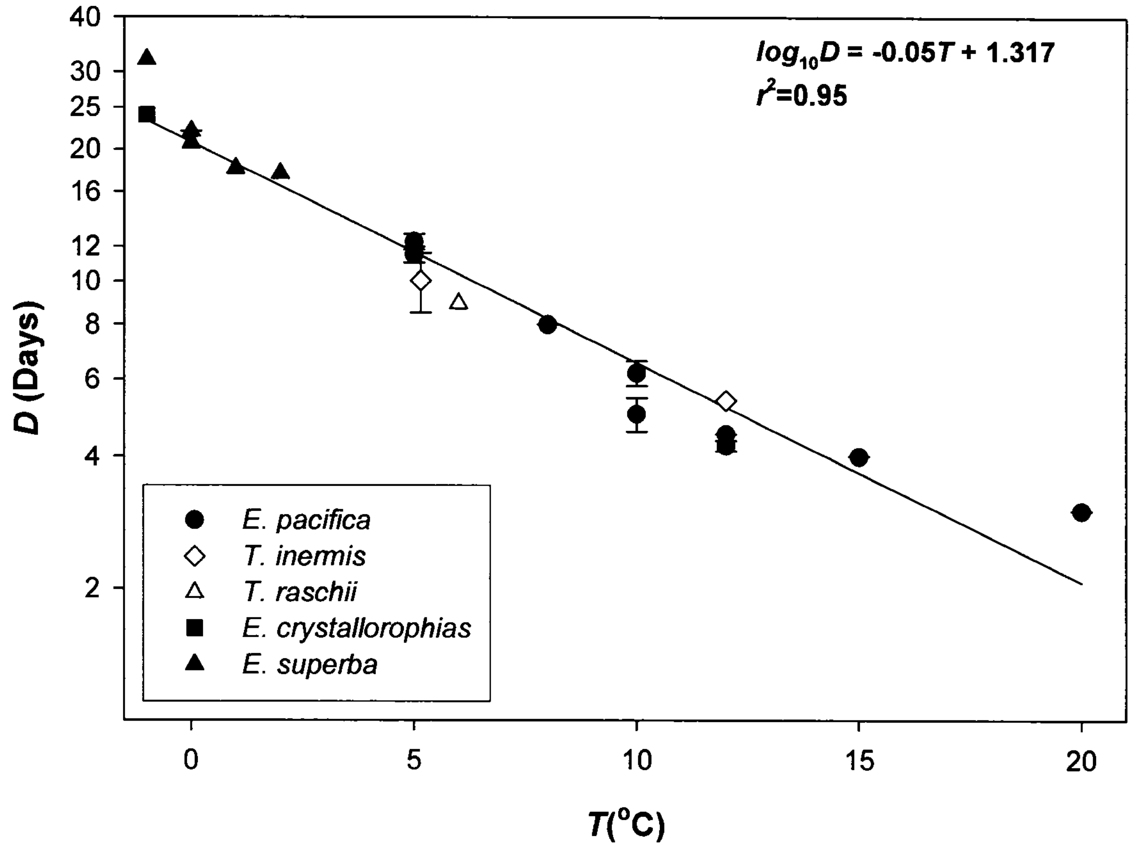

Figure 1.6 Developmental time (D, days with 95% confidence intervals) from hatching to calyptopis 1 and temperature (T, °C) based on our results and on data available in literature (*Euphausia pacifica* from Ross 1981, Iguchi and Ikeda 1994; *E. superba* from Ikeda 1984, Ross et al 1988; *E. crystallorophias* from Ikeda 1986; *Thysanoessa raschii* from Smith 1991).

Table 1.1 Summary of euphausiid egg production experiments in the northern Gulf of Alaska in 2001-2004 indicates season and location where gravid females where collected, temperature the females were incubated (T°C), and number of females that produced eggs (N).

	2001			2002			2003			2004		
	Station	T°C	N	Station	T°C	N	Station	T°C	N	Station	T°C	N
T. inermis												
April		-		GAK11	5	44	GAK4	5	2		-	
				GAK3	5	37	GAK6	5	12		-	
							GAK1	5	19		-	
May		-		GAK4	5	30		-			-	
				GAK7	5	53		-			-	
E. pacifica												
July	GAK9	8	4	GAK5	12	1	GAK8	12	10	GAK3	12	4
	GAK7	8	2									
August	GAK12	12	18	GAK11	12	3		-			-	
	GAK9	12	1									
	GAK6	12	9									
	GAK1	12	26									
October	GAK13	10	7		-						-	

Table 1.2 Egg capsule, embryo and brood sizes in *Thysanoessa inermis* and *Euphausia pacifica* (mean values are with 95% CI unless otherwise noted).

Species/Region	Egg Capsule (um)		Embryo (um)		Brood Size (no. eggs)		Reference
	Mean Diameter	Range	Mean Diameter	Range	Mean	Range	
Euphausia pacifica							
Gulf of Alaska all	439±6	334-643	309±2	240-362	102±12	6-246	Present study
large	561±6	505-643	290±3	240-332			
small	404±3	334-480	314±2	279-362			
Eastern Pacific	400	360-420	330	300-340	-	-	Brinton et al 2000
Yellow Sea	580±30 (SD)	500-680	340±10(SD)	300-380	-	-	Suh et al 1993
Northern Japan Sea	550	425-625	300	250-375	-	-	Pogodin 1982
Southern Japan Sea	460±20	430-505	-	-	-	12-296	Iguchi and Ikeda 1994
Puget Sound							Ross et al 1982
small females	-	-	-	-	60±21	3-265	
large females	-	-	-	-	132±79	71-234	
Thysanoessa inermis							
Gulf of Alaska	641±35	478-792	344±8	300-409	138±19	5-1021	Present study
Western Barents Sea	730	620-860	-	380-400	-	32-110	Dalpadado and Ikeda 1989 Dalpadado and Skjoldal 1991
Southern Barents Sea	-	575-950	-	325-475	-	350-600	Timofeev 1996
Japan Sea	-	560-900	-	-	-	-	Ponomareva 1966
North Atlantic	-	730-760	320	-	-	-	Lebour 1924

Table 1.3 The Intermolt Periods (IP) in days for early stages of *Thysanoessa inermis* and *Euphausia pacifica*, measured at different temperatures.

Stage	*Thysanoessa inermis*						*Euphausia pacifica*							
	5°C		8°C		12°C		5°C		8°C		10°C		12°C	
	IP±95%CI	n	IP±95%CI	n	IP±95%CI	n	IP±95%CI	n	IP±95%CI	n	IP±95%CI	n	IP±95%CI	n
Egg	2.5±0.2	112	1.5±0.4	25	-	-	2.6±0.3	69	1.8±0.2	160	1.2±0.3	70	1.1±0.56	32
N1	1.8±0.2	89	1.5±0.4	25	0.7±0.5	47	1.6±0.3	69	1.2±0.2	159	1.1±0.3	70	0.9±0.5	28
N2	4.1±0.2	84	-	-	1.6±0.5	47	3.6±0.3	69	1.5	3	1.0±0.3	70	1.1±0.5	28
MN	4.3±0.7	9	-	-	2.8±0.4	69	6.4±0.2	144	-	-	2.9±0.3	70	2.3±1.0	7
C1	6.9±0.8	8	-	-	4.8±0.3	44	13.4±0.2	144	-	-	6.9±0.3	70	5.1±1.3	4
C2	6.9±0.8	7	-	-	5.8±0.4	31	9.2±0.2	118	-	-	7.5±0.4	53	4.3±1.5	3
C3	6.3±0.8	7	-	-	5.9±0.4	33	9.1±0.3	86	-	-	6.9±0.7	16	-	-
F1	-	-	-	-	5.3±0.7	9	9.4±1.0	7	-	-	-	-	-	-

CHAPTER 2

Seasonal variations in the growth rates of euphausiids (*Thysanoessa inermis*, *T. spinifera*, and *Euphausia pacifica*) from the northern Gulf of Alaska[2]

2.1 Abstract

The euphausiids *Thysanoessa inermis* (Kroyer, 1846), *Thysanoessa spinifera* (Holmes, 1900) and *Euphausia pacifica* (Hansen, 1911) are key pelagic grazers and also important prey for many commercial fish species in the Gulf of Alaska (GOA). To understand the role of the euphausiids in material flows in this ecosystem their growth rates were examined using the instantaneous growth rate (IGR) technique on the northern GOA shelf from March through October in 2001-2004. The highest mean molting increments (over 5% of uropod length increase per molt) were observed during the phytoplankton bloom on the inner shelf in late spring for coastal *T. inermis,* and on the outer shelf in summer for more oceanic *T. spinifera* and *E. pacifica*, suggesting tight coupling with food availability. The molting rates were higher in summer and lower in spring, for all species and were strongly influenced by temperature. Mean inter-molt periods calculated from the molting rates, ranged from 11 days at 5°C to 6 days at 8°C, and were in agreement with those measured directly during long-term laboratory incubations. Growth rate estimates depended on euphausiid size, and were close to 0 in early spring, reaching maximum values in May (0.123 mm d^{-1} or 0.023 d^{-1} for *T. inermis*) and July (0.091 mm d^{-1} or 0.031 d^{-1} for *T. spinifera*). The growth rates for *E. pacifica* remained below 0.07 mm d^{-1} (0.016 d^{-1}) throughout the season. The relationship between *T. inermis* weight specific growth rate (adjusted to 5°C) and ambient chlorophyll-*a* concentration fit a Michaelis-Menten curve (r^2=0.48) with food saturated growth rate of 0.032 d^{-1} with half saturation (K_d) occurring at 1.65 mg chl-*a* m^{-3}, but such relationships were not significant for *T. spinifera* or *E. pacifica.*

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[2] Pinchuk AI, Hopcroft RR (2006) Seasonal variations in the growth rates of euphausiids from the northern Gulf of Alaska. Mar Biol (in press)

2.2 Introduction

The euphausiids *Thysanoessa inermis* (Kroyer, 1846), *Thysanoessa spinifera* (Holmes, 1900) and *Euphausia pacifica* (Hansen, 1911) occupy a key role in the northern Gulf of Alaska (GOA) ecosystem, both as pelagic grazers and a prey for many vertebrates. These species undergo extensive diel vertical migrations (e.g. Mauchline 1980) and are thought to feed on a variety of phyto- and microzooplankton, as well as suspended organic matter (Ponomareva 1966; Dilling et al. 1998; Bargu et al. 2003; Nakagawa et al. 2001, 2004). They 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 (e.g. Wilson et al. 2006), herring (e.g. Hart 1973), and sablefish (e.g. Sigler et al. 2001), as well as seabirds and baleen whales (Mauchline 1980). In order to appreciate the role of euphausiids in material flow and transformation in the ocean, it is essential that their rates of growth and production, and the factors controlling these rates are understood.

The growth of oceanic zooplankton, including euphausiids, is governed primarily by temperature and food (e.g. Huntley and Boyd 1984; Clarke and Peck 1991; Hirst et al. 2003). Both factors undergo substantial seasonal variability in high latitudes. Euphausiids may respond to changes in these factors in two ways: by altering the duration of the intermolt period, and by changing the growth increment (Buchholz 1991; Iguchi and Ikeda 1995). The intermolt period is thought to be affected mainly by temperature (e.g. Kawaguchi et al. 2006, Tarling et al, 2006) and to a smaller degree by individual size (Fowler et al. 1971; Iguchi and Ikeda 1995). In contrast, the growth increment appears to be strongly influenced by quantity and quality of food (Iguchi and Ikeda 1995; Ross et al. 2000) and may become negative under unfavorable conditions leading to body shrinkage (Nicol et al. 1992; Marinovic and Mangel 1999).

Traditionally, growth rates measurements on *T. inermis*, *T. spinifera* and *E. pacifica* in the North Pacific were estimated using the natural cohort technique (e.g. Smiles and Pearcy 1971; Tanasichuk 1998a, 1998b; Smith 1991). The primary assumptions of this method are that the same population is observed over time, and that mortality of individuals is not size-dependent (Quetin et al. 2003). These assumptions are most likely violated on the northern GOA shelf due to the rugged topography, strong currents and abundant euphausiid predators of different size and hunting habits. An alternative incubation technique, allowing direct measurement of both molting frequency and growth increments, has been applied to *E. pacifica* (Iguchi and Ikeda 1995). However, the long periods of incubation required by this approach at low subarctic temperatures may introduce artifacts and errors to the rates being measured. In contrast, the instantaneous growth rate (IGR) incubation technique (Quetin and Ross 1991) permits measurement of both components of euphausiid growth in relation to environmental factors over relatively small temporal and spatial scales without needing to comply to population constancy and size-independent mortality assumptions (Quetin et al. 2003). With the IGR method, experiments with freshly collected krill are likely to reflect the natural growth rate of individuals in the field (Nicol 2000; Ross et al. 2000). The IGR method has been applied to study various aspects of Antarctic krill growth (e.g. Nicol et al. 1992; Ross et al. 2000; Atkinson et al. 2006; Tarling et al. 2006), and was recently applied to euphausiid populations off the Oregon coast (Shaw et al. 2004).

Despite the evident importance of euphausiids in the northern GOA shelf ecosystem, information on their growth rates within the temperature range of the GOA is absent. The U.S. North Pacific GLOBEC Long Term Observation Program (LTOP) in the northern Gulf of Alaska seeks to address such deficiencies in our knowledge (Weingartner et al. 2002). In the present study, we document seasonal variability in growth rates of the major euphausiid species from the northern GOA measured with the IGR technique, examine factors controlling euphausiid growth throughout the productive season, and compare euphausiid growth rates with those of copepods in the context of the GOA food web.

2.3 Methods

Euphausiids were collected along the Seward Line and within Prince William Sound in the northern Gulf of Alaska (GOA) during GLOBEC LTOP cruises in 2001-2004 (Fig. 2.1). Night-time euphausiid aggregations were located in the upper 50 m of the water column with an HTI acoustic system, then fished using a 1 m^2 MOCNESS equipped with black 100 μm mesh nets and non-filtering cod-ends, towed at 0.25-0.5 m s^{-1}. Collections were immediately diluted into a 20-l pail to facilitate sorting. Active, undamaged euphausiids were gently removed from the catch and placed individually in 750 ml tissue-culture flasks filled with seawater collected simultaneously at the site. No distinction between the euphausiid species were done at the time of collection to minimize handling time. Therefore, most of the experiments contained individuals of more than one species (Table 2.1). Water samples for fluorometric estimation of chlorophyll-*a* concentration were collected at these stations by Niskin bottles and the chl-*a* concentration was averaged over the upper 50 m of the water column (D.A. Stockwell and T.E. Whitledge, unpubl. data). The euphausiids were maintained at near ambient mixed layer water temperature (5°C in March-May, 8-12°C in July-August and 10°C in October) in darkness and were checked every 12-24 hours for molts. If an individual molted, the exuviae and the individual were preserved in 5% formalin. At the end of each experiment, all remaining euphausiids were preserved.

To estimate the magnitude of possible negative growth (body shrinkage), several experiments lasting 10 to 20 days under restricted-food conditions were conducted in April-May (at 5°C) and July-August (at 8°C) of 2001 (Table 1). The euphausiids were placed in filtered seawater upon arrival at the lab (2 to 3 days after collection) with no food subsequently added and water changed once a week. The duration of experiments conducted in 2002-2004 was 48 hours. Molting rates (*MR*, % population day^{-1}) were determined in each experiment only for species that totaled more than 30 individuals. Intermolt periods (*IP*, days) were directly measured during the long-term experiments, and calculated for short-term incubations as the inverse of the observed *MR*.

All length measurements were made digitally to ±1 μm with an accuracy of ±5 μm (Roff and Hopcroft 1986). The lengths of exopodites of both uropods (mm) were measured on all molts (UL_m) and preserved euphausiids (UL_p), and then averaged. Sometimes, one of the uropods was damaged and therefore was not measured. In these cases, the measurements were based on a single molt and postmolt uropod pair. If both uropods were damaged then the individual was used only for the *MR* calculations. Individual length-specific molting increment (*MI*) was computed as:

$$MI = \frac{UL_p - UL_m}{UL_m} * 100 \ (\%).$$

Mean *UL* in experiments was 2.26 mm (range 1.11-2.99 mm, SD=0.35, n=451) for *T. inermis*; 2.21 mm (range 0.77-3.57 mm, SD=0.53, n=227) for *T. spinifera*; and 2.79 mm (range 1.2-3.7 mm, SD=0.43, n=281) for *E. pacifica.*

The relationships between *UR*, *CL* and *TL* were estimated using linear regressions for euphausiids from the GOA collected in March of 1999 as outlined in Coyle and Pinchuk (2005). Carapace length (*CL*, mm) was measured from the tip of the rostrum to the posterior dorsal margin of the carapace. The total length (*TL*, mm) was defined as distance from the tip of the rostrum to the distal end of the telson excluding spines. No correction was made for shrinkage of *TL* in formalin preserved samples. The *TL* range of specimens used to establish equations was 7.6-24.1 mm for *T. inermis*, 10.2-30.4 mm for *T. spinifera* and 3.0-20.5 mm for *E. pacifica*:

$CL = 3.07UL - 1.11(n{=}239, r^2{=}0.88)$ for *T. inermis*

$CL = 2.56UL - 0.69\ (n{=}621, r^2 = 0.85)$ for *T. spinifera*

$CL = 1.48UL + 0.25\ (n{=}340, r^2 = 0.86)$ for *E. pacifica*

$TL = 2.46CL + 2.99\ (n{=}246, r^2{=}0.92)$ for *T. inermis*

$TL = 2.57CL + 2.76\ (n{=}224, r^2{=}0.88)$ for *T. spinifera*

$TL = 3.76CL + 0.87\ (n{=}266, r^2{=}0.94)$ for *E. pacifica*

The relationships between *CL* and dry weight (*DW*, mg) were determined using log-transformed linear regressions. The euphausiids were collected from the study area in 1998-1999 (Coyle and Pinchuk 2005), frozen and transferred to the Seward Marine Center laboratory, where they were thawed, dried at 60°C and weighed to ± 1 μg on a

Cahn microbalance. The *CL* range of specimens used to establish equations was 3.0-10 mm for *T. inermis*, 1.9-12.0 mm for *T. spinifera* and 1.9-7.5 mm for *E. pacifica*:

$\log DW = 2.50 \log CL - 1.162$ (n=838, r^2=0.79) for *T. inermis*
$\log DW = 3.39 \log CL - 1.854$ (n=2531, r^2=0.87) for *T. spinifera*
$\log DW = 3.03 \log CL - 1.161$ (n=945, r^2=0.89) for *E. pacifica*

To facilitate better comparison with published data, these regressions were used to compute length and weight growth rates between moltings as:

$$G_L = \frac{TL_p - TL_m}{IP} \text{ (mm d}^{-1}\text{) and,}$$

$$G_W = \frac{DW_p - DW_m}{IP} \text{ (mg d}^{-1}\text{),}$$

and weight-specific growth rates between moltings as:

$$g_w = \frac{\ln DW_p - \ln DW_m}{IP} \text{ (d}^{-1}\text{).}$$

All data were uploaded into a MS ACCESS database and analyzed using standard STATISTICA and SigmaPlot 8.0 routines. Factorial ANOVA was run to test for inter-annual and seasonal differences in *MI* and *MR* of each species. To elucidate the relative importance of major factors controlling growth, backwards stepwise-regression analyses were done separately on each euphausiid species. The dependent variables were *MI* and *MR,* and the independent variables were daily mean temperature (*T*, °C) and chl-*a* concentration (*Chl*, mg m^{-3}). Since euphausiids display an asymptotic growth pattern (e.g. Tanasichuk 1998a, 1998b), their length-specific growth increments tend to decrease when individual size increases. While the proportion of *CL* to TL in euphausiids is known to change when mature, and often differs between males and females (e.g. Miller 1983; Timofeev 1996), *TL* is subject to severe shrinkage after preservation (e.g. Kulka and Corey 1982). Since we did not have an opportunity to freeze the individuals after the shipboard experiments, rigid *CL* was chosen to provide a measure of individual size.

Therefore, CL_m was added as an independent variable when analyzing *MI*. Euphausiid size was not included when analyzing *MR*, since the estimates of *MR* were obtained for a population in an experiment, rather than derived from individual measurements. P-to-enter was set at 0.049 and P-to-remove at 0.05. Then multiple linear regressions relating *MI* and *MR* to the remaining variables were completed and standardized regression coefficients computed.

To quantify relationships between g_w and *Chl* alone, the individual values were averaged for each experiment, adjusted to 5°C using Q_{10} of 2.25 (Winberg 1983; Iguchi and Ikeda 1995), and then fit to a Michaelis–Menten uptake function curve expressed as:

$$g_w = \frac{g_{w_{\max}} Chl}{K_d + Chl}, \text{ where}$$

$g_{w_{\max}}$ is the asymptotic g_w, and K_d is half-saturation constant. Since euphausiids may experience negative growth, the data were transformed by adding a positive factor of 0.004 before fitting and estimated values $g_{w_{\max}}$ were converted back afterwards.

2.4 Results

2.4.1 Seasonal variability in the environment

The mean temperature was ~5°C throughout the water column from March through May (Fig. 2.2a). 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 6°C) throughout the year. The mean water column chl-*a* content was low (<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. 2.2b). In summer and fall, chl-*a* content decreased to ~0.7 mg m^{-3}, and in December it was <0.5 mg m^{-3}.

2.4.2 Seasonal variability in euphausiid growth

While there were no significant inter-annual differences in euphausiid length-growth, seasonal patterns affecting both *MI* and *MR* were distinctive for all three species, despite the large individual variability observed. The minimal *MI* values were observed in

March, indicating close to zero growth or shrinkage (Fig. 2.3). Growth intensified through the spring, peaking in May with ~5% change in *UL* per molt for *T. inermis*. By the mid-summer, the *MI* values decreased significantly for *T. inermis*, while remaining high for other species. In late summer, *MI* values of *T. inermis* were near 0%, with a slight increase during October. In contrast, *T. spinifera* had a less modulated *MI* of ~2 to 4% change in *UL* from April through the end of production season. For *E. pacifica* the pattern was most similar to that of *T. inermis*, but it maintained a positive *MI* throughout the summer and fall. In contrast to *MI*, the highest mean *MR* (14-16% of population d^{-1}) were recorded in July-August for all species, while the lowest mean *MR* (~6-10% of population d^{-1}) were consistently observed in March through May (Fig. 2.4). In October, the mean *MR* was intermediate (~10% of population d^{-1}).

The major factors controlling the *MI* in the experiments were chl-*a* concentration (positive correlation) and body size (negative correlation), while the *MR* depended almost exclusively on water temperature (positive correlation) for all species (Table 2.2). Only *T. inermis* showed a weak negative correlation between the *MI* and temperature, and a positive correlation between the *MR* and chl-*a* content.

Two distinctive size groups were found in experimental populations for all three species, visually separated at 2.2 mm UL (16.9 mm TL) for *T. inermis,* 2.5 mm UL (17.4 mm TL) for *T. spinifera,* and 2.6 mm UL (16.3 mm TL) for *E. pacifica* (Fig. 2.5, insets). Therefore, mean growth rates were calculated per month separately for each size group to account for the effect of body size, revealing that smaller euphausiids grew faster both in terms of length increase (Fig. 2.5) and weight-specific rates (Table 2.3). Distinctive seasonal patterns of growth emerged for *Thysanoessa* species, similarly starting at 0 or negative growth of both size groups in March. In *T. inermis*, small individuals increased growth in April (0.044 mm d^{-1} or 0.034 mg d^{-1}), reached maximal growth in May during the spring bloom (0.123 mm d^{-1} or 0.109 mg d^{-1}), remained high in July and decreased (0.019 mm d^{-1} or 0.013 mg d^{-1}) in October (Fig. 2.5). Large euphausiids also maintained positive growth in April (0.023 mm d^{-1} or 0.029 mg d^{-1}), with maximum rates in May (0.102 mm d^{-1} or 0.121 mg d^{-1}), but showed negative or 0 growth from July through

October (to −0.025 mm d^{-1} or −0.028 mg d^{-1}). While small *T. spinifera* also showed highest growth rates in May (0.091 mm d^{-1}), they grew steadily throughout the season decreasing to 0.02-0.03 mm d^{-1} only in October. The growth of large *T. spinifera* was constantly low (<0.02 mm d^{-1}) through most of the season. In contrast, *E. pacifica* did not show any distinctive seasonal growth pattern, with growth rates for small individuals remaining constantly low (<0.07 mm d^{-1}) from spring to fall, and large individuals growing slightly slower (Fig. 2.5).

After removing temperature effect on growth, through Q_{10} standardization, the relationship between the mean g_w and ambient chl-*a* concentration fit to a Michaelis-Menten form best for *T. inermis* (r^2=0.48) with food-saturated weight specific growth rate ($g_{w_{\max}}$) of 0.032±0.008 (*SE*, p<0.001) d^{-1} and half saturation (K_d) occurring at 1.65±0.74 (p=0.03) mg chl-*a* m^{-3}. There were poor fits (r^2<0.1) for *T. spinifera* and *E. pacifica* (Fig. 2.6), suggesting that other factors contribute substantially to variations in the g_w of these species. Inclusion of body weight in addition to the Michaelis-Menten relationship to chl-*a* did not substantially improve the model, likely because the weight ranges of euphausiids used in the experiments were not broad enough to resolve the differences in the weight specific growth rates.

2.4.3 The influence of starvation on euphausiid growth

While individual euphausiid *MI* remained positive during the first 4 days following collection, shrinkage in length was subsequently observed for all species, reflecting generally unfavorable food conditions (Fig. 2.7). Once turned negative after day 5, the *MI* appeared to remain constant averaging −4.37±0.27% (SE, n=166) for *E. pacifica*, −3.07±0.33% (n=110) for *T. inermis,* and −3.22±1.05% (n=11) for *T. spinifera*, with minimal values of about −10% occurring in all species. The intermolt periods measured directly during the long-term incubations were significantly (P<0.05) different for selected temperatures and closely corresponded to our estimates derived from the shipboard experiments (Table 2.4). There were no substantial differences between consecutive intermolt periods for all species at any given temperature (Table 2.4).

2.5 Discussion.

In this study, strong and distinct seasonal patterns were found in several of the metrics used to describe growth in euphausiids. Molt rate was most strongly governed by temperature, while growth increment was affected by food and body-size. Weight-specific growth was governed by all three. While the effect of temperature on the euphausiid *MR* and intermolt period (*IP*) has long been recognized (e.g. Lasker 1966; Fowler et al. 1971; Sameoto 1976; Dalpadado and Ikeda 1989; Quetin et al. 1994), the effects of food and body size remain less studied. Consistent with our observations, growth increment appears to remain uninfluenced by temperature in euphausiids (Iguchi and Ikeda 1995) as well as other pelagic crustaceans such as mysids and amphipods (Gaudy and Guerin 1979; Ikeda 1990). However, Atkinson et al (2006) showed a significant relationship between growth increment and temperature for Antarctic krill (*Euphausia superba*) with the former being maximal at 0.6°C. The IP of *E. pacifica* also tends to increase with increasing individual size (Fowler et al. 1971; Iguchi and Ikeda 1995). Extensive field studies on *E. superba* indicate that effects of food availability, size and other factors (such as synchrony of molting) are superimposed on the effect of temperature (Quetin et al. 1994). In contrast to initial observations on *E. pacifica* (Lasker 1966), it has now been shown that food-deprived conditions can significantly extend the IP of *E. superba* (Ikeda and Dixon 1982; Ikeda and Thomas 1987). Consistent with our observations, feeding studies on Antarctic krill revealed that their MI is also dependent both on food quantity and quality (Ross et al. 2000).

In the present study, the increase in the MI in May coincided with the increased content of chl-*a* in the water due to the spring phytoplankton bloom. In contrast, the MR increased later in the season when the summer stratification resulted in development of warm surface layer. The multiple regression analysis also confirmed that temperature is the major factor controlling molting, while growth increment is limited mainly by food availability. The only exception was *T. inermis,* which showed weak interdependence between MR and chl-*a*, and between MI and temperature. The higher summer temperatures may suppress growth of this cold water species changing the balance of parameters in metabolic responses.

The strong functional relationship between weight-specific growth rates and ambient chl-*a* concentration in *T. inermis* indicates that the growth rate in this species is closely coupled with the availability of phytoplankton. In contrast, the lack of similar relationship in *T. spinifera* and *E. pacifica* suggests that these species rely on prey items other that phytoplankton (see below). Interestingly, the egg production of *E. pacifica* was closely coupled with chl-*a* content (Pinchuk and Hopcroft 2006), which suggests that a phytoplankton diet might be of particular importance for *E. pacifica* reproduction. Recent studies indicate that sex and maturity can influence MI and MR (Atkinson et al. 2006; Tarling et al. 2006). We did not distinguish between males, females and juveniles nor determine maturity stage of euphausiids in our experiments, and this may account for some of the scatter in our data.

The mean weight-specific growth rates of *T. inermis* were highest (0.016-0.023 d^{-1}) in the midst of the phytoplankton bloom in May, while later they decreased to 0.004 d^{-1} for small individuals and to −0.004 for large individuals. Similarly, in the Bering Sea estimated *T. inermis* growth rates were highest in late April and May (0.045-0.06 d^{-1}), decreasing to 0.01-0.013 d^{-1} by June (Smith 1991). In the North Sea, adult *T. inermis* grew at 0.044 mg DW d^{-1} and 0.153 mg DW d^{-1} before and after the bloom, respectively (Lindley and Williams 1980), which is comparable with our estimate of 0.028-0.034 mg DW d^{-1} for April and 0.109-0.120 mg DW d^{-1} in May. Negative growth of −0.0005 d^{-1} for *T. inermis* in winter has been observed off Northern Norway, while the summer growth rates ranged between 0.012-0.007 d^{-1} for different size groups (Hopkins et al. 1984). Our measurements also show negative (−0.001 d^{-1}) or zero growth for *T. inermis* in March. These comparisons emphasize the importance of the spring bloom as a major source of energy for *T. inermis* growth, and suggest that the Bering Sea environment provides better conditions for *T. inermis* growth than more northern and southern parts of its range.

The growth rates of *E. pacifica* also increased slightly during the bloom, but, unlike those of *T. inermis* and *T. spinifera,* did not change throughout the production season, suggesting that this species relies on food sources other than spring diatoms. The morphology of the *E. pacifica* feeding basket allows effective retention of particles >5μm (Suh and Choi 1998), enabling them to consume smaller diatoms, dinoflagellates and microzooplankton, which are usually abundant throughout the summer in the North Pacific (Landry et al. 1993). Our estimates of small *E. pacifica* growth rates (0.02-0.08 mm d^{-1}) are close to those reported for specimens of similar size from Washington (0.05-0.08 mm d^{-1}) (Cooney 1971; Bollens et al. 1992), British Columbia (0.047-0.075 mm d^{-1}) (Hulsizer 1971; Heath 1977, cited after Bollens et al. 1992) and Northern Japan (0.056 mm d^{-1}) (Taki and Ogishima 1997). Not surprisingly, they are lower than growth rates measured at the warmer, southernmost parts of *E. pacifica*'s range (0.07-0.09 mm d^{-1}) off Southern California and Oregon (Smiles and Pearcy 1971; Brinton 1976).

Euphausiids can employ various mechanisms to survive in high latitudes during periods of low food availability in winter. They can rely on lipid reserves accumulated during spring and summer blooms, switch to suitable food, or cease feeding. The latter would result in shrinkage or reduction of metabolic rates. Our mean long-term food-deprivation MI estimates of ~ −3% are similar to those reported for Antarctic krill (Nicol et al. 1992), and it appears that under experimental conditions both the North Pacific and Antarctic euphausiids can achieve a relatively constant shrinkage rate within a few days of food limitation. Our estimates of natural MI show zero or negative growth for all three species in March, suggesting shrinkage occurs November through February. However, the natural shrinkage was substantially less than that observed during food deprivation experiments. This implies that shrinkage and starvation do not reach critical levels and that euphausiids are able to find enough food or to store sufficient reserves to survive through the winter in the northern GOA. Long starvation tends to extend IP of *E. superba* and *Meganyctiphanes norvegica* (Ikeda and Dixon 1982; Buchholz 1985), but the effect does not necessarily become significant after the first sequential molts. The lack of a significant increase in IP in our long-term experiments suggests that their duration was not long enough (at the given temperature), or that the euphausiids were still using lipid reserves to maintain constant metabolic rates.

An important caveat in the interpretation of our results is that that length is an imperfect estimate of growth in terms of mass. The IGR technique as employed here only considers somatic growth in length, and length increase for females may be curtailed when resources are shifted into ovary development and egg production, or to lipid deposition rather than structural tissue as the autumn approaches, resulting in increased weight without increasing length. Our observations of the lack of positive growth in *T. inermis* in winter, intensive growth during the spring bloom, and its consequent decrease, reflect these ontogenetic changes. The cold water *T. inermis* is known to be herbivorous and heavily dependent on spring and summer phytoplankton blooms for accumulating wax esters (up to 50% of its dry weight) and achieving quick somatic growth (Falk-Petersen et al. 1981, 2000), while during winter only minor food intake occurs, and the lipid stores are mobilized to sustain the animals and to fuel the single reproductive effort the following spring (Falk-Petersen et al. 2000, Pinchuk and Hopcroft 2006). *E. pacifica* is capable of producing multiple broods (average 102 eggs brood^{-1}) every 8 days throughout summer in the northern GOA (Pinchuk and Hopcroft 2006). Assuming egg DW of 3.3 μg (Iguchi and Ikeda 1994), this would require additional investment of 0.042 mg DW d^{-1} not accounted for in IGR estimates. Both these possibilities may have hampered our ability to fully understand the factors affecting somatic growth in all three species in terms of length increment and the predicted weight-specific growth.

Given our new appreciation of euphausiid rates in the GOA, it is instructive to consider their potential importance in comparison to the calanoid copepods that generally dominate this ecosystem both by abundance and biomass (Coyle and Pinchuk 2003). The temperature-adjusted weight-specific growth rates of euphausiids are considerably lower than those of the dominant copepods from the northern GOA (Table 2.5). This may lead to a hasty conclusion that euphausiids have limited impact on phytoplankton compared to copepods. However, euphausiids on average use ~66-75% of their assimilated carbon in respiration (Lasker 1966; Ross 1982), while copepods respire ~50% (Vidal 1980), a difference likely reflecting the more active swimming behavior of euphausiids. Furthermore, the weight-specific assimilation of *Calanus pacificus* at 12°C ranges between 29-66% d^{-1} (Vidal 1980), while that of *E. pacifica* is only 5-7% d^{-1} (Lasker 1966; Iguchi and Ikeda 1999). This is not surprising, since the assimilation rate must be equal to the sum of rates of anabolic and catabolic processes, and, therefore, the weight-specific rate of assimilation typically decreases with increasing body size (Vidal 1980). Since the dry weight of *C. pacificus* is generally 10 folds less than that of *E. pacifica*, it thus appears that, on balance, the weight-specific feeding demands of euphausiids are similar to those of copepods.

On the GOA shelf, copepod biomass is usually 6-35 times more than that of euphausiids during the spring bloom, but becomes almost the same in late summer and fall (Coyle and Pinchuk 2003). At the same time, euphausiids can form short-lived dense aggregations (Endo et al. 1985; Hanamura et al. 1989) ultimately dominating other zooplankton taxa. Because of such enormous seasonal and spatial disproportions in their distributions, mesoscale advection processes and predation likely determine the relative biomass, and hence importance, of these two groups in the zooplankton community at a given place and time.

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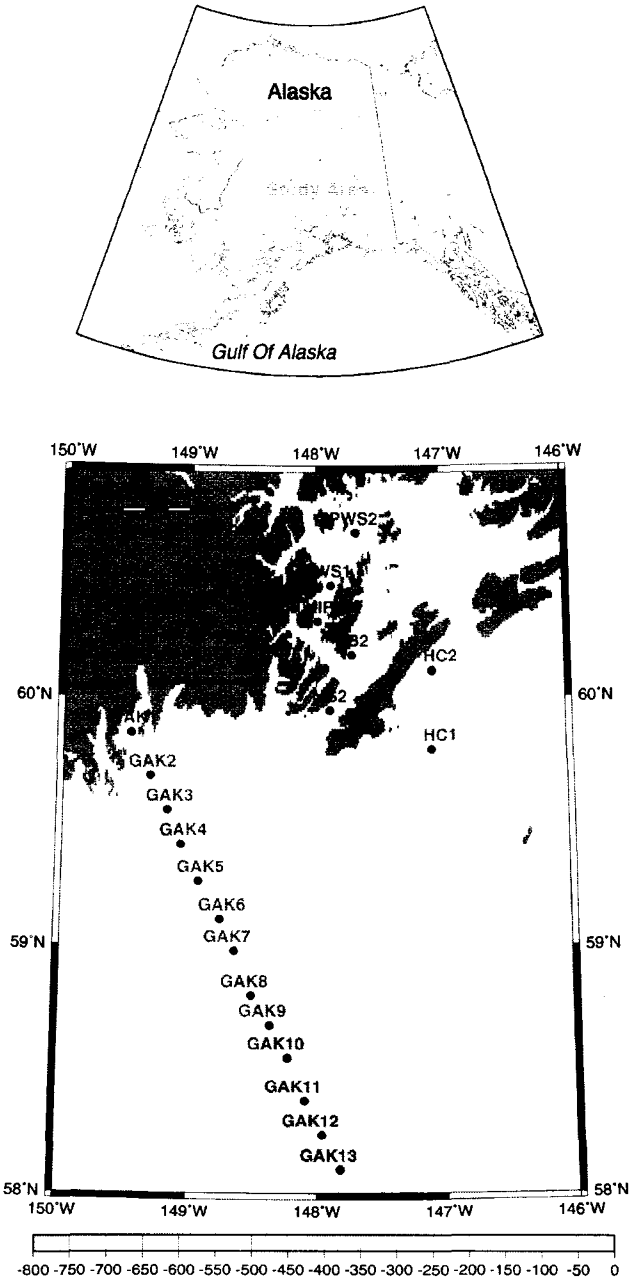

Figure 2.1 Map of sampling locations in the northern Gulf of Alaska.

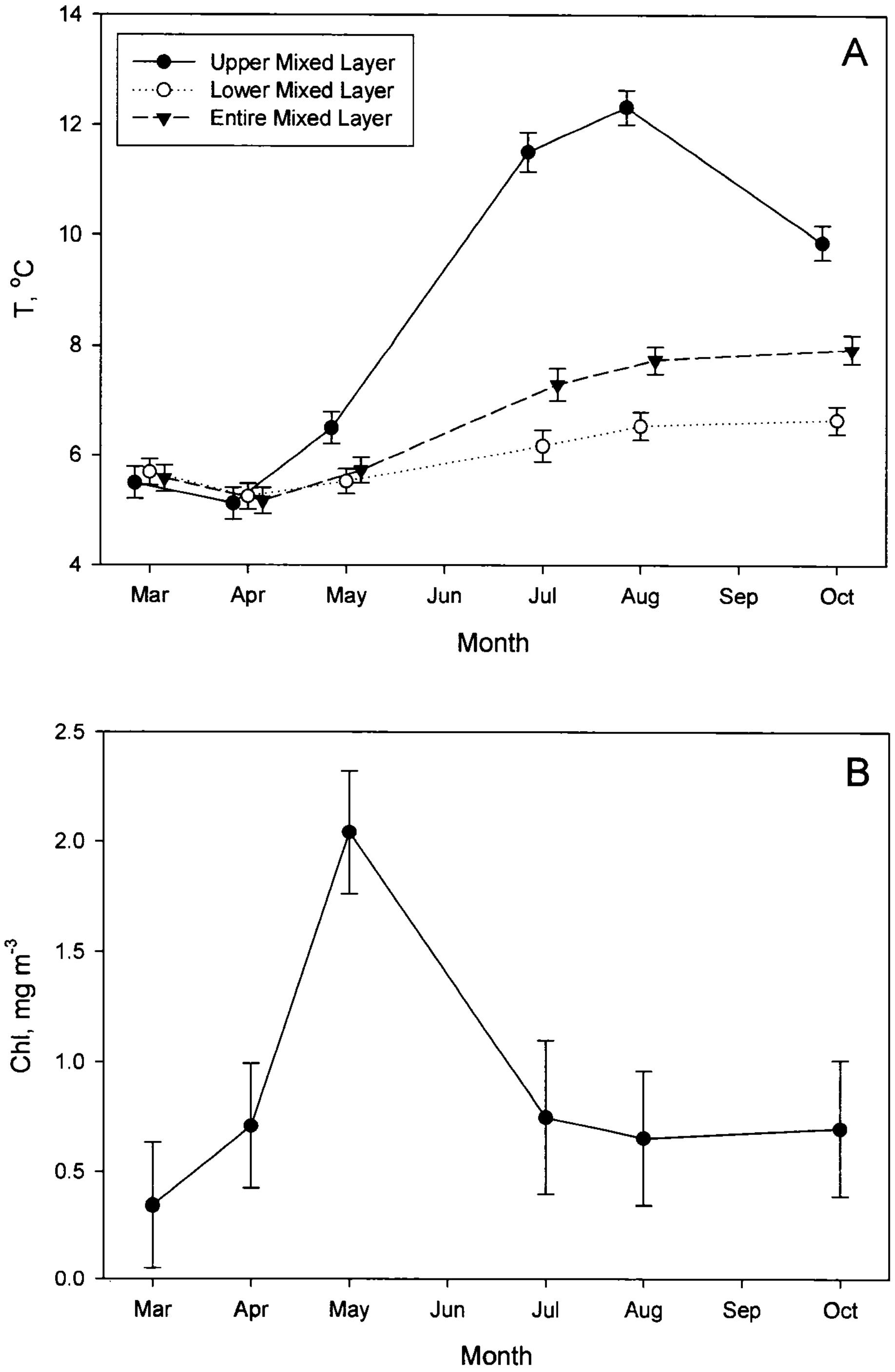

Figure 2.2 Seasonal variations in temperature and chlorophyll-*a* concentrations along the Seward line in the northern Gulf of Alaska in 2001-2003: A - temperature above and below the thermocline, and through the entire mixed layer (0 -100 m); B - chlorophyll-*a* concentrations in the 0-50 m (vertical bars are 95% CI).

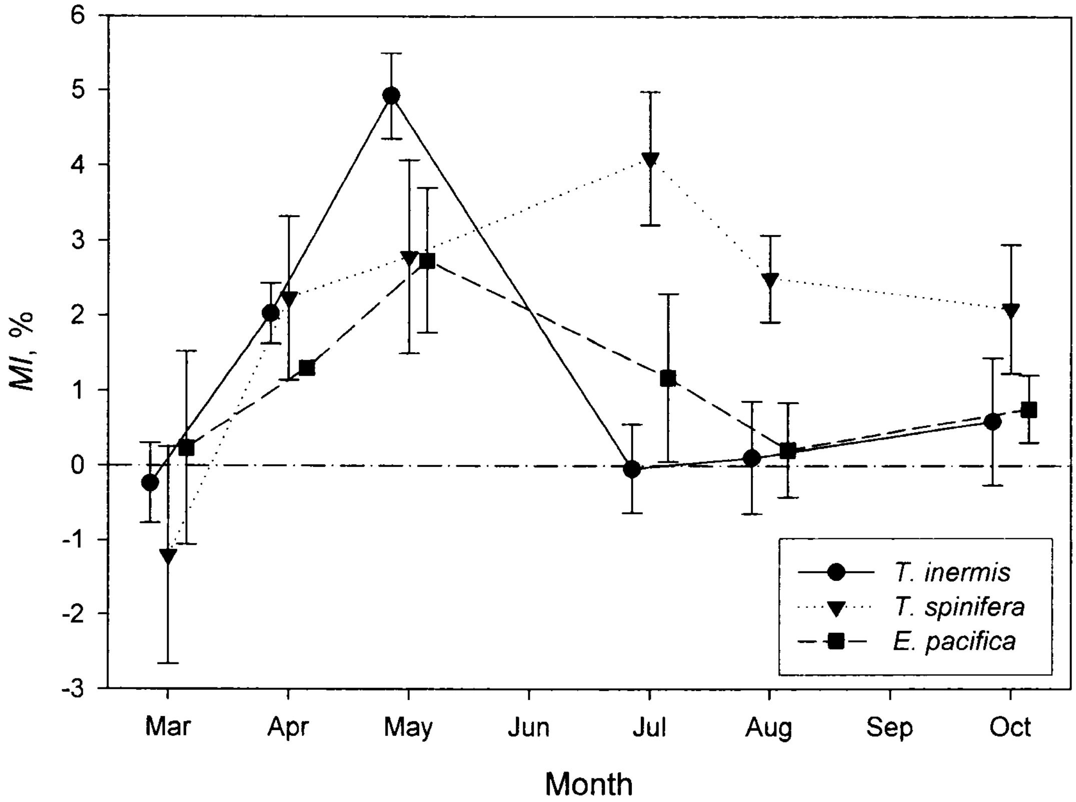

Figure 2.3 Seasonal variations in the mean length-specific molting increments (MI, % of uropod length) of *Thysanoessa inermis*, *T. spinifera* and *Euphausia pacifica* in the northern Gulf of Alaska in 2001-2003 (vertical bars are 95% CI, reference line drawn at 0 increment to denote negative/positive growth).

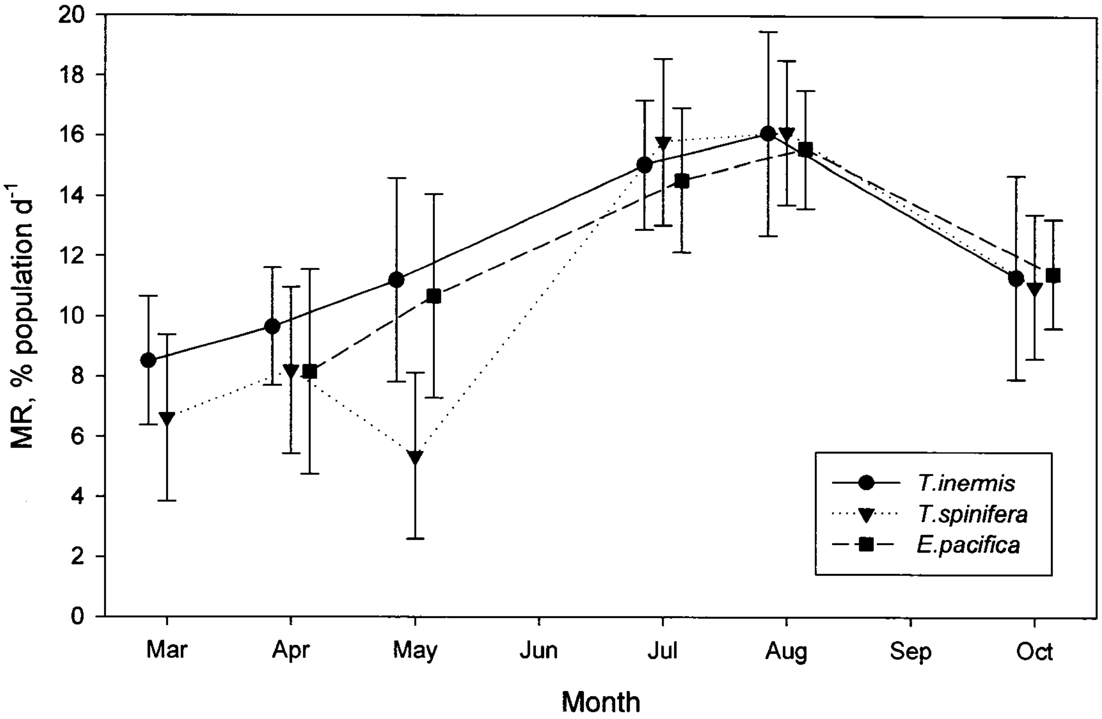

Figure 2.4 Seasonal variations in the mean molting rates (MR, % population day^{-1}) of *Thysanoessa inermis, T. spinifera* and *Euphausia pacifica* in the northern Gulf of Alaska in 2001-2003 (vertical bars are 95% CI).

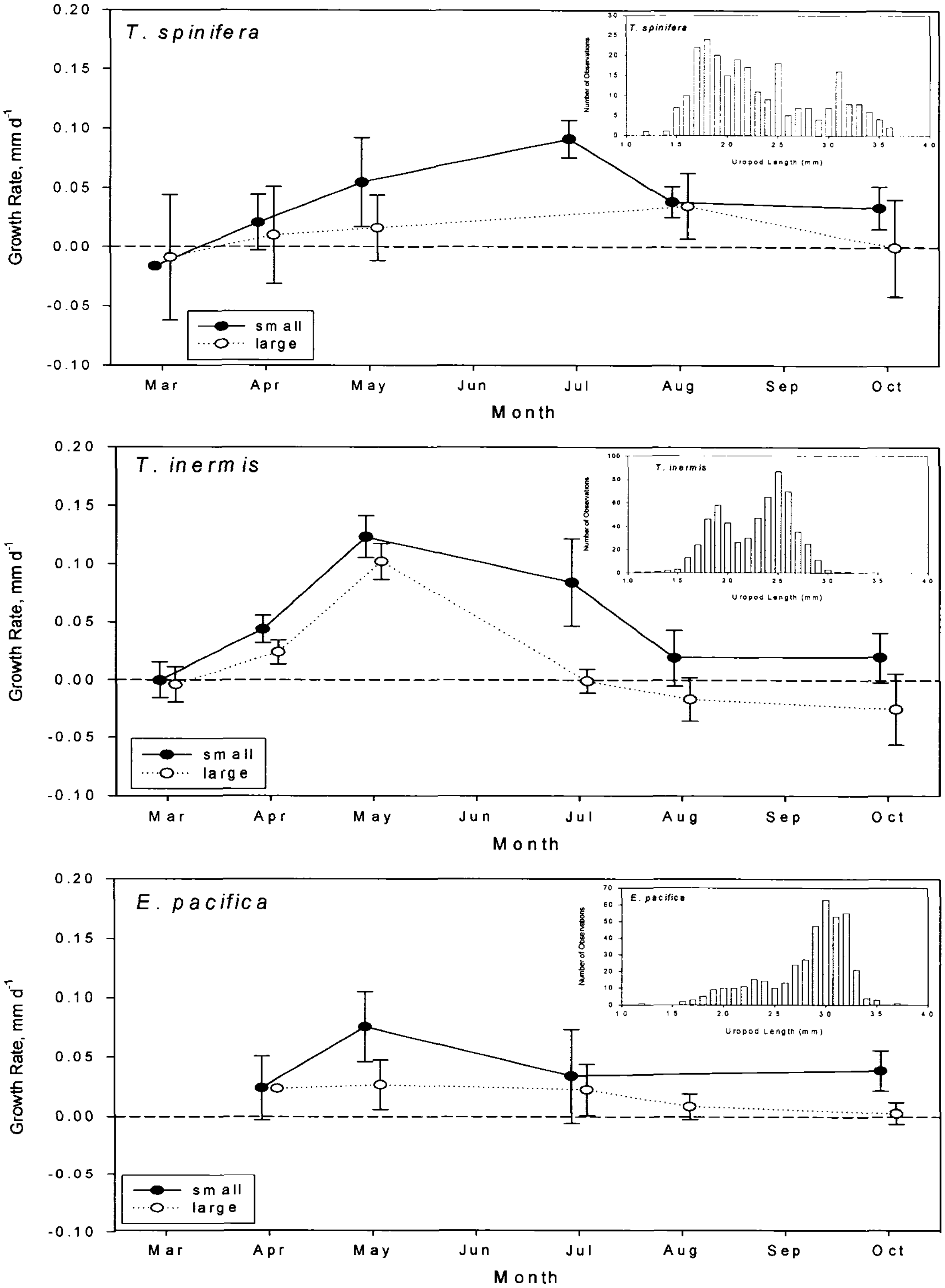

Figure 2.5 Seasonal variations in mean length growth rates (mm d^{-1}) of two major size groups of euphausiids (based on length-frequency distributions) in the northern Gulf of Alaska with a reference line marking 0-growth.

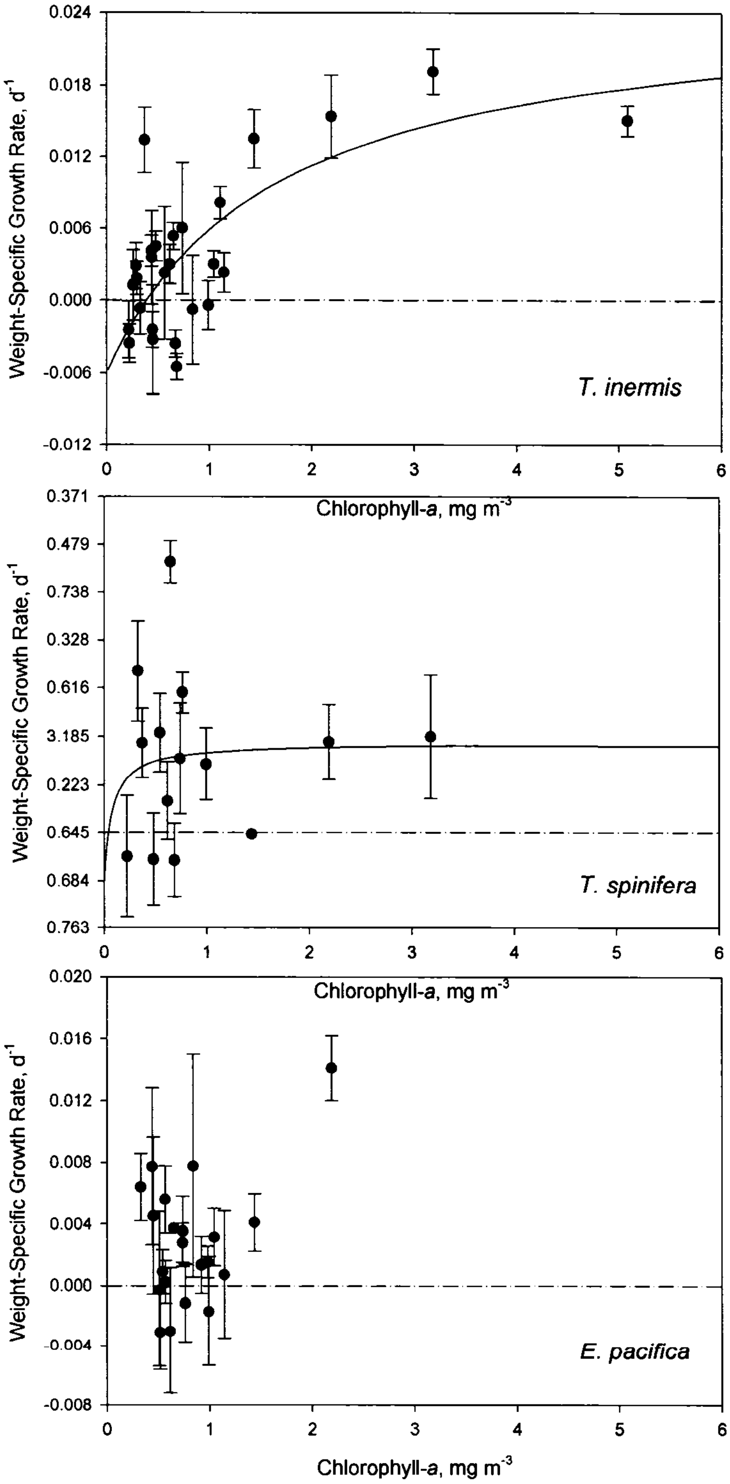

Figure 2.6 Functional relationships between ambient chlorophyll-*a* concentrations and weight-specific growth rate of euphausiids from the northern Gulf of Alaska approximated with Michaelis-Menten curve.

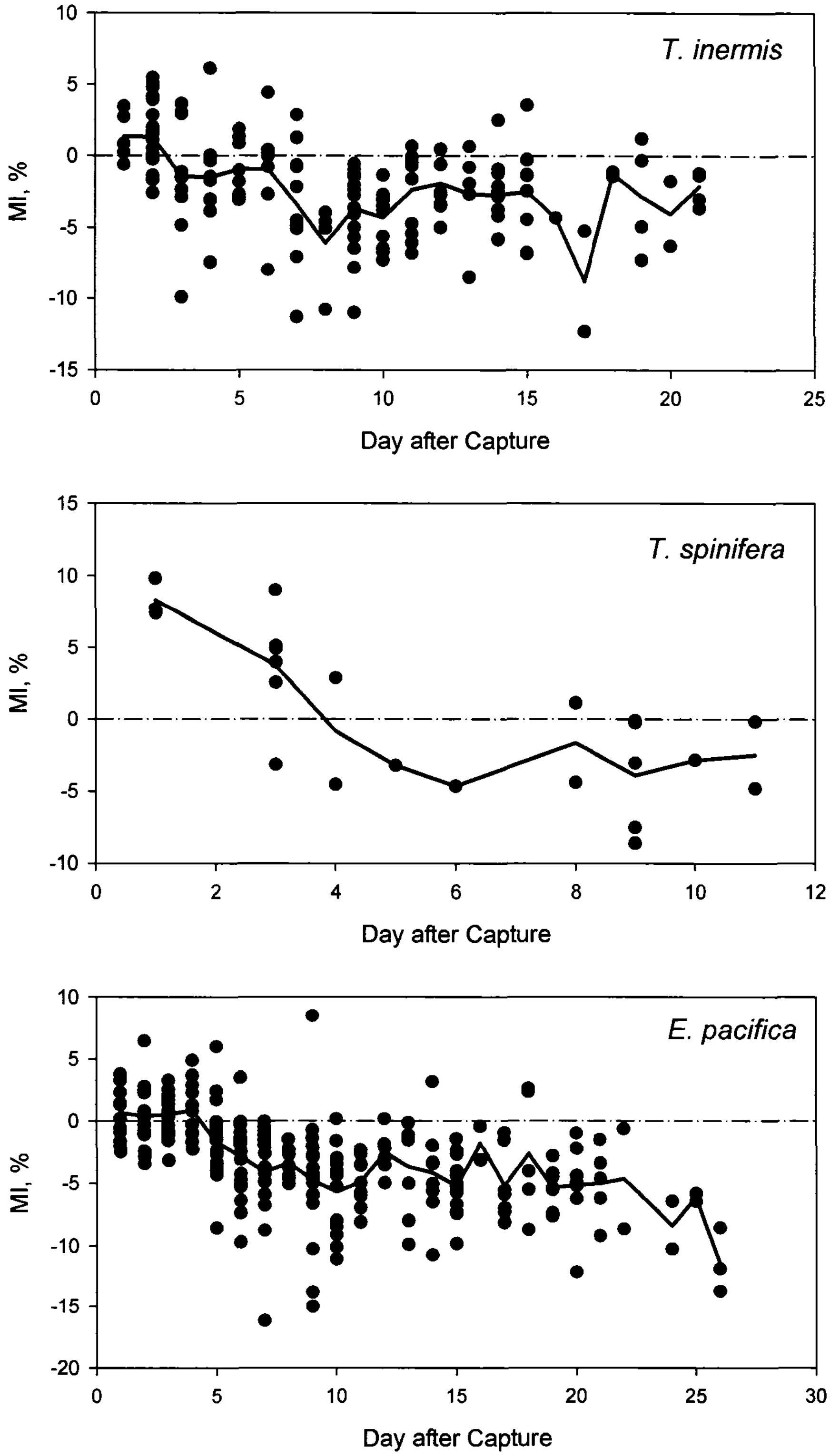

Figure 2.7 Shrinkage of euphausiids under starvation as indicated by molt increment (MI), solid line is the running mean.

Table 2.1 Summary of growth and molting rates experiments in the northern Gulf of Alaska showing the number of euphausiids incubated per experiment (TI - *Thysanoessa inermis*, TS - *Thysanoessa spinifera*, EP - *Euphausia pacifica* , * - long-term experiments lasting more then 48 hours, only molted euphausiids included).

Month	2001				2002				2003				2004			
	Station	TI	TS	EP	Station	TI	TS	EP	Station	TI	TS	EP	Station	TI	TS	EP
March	PWS1*	9	5	-	GAK6	128	15	2	GAK12	2	18	99				
					GAK3	58	20	3	GAK2	112	51	7				
					GAK1	129	48	3								
April	GAK13*	5	2	74	GAK11	177	1	28	GAK4	132	34	4				
					GAK3	172	18	-	GAK6	189	17	-				
									GAK1	51	141	-				
May	GAK13*				GAK1	81	43	1	GAK2	52	35	92	GAK1-2	24	72	74
	GAK9*				GAK7	192	5	-								
July	GAK9*	21	3	7	GAK7	1	180	5	GAK8	110	6	73				
	GAK7*	17	4	20	GAK5	131	33	9								
August	GAK12*	2	-	35	GAK11	-	158	25	PWS1	33	100	1				
	GAK9*	4	19	9	GAK5	164	29	7	GAK4	34	58	64				
	GAK6*	13	2	16					GAK3	2	19	153				
October					GAK2	19	44	83	GAK12	-	-	207	GAK4	-	54	128
					GAK4	77	66	21					GAK11	-	29	111
					GAK1	66	30	57					GAK6	3	-	192

Table 2.2 Relationships between dependent variables molt increment (MI) and molting rate (MR) and independent variables temperature (T), chlorophyll-*a* concentration (Chl) and pre-molt carapace length (CL). The coefficients β_T, β_{Chl}, β_{CL} correspond to T, Chl and CL respectively.

Species	Backwards stepwise regression	Multiple linear regression					N
		MI					
		β_T	β_{Chl}	β_{CL}	r^2	p(*T*; *Chl*; *CL*)	
T. inermis	all included	-0.175	0.436	-0.236	0.31	<0.001;<0.001;<0.001	427
T. spinifera	*T* removed		0.255	-0.440	0.18	-; <0.001; <0.001	166
E. pacifica	*T* removed		0.196	-0.303	0.14	-; <0.001; <0.001	255
		MR					
		β_T	β_{Chl}				
T. inermis	all included	0.850	0.401		0.74	<0.001; 0.006	22
T. spinifera	*Chl* removed	0.867			0.75	<0.001	20
E. pacifica	*Chl* removed	0.625			0.39	0.002	22

Table 2.3 Seasonal mean weight-specific growth rates (g_w, d^{-1}) for two major size groups of euphausiids in the northern Gulf of Alaska. SE is standard error and (*n*) is number of observations.

Month	*Thysanoessa inermis*		*Thysanoessa spinifera*		*Euphausia pacifica*	
	Small	Large	Small	Large	Small	Large
	g_w ± SE (*n*)	g_w ± SE (*n*)	g_w ± SE (*n*)	g_w ± SE (*n*)	g_w ± SE (*n*)	g_w ± SE (*n*)
March	0 ± 0.001 (*37*)	−0.001 ±0.001 (*37*)	-0.004 ± N/A (*1*)	-0.001 ± 0.008 (3)		
April	0.009 ± 0.001 (*61*)	0.004 ± 0.001 (*79*)	0.005 ± 0.004 (*15*)	0.002 ± 0.006 (*5*)	0.006 ± 0.003 (*11*)	0.004 ± N/A (*1*)
May	0.023 ± 0.002 (*27*)	0.016 ± 0.001 (*35*)	0.014 ± 0.006 (*6*)	0.003 ± 0.004 (*11*)	0.016 ± 0.003 (*9*)	0.005 ± 0.002 (*18*)
July	0.022 ± 0.003 (*6*)	0 ± 0.001 (*78*)	0.031 ± 0.002 (*34*)		0.007 ± 0.004 (*5*)	0.004 ± 0.002 (*17*)
August	0.005 ± 0.002 (*15*)	−0.003 ± 0.002 (*24*)	0.012 ± 0.002 (*49*)	0.006 ± 0.004 (*11*)		0.001 ± 0.001 (*69*)
October	0.004 ± 0.002 (*19*)	−0.004 ± 0.003 (*9*)	0.011 ± 0.003 (*26*)	0 ± 0.006 (*5*)	0.009 ± 0.002 (*27*)	0.001 ± 0.001 (*96*)

Table 2.4 Intermolt periods (IP) calculated from IGR experiments and consecutive intermolt periods (IP1 and IP2) measured directly during long term incubations. Temperatures for IGR experiments are estimated daily mean temperatures computed with respect to approximate time euphausiids spent above and below thermocline during 24 hour day and rounded to the nearest degree, *n* is number of observations.

Species	Temperature				
	5°C		7°C	8°C	
From IGR experiments	IP±CI (*n*)		IP±CI (*n*)	IP±CI (*n*)	
T. inermis	10.1±1.4 (*13*)		8.8±3.6 (*2*)	6.5±1.9 (*7*)	
T. spinifera	16.4±1.7 (*9*)		9.5±2.5 (*4*)	6.4±1.9 (*7*)	
E. pacifica	10.6±2.3 (*5*)		9.0±1.9 (*7*)	6.9±1.6 (*10*)	
Direct measurements	IP1±CI (*n*)	IP2±CI (*n*)		IP1±CI (*n*)	IP2±CI (*n*)
T. inermis	10.3±0.9 (*13*)	11.6±2.6 (*5*)		6.6±0.3 (*67*)	7.0±0.5 (*29*)
T. spinifera	10.1±1.5 (*7*)	-		7.0±1.1 (*8*)	7.5 (*2*)
E. pacifica	10.9±0.5 (*58*)	11.1±1.0 (*9*)		6.7±0.3 (*57*)	8.2±0.7 (*13*)

Table 2.5 Weight-specific growth rates (standardized to 5°C) of euphausiids compared with dominant copepods from the northern Gulf of Alaska.

Species	g_w	Source
Euphausiids:		
Thysanoessa inermis	0.003	this study
Thysanoessa spinifera	0.007	this study
Euphausia pacifica	0.0025	this study
Copepods:		
Centropages abdominalis	0.08	Slater and Hopcroft (2005)
Neocalanus flemingeri/plumchrus	0.105	Liu and Hopcroft (2006a)
Metridia pacifica	0.083	Liu and Hopcroft (2006b)
Calanus marshallae	0.118	Liu and Hopcroft (unpublished)
Calanus pacificus	0.074	Liu and Hopcroft (unpublished)

CHAPTER 3

Climate-related changes in abundance and reproduction of dominant euphausiids in the northern Gulf of Alaska in 1998-2003[3]

3.1 Abstract

Interannual variability in abundance of the dominant euphausiids *Thysanoessa inermis, Thysanoessa spinifera* and *Euphausia pacifica* were studied in the northern Gulf of Alaska during the production season from 1998 to 2003. *Thysanoessa inermis* abundance increased significantly over the shelf from 1998 to 2002. In contrast, the abundance of *T. spinifera* (which also inhabits the shelf) and *E. pacifica* (usually common on the outer shelf) did not chang. Based on the incidence of spermatophores on the females, reproduction of *T. inermis* occurred during April in 1998 and 2003, and was extended through May in 1999-2002. 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 early spawning *T. inermis* on the inner shelf.

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[3] Pinchuk AI, Coyle KO, Hopcroft RR (2006) Climate-related changes in abundance and reproduction of dominant euphausiids in the northern Gulf of Alaska in 1998-2003. Prog Oceanogr (in review)

3.2 Introduction

The Gulf of Alaska (GOA) continental shelf supports a rich and diverse marine ecosystem including the most important commercial fisheries in the United States EEZ such as crustacean, salmon, pollock, halibut and sablefish (Weingartner et al., 2002) as well as sea bird 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 (e.g. Albers & Anderson, 1985), king crab (Blau, 1986), walleye pollock (Hollowed et al., 1994), pacific cod (Thompson & Zenger, 1994), and salmon (e.g. Mantua et al., 1997), which appears to be related to North Pacific basin-scale climate changes (Francis & Hare, 1994; Trenberth & Hurrell, 1994; Anderson & 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 condition of zooplankton, with consequences for feeding success, growth and survival of juvenile and planktivorous fish.

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” 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 fuller knowledge of the mechanisms affecting euphausiid population dynamics is important for understanding the GOA ecosystem.

The euphausiid fauna of the northern GOA comprises seven species of which three are predominant: *Thysanoessa inermis*, *T. spinifera*, and *Euphausia pacifica* (Coyle & 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 & 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 inter-annual differences in abundance, timing and magnitude of spawning of the major euphausiid species in relationship to temperature, salinity and chlorophyll-*a* distribution during the production season in the northern Gulf of Alaska from 1998-2003.

3.3 Methods

Zooplankton samples, conductivity-temperature-depth (CTD) and fluorescence profiles were taken along the Seward Line in the northern GOA during US GLOBEC LTOP cruises from 1998-2003 (Fig. 3.1, Table 3.1). CTD profiles were taken with a Seabird model 911 Plus with dual conductivity and temperature sensors. Water samples for fluorometric estimation of chlorophyll-*a* concentrations were collected by Niskin bottles and the chlorophyll concentration was averaged over the upper 50 m of the water column (D. A. Stockwell and T. E. Whitledge, unpubl.data). Euphausiids were collected using a 1-m^2 MOCNESS fitted with 500 μm 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 m^3 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 species and stage of euphausiids. The presence of spermatophores on females, indicating mating since her last molt (Mauchline, 1980), was also recorded. The proportion of the total sample in the sub-sample varied according to the abundance of zooplankton. Blotted wet weights of all specimens of each species, sex and stage were measured and recorded individually for each sample. Wet-weight measurements were made on a Cahn electrobalance or Mettler top loading balance, depending on the size of the animals.

The data were uploaded to a Microsoft Access database, and analysis was performed using STATISTICA 6 software. Analysis included a total of 2826 MOCNESS samples. Due to uneven spatial distribution of euphausiids, the abundance/biomass data were transformed using a power of 0.15 to stabilize the variance, the means and 95% confidence intervals were computed for each species, and the results were converted back to the arithmetic values for plotting. The non-parametric Kuskal-Wallis test was used to analyze chlorophyll-*a* data since even after transformation the data failed to meet the normality assumption.

3.4 Results

3.4.1 Cross-shelf distribution

Cross-shelf differences in euphausiid abundance where obvious (Fig. 2.2) despite the broad confidence intervals arising from substantial patchiness in euphausiid distribution. *T. inermis* was usually abundant (~50 ind 1000 m^{-3}) within 100-120 km of shore, but sharply declined at the shelfbreak, and *T. spinifera* generally mirrored the distribution of *T. inermis* (Fig. 3.2). In contrast, *E. pacifica* was most abundant beyond 150 km from shore. The broad confidence intervals arose from substantial patchiness in euphausiid distribution. The cross-shelf distribution of *E. pacifica* also showed seasonal variability (Fig. 3.3). In spring (March-May) it was virtually absent from the shelf, but it was abundant (~20 ind 1000 m^{-3}) over the slope. In contrast, by the end of the summer it appeared on the shelf in quantities similar to those beyond the shelfbreak (~20-60 ind 1000 m^{-3}).

3.4.2 Interannual variability

The mean abundance of *T. inermis* steadily increased from 1998 through 2002 followed by a sharp decline in 2003 (Fig. 3.4a). In contrast, the abundance of *E. pacifica* decreased slightly in 2001-2002 but appeared to recover in 2003. The abundance of *T. spinifera* was not significantly different between the years except for a peak in 2000. These changes resulted in a shift of dominant species: the euphausiid population was dominated by *T. spinifera* and *E. pacifica* in 1998-2000 and in 2003, while in 2001 and 2002 *T. inermis* prevailed. In contrast, there were no significant interannual changes in euphausiid abundance beyond the shelfbreak, except for exceptionally low numbers of *E. pacifica* in 1998, and high abundance of *T. spinifera* in 2000 (Fig. 3.4b).

The abundance of adult females carrying spermatophores also showed interspecific and interannual variability (Fig. 3.5). Female *T. inermis* with spermatophores occurred in April-May in the most of the years; in 1998 and 1999 they were restricted to April only. The abundance of fertilized *T. inermis* females was an order of magnitude higher in 2002 than in other years. Adult females of *T. spinifera* started to appear in March in 1998-1999, but were most abundant in April and May. Ovigorous females were occasionally found throughout summer, and as late as October. The number of spawning females was higher in 2000 than in other years. In contrast, adult female *E. pacifica* were present from July through October, with the exception of 1999 and 2000 when adult females were found as early as May. The peak abundance of adult females of *E. pacifica* was consistently lower than that of the other euphausiid species.

The average temperature of the upper 100 m in spring was significantly warmer (>6°C) in 1998 and 2003 than in 1999-2002, both on the shelf and beyond the shelf break, with the coldest temperature observed on the shelf in 1999 and 2002 (Fig 3.6a). In contrast, the mean summer/fall temperature showed little interannual variability over the study area and remained around 9°C (Fig. 3.6b). During the warm springs the mean chlorophyll-*a* concentrations in the upper 50 m were slightly higher in March and substantially lower in May compared to those during the cold years, indicating earlier and weaker spring blooms in 1998 and 2003 (Table 3.2). The highest mean chlorophyll-*a* concentrations (2.63 mg m^{-3}) were usually observed during the cold years in May. There were no significant differences in chlorophyll-*a* content during the summer months.

3.5 Discussion

3.5.1 Cross-shelf distribution

The inter-specific differences in euphausiid cross-shelf distribution found in this study generally confirm our earlier findings. 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 & 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, a shelf break and beyond influenced by the warmer and saline oceanic Alaska Current, and a broad transition 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 & Pinchuk, 2005), while the onshore movement of water due to Ekman transport persists throughout the most of the year (Livingstone & Royer, 1980).

T. inermis was most abundant on the inner shelf within 60 km of shore, *T. spinifera* was numerous in the transition zone, and *E. pacifica* apparently originated from the oceanic Alaska Current (Coyle & Pinchuk, 2005). 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 parts of the continental shelf in the North Atlantic, Arctic and Bering Sea (Smith, 1991; Dalpadado & Skjoldal, 1996; Astthorsson & Gislason, 1997; Coyle & Pinchuk, 2002) The shelf break fronts mark the transition between the colder and fresher shelf water and 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 & Coyle, 2005). Typically, these fronts are well developed in winter, when the shelf water is well mixed, and the offshore water is mildly stratified, while in summer the shelf becomes stratified and the fronts weaken (e.g. Mann & 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 attachment of the bottom-advected front separating buoyant shelf water from homogeneous offshore water migrates 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 & Denman, 1982), and shelf break eddies and flow meanders forming primarily in years of anomalously strong cyclonic winds (Bower, 1991; Meyers & Basu, 1999; Crawford & 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., in review), indicating that the summer influx of *E. pacifica* on the shelf might have important consequences for shelf biota.

3.5.2 Interannual variability

We found distinctive patterns of interannual variability in abundance of *T. inermis* (steady increases of over an order of magnitude from 1999 through 2002) and *E. pacifica* (slight increases in 1998 and 2003), and no pattern for *T. spinifera* on the northern GOA shelf. The increase in *T. inermis* abundance coincided with 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 collapsed. 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 may 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 no 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) could result in slower or negative euphausiid growth rates in years of lower euphausiid abundance, and faster growth coud result in years of higher food abundance. Food limitation is not generally supported by field measurements of euphausiid growth rates in the northern GOA; strong seasonal patterns occur, but no significant interannual differences have been observed (Pinchuk & Hopcroft, in review). Since we did not detect much interannual variability in temperature and chlorophyll-*a* concentration in summer and fall (Fig. 3.6, Table 3.2), 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 & Hopcroft, in review). Additionally, the spermatophore technique provides no information on interannual variability in individual brood sizes.

Our data show that timing and magnitude of euphausiid spawning events do have 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 diatom 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 timings of spawning events are known for *E. pacifica* and *T. spinifera* off Oregon and British Columbia coast (Smiles & Pearcy, 1971; Tanasichuk, 1998a, 1998b), and for *T. inermis* from other regions of subarctic Atlantic and Pacific (Kulka & Corey, 1978; Astthorson, 1990; Smith, 1991; Dalpadado & Skjoldal, 1991; Timofeev, 1996).

T. inermis are 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 & Skjoldal, 1996; Timofeyev, 1996; Pinchuk & Hopcroft, 2006). The data on seasonal dynamics of fatty acid 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 & Hopcroft, in review). 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 & 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 µm (Suh & 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 & 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 & Hopcroft, in review).

T. spinifera releases large numbers of eggs with an unknown frequency (Pinchuk & 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, 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* largely depends 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 would 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 is thermal conditions except for the years re-adjustment occurs 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 substantially influence metabolic rates over a period of several months, assuming that the euphausiids occur in the mixed layer in winter. Little is known about winter behavior of *T. inermis*, but 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* collected from the Gulf of St. Lawrence (Sameoto, 1976) and *E. pacifica* from the southern Japan Sea (Iguchi & Ikeda, 1995). The weight-specific respiration rate at 4°C for *T. inermis,* ranging from 6.2 to 35 mg dry weight (DW), was 1.41 $\mu l\ O_2\ h^{-1}\ mg\ DW^{-1}$ (Sameoto, 1976). At the same temperature for *E. pacifica* of comparable DW range, the weight-specific respiration rate was similar, 1.39 $\mu l\ O_2\ h^{-1}\ mg\ DW^{-1}$ (Iguchi & Ikeda, 1995). The weight-specific respiration rates of *E. pacifica* and *T. inermis* calculated using the respiration/temperature relationship (Iguchi & Ikeda, 1995), 1.503 $\mu l\ O_2\ h^{-1}\ mg\ DW^{-1}$ and 1.629 $\mu l\ O_2\ h^{-1}\ mg\ DW^{-1}$ 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 & 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 overwintering *T. inermis* may consume about 45% more energy 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. 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* larvae. While the non-feeding larval stages rely on internal energy reserves and their growth and developmental rates are primarily controlled by environmental temperature (e.g. Pinchuk & 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 & Gruner, 1956). From this moment the quantity and quality of diet determines krill growth and development in addition to temperature (Huntley & Boyd, 1984). Depending on available food, larval development and growth may progress, be delayed or terminated (Ross et al., 1988; Huntley & 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 & Quetin, 1989). It takes about 10 days for *T. inermis* to reach the calyptopis 1 stage at 5°C in the GOA (Pinchuk & 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 ultimately influence euphausiid population dynamics by determining the recruitment of the postlarval 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, ultimately decreasing or increasing population abundance depending on which climatic phase is occurring. 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) and associated phenomena appear to be major sources of oceanographic and biological variability (Mantua et al., 1997). The most prominent feature of the PDO and the climate in the GOA is the Aleutian Low (AL), for which the average geographic location changes periodically during the winter (Mundy & 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 lots of 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 & 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 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-than-optimal 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 run-up of deepwater onto the shelf, leading to an earlier and less intense phytoplankton bloom on the shelf and lower biological production afterwards (Mundy & Spies, 2005). During 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 & 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 become overrun by seasonal variability. Therefore, climatic changes may greatly influence the onset of production season controlling the timing, span and magnitude of the spring bloom, thereby affecting the structure and recruitment success of zooplankton communities and sending a signal that propagates through the higher trophic levels of the shelf marine 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.

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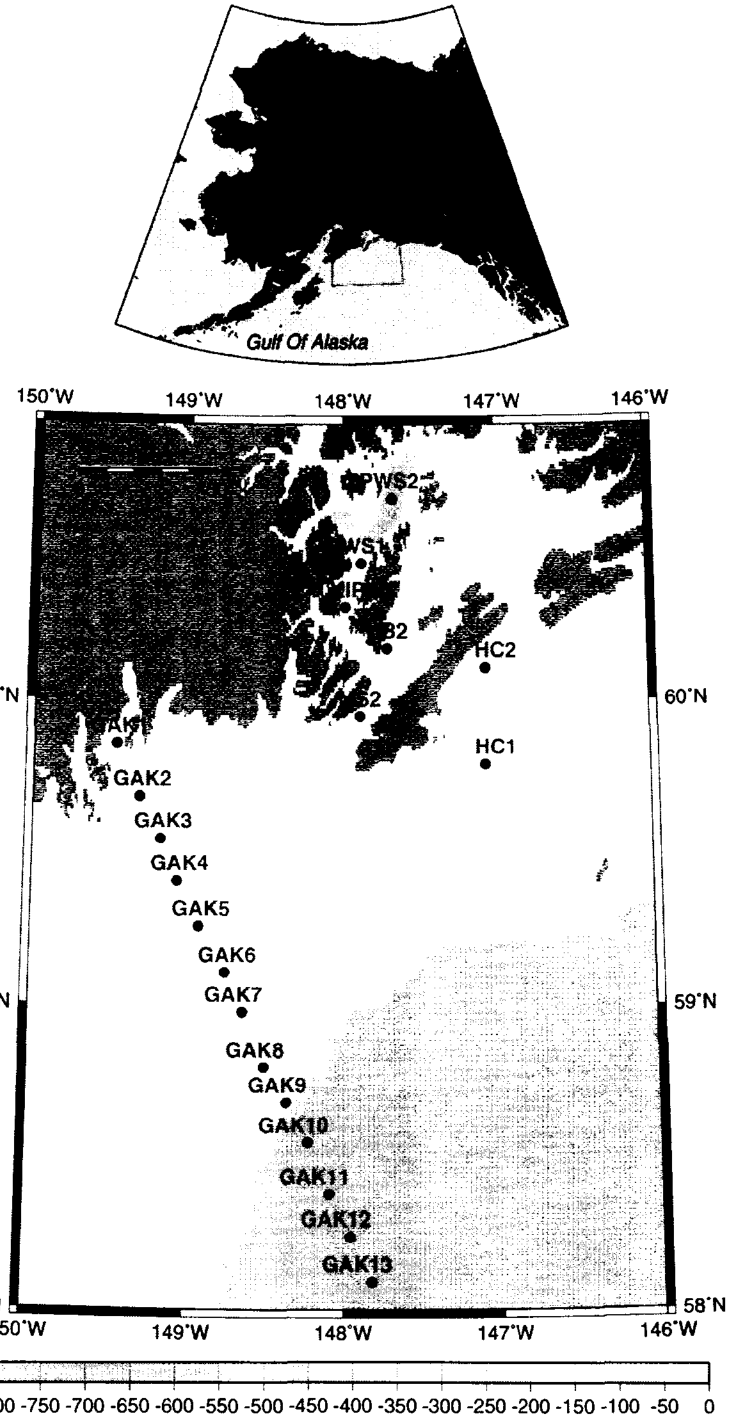

Fig. 3.1 Map of sampling locations in the northern Gulf of Alaska.

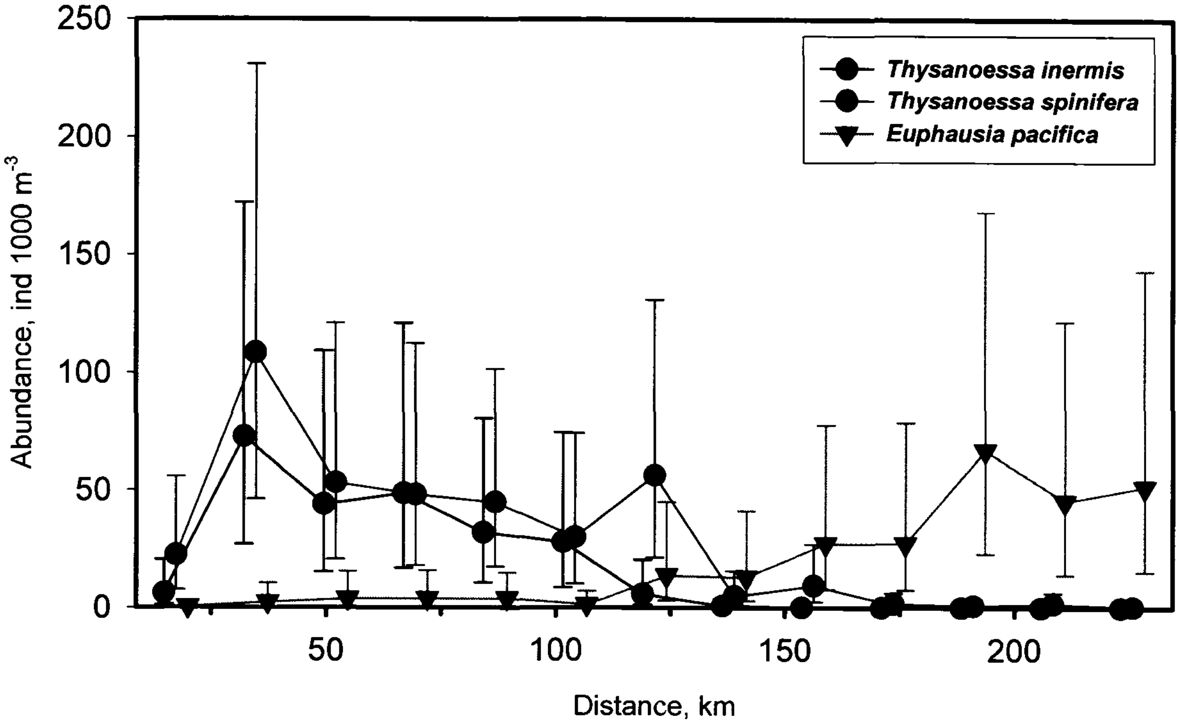

Fig. 3.2 Cross-shelf (from the coast to offshore) distribution of dominant euphausiid species in the northern Gulf of Alaska. Symbols offset slightly to improve presentation.

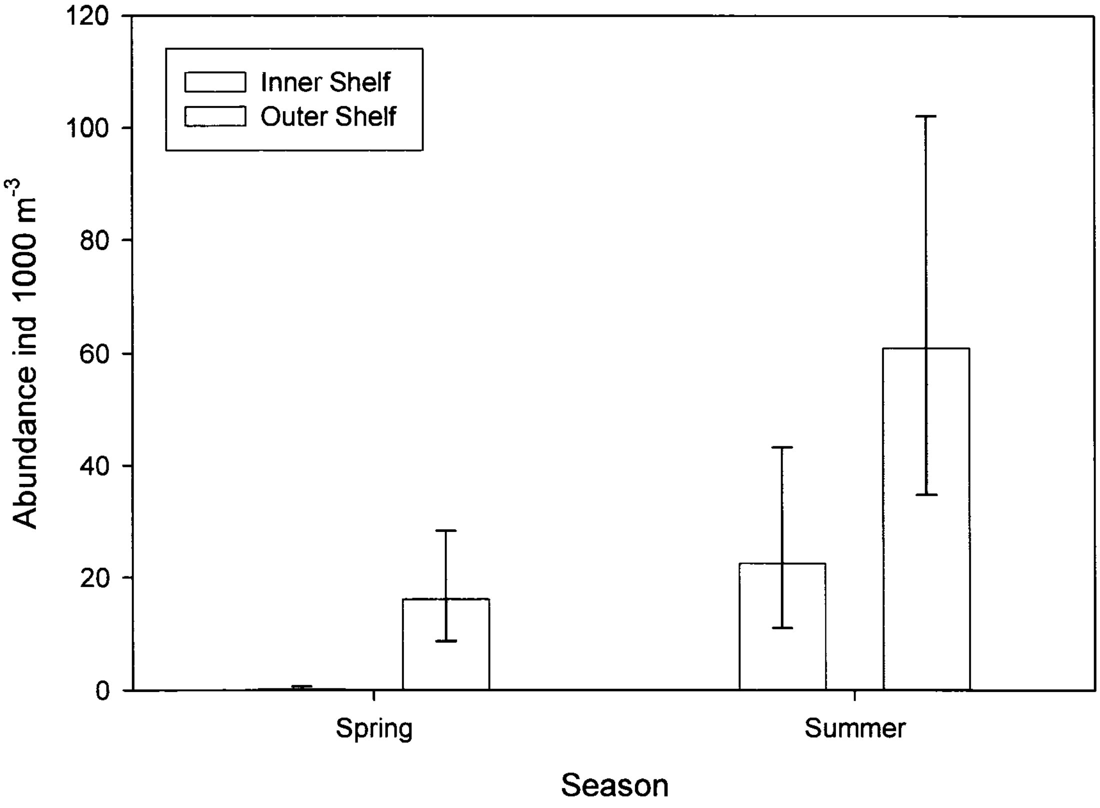

Fig. 3.3 Seasonal change on *Euphausia pacifica* cross-shelf distribution. in the northern Gulf of Alaska over the 1998-2003 period. Inner shelf is characterized from Gak1-7, and outer shelf from Gak8-13 (error bars - 95% confidence intervals).

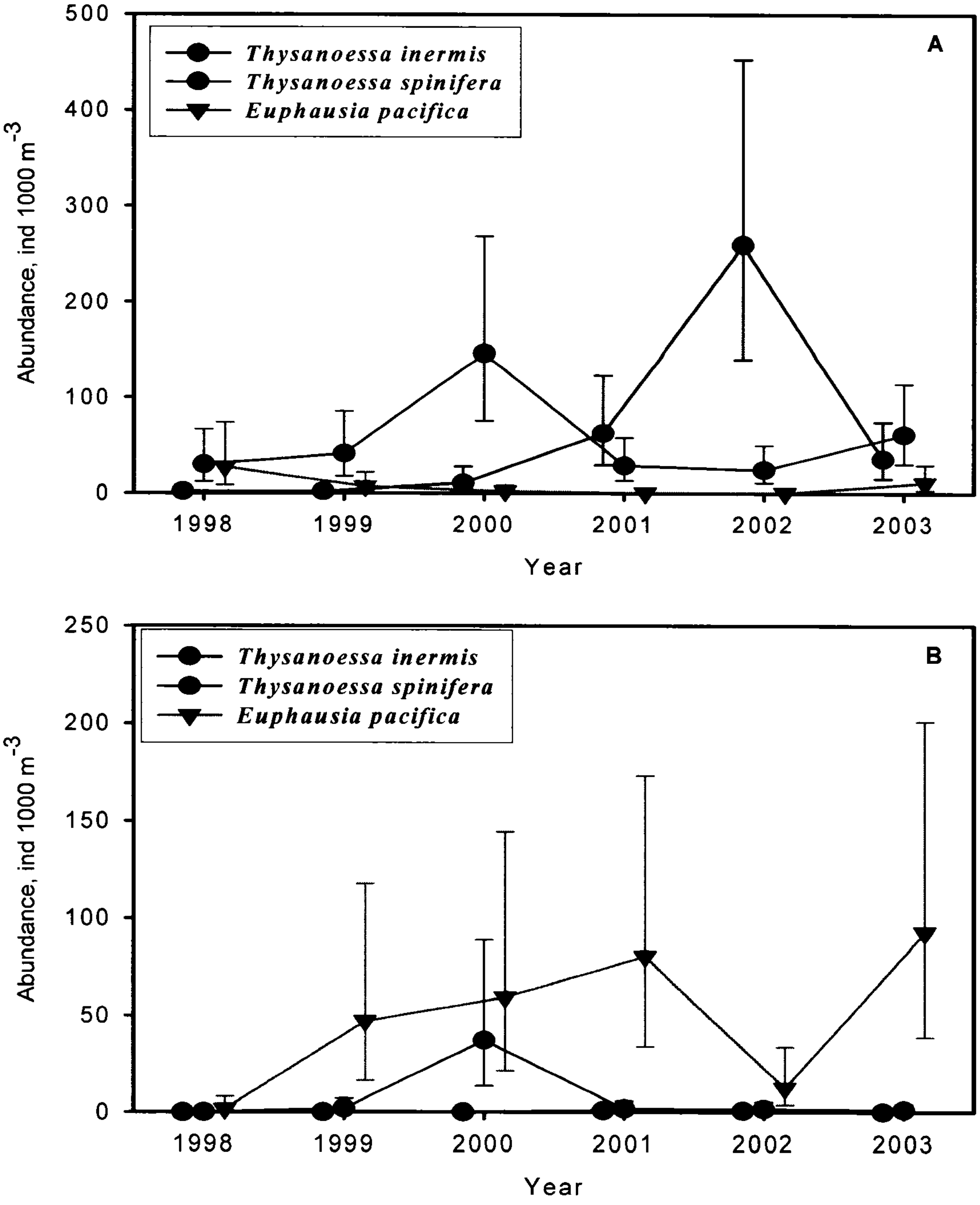

Figure 3.4 Interannual changes in abundance of dominant euphausiid species in the northern Gulf of Alaska on the shelf (A), and at the shelf break and beyond (B) (error bars – 95% confidence intervals).

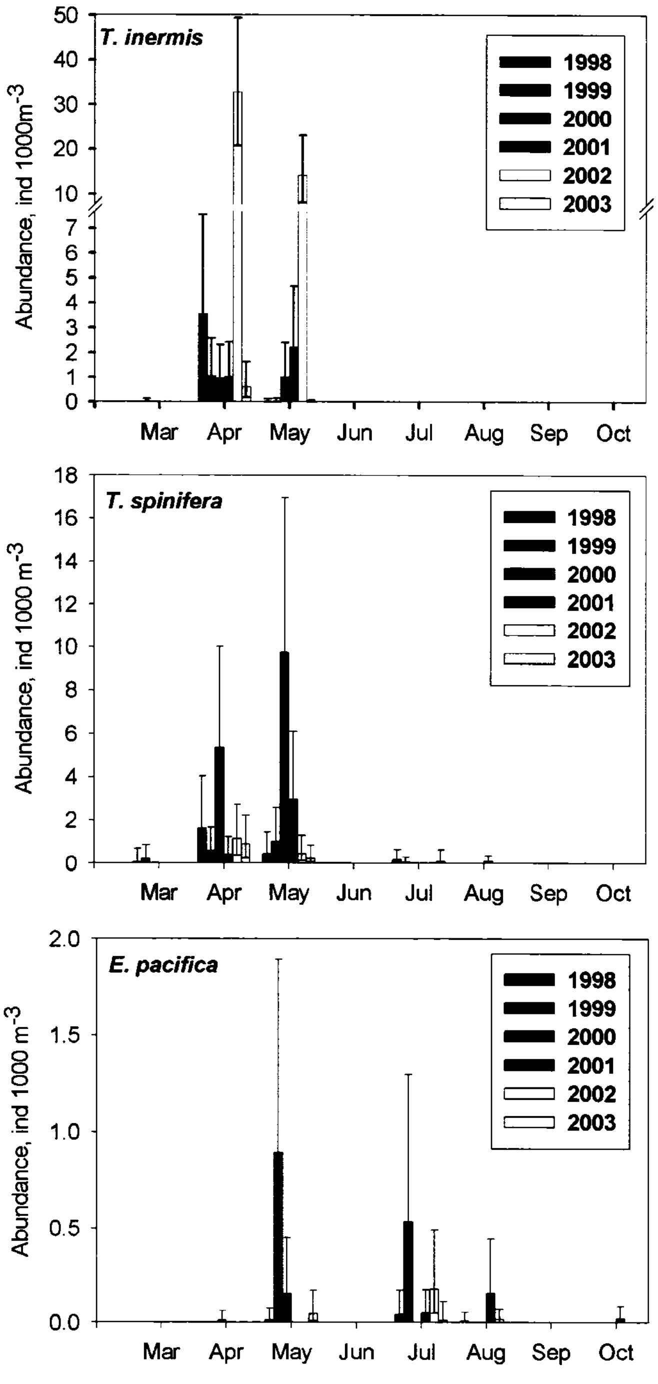

Fig. 3.5 Interannual abundance of adult female euphausiids with attached spermatophores on the northern Gulf of Alaska (error bars – 95% confidence intervals).

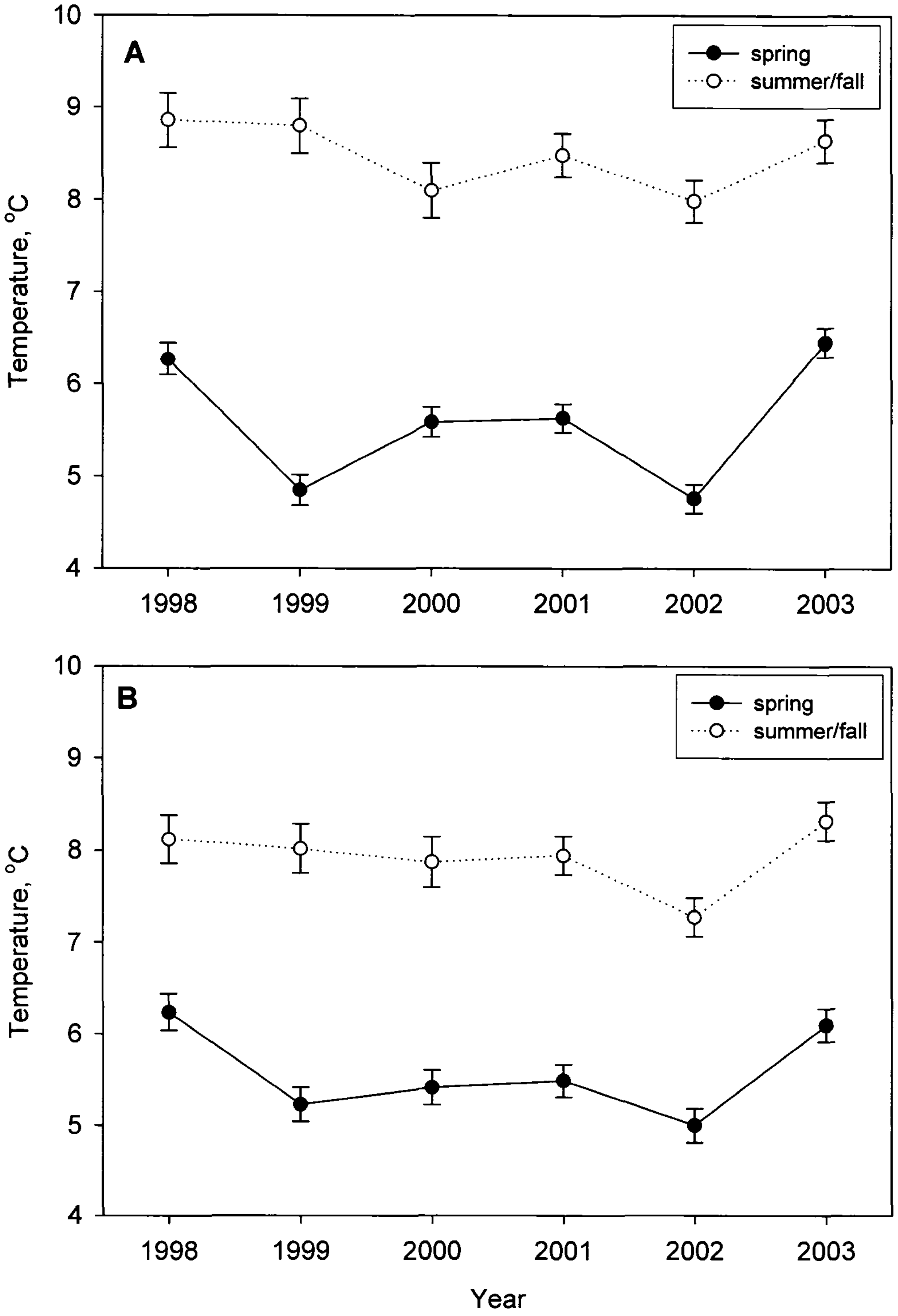

Fig. 3.6 Interannual variability in the upper 100 m layer temperature in the northern Gulf of Alaska averaged for spring and summer/fall over the shelf (A) for GAK1-7 and beyond the shelf break (B) for GAK8-13 (error bars – 95% confidence intervals).

Table 3.1 Summary of GLOBEC LTOP cruises in the northern Gulf of Alaska.

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

Table 3.2 The Kruskal-Wallis test of the significance of mean chlorophyll-*a* concentrations in the upper 50 m during spring months in warm and cold years in the northern Gulf of Alaska (p- probability level).

Month	Chlorophyll-*a* (mg m^{-3})		p
	Warm (1998,2003)	Cold (1999-2002)	
March	0.37	0.27	0.0036
April	0.41	0.77	0.052
May	0.92	2.63	0.0001
July/August	0.90	0.81	0.1

CONCLUSION

This thesis provides the first account of egg production, growth, development, and temporal variability of the three dominant euphausiid species in the northern Gulf of Alaska in relation to environmental variations. Overall, this information helps clarify the life history patterns of these species, and lays the foundation for estimating and modeling the secondary production of euphausiids within the Gulf of Alaska.

The combination of field incubations of gravid females, concurrent with the IGR technique, executed over the complete production season, allows us to obtain rates applicable to *in situ* populations and to identify those factors influencing them. Supplemental laboratory experiments on larval development and frequency of spawning provide valuable information for interpretation of euphausiid life cycles in the GOA. Our results confirm that euphausiids employ species-specific reproductive and growth strategies enabling them to cope with highly seasonal fluctuations of subarctic marine environment (Falk-Petersen et al. 2000). The cold-water, mostly herbivorous *T. inermis* relies on lipids accumulated during summer and fall to survive through winter and to fuel its reproductive effort the following spring. The investment of consumed energy into lipid reserves results in cessation of spawning and limited growth through most of the summer and fall. Consequently, the spent animals depend heavily on the spring bloom to restore their energetic needs and to achieve maximum growth during the bloom's development.

In contrast, *T. spinifera* and *E. pacifica* reproduce through the whole summer, with *T. spinifera* starting earlier. At least *E. pacifica* has been shown to be capable of producing multiple broods. Moreover, while their growth rate increases during the bloom, both these euphausiids appear to be able to maintain high growth rates throughout the production season as well. The lack of substantial lipid storage and the comparative eye and feeding basket morphology (Ponomareva 1966; Suh and Choi 1998) suggest that these species are able to efficiently utilize a variety of food sources from protozoans and “marine snow” to small copepods (Bargu et al. 2003; Dilling et al. 1998; Nakagawa et al. 2001, 2004), thus successfully maintaining their growth and reproduction rates throughout the season.

Early development of these species (together with other euphausiid species inhabiting temperate waters) shows a remarkably similar response to changes in temperature, expressed in the form of single linear function, enabling us to predict the appearance of first-feeding larval stages from knowledge of the spawning periods and environmental temperature. Since first-feeding krill larvae are extremely sensitive to food availability (Mullin and Brooks 1970; Ross et al. 1988; Ross and Quetin 1989; Huntley and Brinton 1991), such knowledge, combined with estimates of their food resource fields, allows forecasting of larval survival and, therefore, post-larval recruitment of a year-class to the krill population.

The different reproductive and growth strategies of the euphausiid species in this study profoundly affects their populations in northern waters. These strategies help provide the mechanistic explanation of the observed multi-annual population cycles linked to variability in the marine environment. Climatically induced fluctuations in temperature and water column stability alter the timing and magnitude of spring phytoplankton blooms, and result in changes in metabolic rates of euphausiids, thus diminishing or enhancing euphausiid survival. In addition, changes in wind strength and direction, as well as in precipitation, ultimately reinforce or weaken the development of buoyancy driven coastal currents (Mundy and Olsson 2005), thereby modifying cross-shelf water exchange, and thus leading to a greater or lesser penetration of oceanic euphausiids into the coastal shelf ecosystem (Weingartner et al. 2005; Coyle and Pinchuk 2005). Colder years are likely to promote overall euphausiid production on the northern GOA shelf by facilitating better overwintering survival and reproductive success of *T. inermis*. In contrast, warmer and windier years will diminish the *T. inermis* population, but the on-shore flow might compensate for a decreased *T. inermis* by advecting *E. pacifica* onto the shelf from offshore. It appears that *T. spinifera* is most versatile in terms of feeding and reproductive strategies, which may lead to its long-term success on the shelf.

Determining growth and egg production rates of euphausiid species is but one step towards understanding their ecological function within marine systems. Numerous gaps in our understanding of euphausiids still need to be addressed. Understanding how the observed differences and similarities between these species affect food web interactions (i.e. diet composition, ingestion and clearance rates) would be a useful next step. A combination of traditional feeding experiments (Bamstedt et al. 2000) with novel biochemical (Ju and Harvey 2004) and molecular (Martin et al. 2006) approaches appear to be an especially promising technique to explore such relationships. Data on energetic demands and metabolic rates during winter are needed to determine on how much lipid is required for survival through warmer or colder winters and how variations in storage impact the subsequent reproductive potential for *T. inermis*. Information on energetic content of different prey available in coastal and oceanic environments is needed to define growth, and reproductive potential of *T. spinifera* and *E. pacifica* throughout summer. A consistent monitoring of euphausiid population size structure, to calculate meaningful estimates of krill production from growth and egg production rates (Tanasichuk 1998a, 1998b), remains essential in understanding their role in the pelagic ecosystems. Given that euphausiids are a key prey items for many vertebrates occurring in the northern GOA (Armstrong et al. 2005; Wilson et al 2006; Hart 1973; Sigler 2001), quantifying mechanisms of top-down control of euphausiid populations should also be pursued through investigations of krill mortality due to predation, and studies on the relative abundance and stage-specific demands of their predators. Finally, determining life history traits of other euphausiids occurring within the Gulf of Alaska, such as *T. longipes*, *T. inspinata*, and *T. raschii* (Coyle and Pinchuk 2003), will help round out our understanding of ecosystem processes in this region as well as improve the precision of secondary production models. Several of these needs are currently being pursued.

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APPENDIX A

Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000[4]

A-1. Abstract

Zooplankton abundance from March through October on the northern Gulf of Alaska shelf in 1998, 1999 and 2000 was dominated by calanoid copepods; the biomass was dominated by calanoids and cnidarians. Although we sampled during the 1997-1998 El Niño, marked interannual differences in the major copepod taxa were not observed. Zooplankton abundance and species composition was influenced primarily by mean water-column salinity, secondarily by the mean temperature above the thermocline. An annual biomass peak, averaging about 0.5 g wet weight m^{-3}, occurred in May and consisted primarily of the oceanic copepod species *Neocalanus cristatus, Neocalanus plumchrus* and *Neocalanus flemingeri.* A second biomass peak, 0.5 g wet weight m^{-3}, was observed in August and consisted mainly of the cnidarian *Aequorea* spp. Copepod production estimated from daily growth rates using temperature-body size regressions peaked in May at about 35 mg C m^2 d^{-1}. Initial calculations suggest an annual copepod production on the order of 6 g C m^2 y^{-1}, probably less than 10% of the annual primary production. The apparent resilience of the zooplankton assemblage on the northern Gulf of Alaska shelf to the 1997-1998 ENSO may have been due to its large geographic separation from the faunal boundary between zooplankton communities in the California Current and North Pacific subarctic gyre.

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[4] Coyle, K.O., Pinchuk A.I. 2005. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 20. Fisheries Oceanography 12: 327-338

A-2. Introduction

The northern shelf of the Gulf of Alaska (GOA) supports a diverse and rich ecosystem and sustains a number of important fisheries resources, including millions of hatchery salmon smolts which are released annually into the GOA ecosystem through Prince William Sound (Willette et al., 2001). Nevertheless, the GOA shelf ecosystem is poorly understood. In contrast to most eastern boundaries of the Pacific Ocean, where wind-forced coastal upwelling regularly replenishes the euphotic zone with nutrients, the GOA shelf is deep and subject to persistent coastal downwelling. Presumably, this downwelling leads to nutrient depletion in the euphotic zone and low productivity during much of the summer following the initial spring bloom.

In addition, fisheries populations in the GOA ecosystem have undergone substantial changes. In the mid 1970's, the crab and shrimp populations declined while salmon and ground fish populations increased (Anderson and Piatt, 1999; Albers and Anderson, 1985; Blau, 1986; Hollowed et al., 1994; Thompson and Zenger, 1994; Francis and Hare, 1994). These changes coincided with decadal-scale North Pacific adjustments in the atmosphere and ocean (Trenberth and Hurrell, 1994; Mantua et al., 1997). Subsequent ecosystem changes followed in the 1980s with declines in marine mammal and seabird populations (Merrick et al., 1987; Hatch and Sanger, 1992; Springer, 1998). While such correlations suggest that the GOA ecosystem is sensitive to long-term climate variations, the mechanistic links between climate variability and ecosystem change are unknown.

The GOA GLOBEC program seeks to understand the mechanisms linking climate variability to the ecosystem response. Identification of long term ecosystem variability and its causes requires consistent data sets collected at time scales comparable to the decadal climate variations hypothesized to drive the ecosystem response. GOA GLOBEC is currently undertaking a long term observation program (LTOP) to gather the required data. The LTOP began in October 1997 and is projected to continue through August 2004. It consists of a number of components, including physical oceanography, nutrient cycling and primary production, zooplankton population assessments and a study of zero-class pink salmon populations on the GOA shelf. This paper summarizes the first three years of zooplankton observations, from October 1997 through October 2000.

GOA shelf waters are characterized by two major currents, the Alaska Stream which flows westward at or near the shelf break, and the Alaska Coastal Current, a buoyancy driven current flowing westward within 20 to 50 km of the shore line. The northern Gulf of Alaska coast is rugged with numerous bays, inlets and fjords. The bottom topography includes submarine canyons, ridges and submerged fjords. In addition to the main currents, the rugged topography and strong semidiurnal tides generate numerous eddies and meanders, which probably influence the species composition and distribution of zooplankton along the shelf.

Previous zooplankton studies on the GOA shelf focused primarily on Prince William Sound and Shelikoff Strait (Incze et al., 1996; Cooney et al., 2001). The zooplankton community in the above regions consists of a combination of oceanic and neritic herbivorous and omnivorous species (Cooney, 1986a, 1986b; Incze et al., 1996). The major oceanic taxa include the large calanoid species *Neocalanus plumchrus, N. flemingeri, N. cristatus, Eucalanus bungii* and *Metridia pacifica.* During spring and summer, 25-78% of the copepod biomass over the shelf is dominated by the oceanic species complex (Cooney, 1986a; 1986b, Incze et al., 1996). The distribution of oceanic copepods is presumably determined by cross shelf transport (Cooney, 1986a) and water mass type (Incze et al., 1996; Napp et al., 1996). The shelf species include the copepods *Pseudocalanus* spp. and *Calanus marshallae.* In addition to copepods, a number of micronektonic species contribute to the overall density of forage for fish on the GOA shelf. The euphausiid species include primarily *Thysanoessa inermis*, *T. spinifera* and *Euphausia pacifica*, with lower abundances of *Thysanoessa raschii, T. longipes, T. inspinata*, and *Tessarabrachion oculatum.* Amphipods include *Cyphocaris challengeri, Parathemisto pacifica*, and *Primno macropa* (Incze et al., 1996, Sugisaki et al., 1998). The above studies were done primarily in spring and early summer. Little information is available on zooplankton stocks for the entire production season. In the following paper, we describe the major features of the zooplankton production season on the GOA shelf, starting in March and ending in October. The seasonal cycle of the major species is presented and an estimate of the annual copepod production is computed. In addition, factors influencing species composition on the GOA shelf are outlined.

A-3. Methods

Zooplankton samples and conductivity-temperature-depth (CTD) profiles were taken along the Seward Line and in Prince William Sound (Fig. A-1) from October 1997 through October 2000 (Table A-1). CTD profiles were taken with a Seabird model 911 Plus with dual conductivity and temperature sensors. Large zooplankton and micronekton were collected with a 1-m^2 MOCNESS (Wiebe et al., 1976) with 500 μm mesh nets. The MOCNESS was equipped with a flowmeter positioned outside the mouth of the net. Additional sensors included Seabird 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. The small zooplankton component was sampled with a 25 cm diameter CalVET system (CalCOFI Vertical Egg Tow; Smith et. al., 1985) having 150 μm mesh nets. Each net was equipped with General Oceanics flowmeters in the mouth of the nets to monitor volume filtered. The net was fished vertically from 100 m depth to the surface. The samples were preserved in a 10% formalin seawater solution for later analysis.

The zooplankton samples were processed as follows: Each sample was poured into a sorting tray and large organisms, primarily shrimp and jellyfish, were removed and enumerated. The sample was then sequentially split using a Folsom splitter until the smallest subsample contained about 100 specimens of the most abundant taxa. The most abundant taxa were identified, staged, enumerated and weighed. Each larger subsample was examined to identify, enumerate and weigh the larger, less abundant taxa. The CalVET samples were subsampled with a Stempel pipet to produce subsamples with about 100 specimens of the most abundant taxa. Blotted wet weights of all specimens of each taxa and stage were taken on each sample and the coefficient of variation in average wet weight was computed. If the coefficient of variation for any given taxa and stage changed by less than 5% when additional weights were taken from subsequent samples, wet weights were no longer measured for that taxa for that cruise, and the wet weight biomass was estimated by multiplying the specimen count by the mean wet weight. In practice, only calanoid copepods had consistent wet weights after weighing each taxon and stage in about 10-15 samples. Therefore, wet weights on euphausiids, shrimp and other larger taxa were measured and recorded individually for each sample. Wet weight measurements were done on a Cahn Electrobalance or Mettler top loading balance, depending on the size of the animal. All animals in the samples were identified to the lowest taxonomic category possible. Copepodid stages were identified and recorded. The data were uploaded to a Microsoft Access data base, and analysis was done with standard statistics software. Counts and wet weights were taken for all taxa encountered in the subsamples.

Only adult and occasionally stage V *Acartia* were identified to species. Earlier copepodids were identified as *Acartia* spp. The specimens identified to species were *A. longiremis* and *A. hudsonica. Pseudocalanus* were not identified to species but referred to as *Pseudocalanus* spp. Species likely to occur in the northern Gulf of Alaska include *P. minutus, P. moultani, P. newmani* and *P. mimus.* Species previously identified from Shelikof Strait include all of the above except *P. moultani* (Siefert, 1994).

The depth of the thermocline and halocline was computed from the CTD data for each station by locating the depth where dT/dZ and dS/dZ was maximum (S = salinity, psu; T = temperature, °C; Z = depth, m). The mean water column temperature and salinity above and below the thermocline and halocline respectively, and the total mean water column temperature and salinity were then computed. In addition, the maximum value of dT/dZ and dS/dZ was recorded for each station. A general linear regression was used to identify relationships between zooplankton abundance, temperature, salinity and maximum halocline and pycnocline values. In practice, zooplankton density was related to mean salinity and temperature above the thermocline only.

The daily production of calanoid copepods was estimated from daily growth rates computed with a temperature-body size regression (Hirst & Lampitt, 1998). Body size in mg C was computed from formalin-preserved wet weights for each taxon and stage using the regression equations in Wiebe (1988). The biomass of specimens with individual wet weights greater than or equal to 0.3 mg was computed from the MOCNESS samples. Biomass for smaller specimens was computed from the CalVET samples. The biomass for each taxon and stage was integrated for the water column and converted to mg C m^{-2} using the literature regressions (Wiebe, 1988). Mean water column temperature was used in the growth equation. Water temperature for the MOCNESS samples was taken from the MOCNESS header file for each tow. Temperature for the CalVET samples was taken from the CTD water column profile at each CalVET station. We used the regression for broadcast spawners on data for the *Metridia*, *Neocalanus*, *Eucalanus*, *Mesocalanus* and *Calanus* species: $\log_{10} g = 0.0087(T) - 0.4902\log_{10}(BW) - 0.7568$, where g is the growth rate (d^{-1}), T is the temperature in ^{o}C and BW is the body weight in mg C individual^{-1}. The equation for sack spawners [$\log_{10} g = -1.7255 + 0.0464(T)$] was used to compute production for all other copepods, which consisted primarily of *Pseudocalanus* spp. and *Oithona similis*. The taxa and stages in the two size categories are listed in Table A-2.

A-4. Results

The annual cycle of zooplankton abundance and biomass on the Gulf of Alaska shelf during 1997-2000 showed a strong seasonal pattern (Fig. A-2). The mean monthly abundance of mesozooplankton during the production season was dominated by calanoid copepods, with a distinct abundance peak in May (Fig A-2A). Biomass during spring was also dominated by large calanoids, however, increases in abundance of large cnidarians resulted in a distinct cnidarian biomass peak in August (Fig A-2B). Cnidarian abundance was dominated by *Aglantha digitale*, *Dimophyes arctica* and bracts from unidentified siphonophores. Biomass was dominated by a small number of the large hydrozoans, predominantly *Aequorea victoria*. Pteropod abundance increased during summer with peak abundance and biomass in August. The mean monthly biomass and abundance of euphausiids was relatively constant throughout the production season. Although hyperiid amphipods (primarily *Parathemisto pacifica*), the larvacean genus *Oikopleura* and chaetognaths (primarily *Sagitta elegans* and *Eukrohnia hamata*) were present, they were minor constituents of abundance and biomass in the MOCNESS samples.

Small calanoids and cyclopoids dominated copepod abundance in the CalVET samples (Fig. A-3). The small calanoids consisted primarily of *Pseudocalanus* spp., with low abundances of *Microcalanus* spp., *Racovitzanus antarctica, Calanus pacificus* and *Mesocalanus tenuicornis*. The cyclopoid copepod *Oithona similis* was also very abundant, particularly during May through August. Despite their lower abundance, the mean monthly copepod biomass was dominated by the large calanoids, particularly in May, when the oceanic species (*Neocalanus cristatus, N. flemingeri* and *N. plumchrus*) were most abundant.

Although copepod biomass in April and May was dominated by the *Neocalanus* species, as the season progressed, *Neocalanus* disappeared from shelf waters, and copepod biomass was made up of the smaller species, *Pseudocalanus* spp. and *Metridia pacifica* (Fig. A-3). Prince William Sound contained a unique species assemblage, consisting of *Metridia okhotensis*, the shrimp *Pasaphaea pacifica*, the lyassianasid amphipod *Cyphocaris challengeri*, unusually high numbers of pelagic ostracods and the arctic hyperiid *Parathemisto libellula*, with high concentrations of *N. flemingeri* in April and May. *P. libellula*, *Pasapheae pacifica* and *C. challengeri* were generally absent from shelf waters.

Copepod production was approximately 20 mg C m^{-2} d^{-1} during March, it gradually increased throughout the spring and peaked at about 35 mg C m^{-2} d^{-1} during May, it remained around 30 mg C m^{-2} d^{-1} through much of the summer, and declined between August and October (Fig. A-4). *Metridia pacifica* dominated the production throughout the year, comprising about half of the total annual copepod production. The sack spawners *Pseudocalanus* spp. and *Oithona similis* were responsible for an additional third of the total production, and about half of the production in July. Most of the remaining production was generated by the oceanic copepods of the *Neocalanus* and *Eucalanus* genera, primarily in April and May. Total copepod production between March and October was estimated at about 6 g C m^{-2} (Table A-3).

The copepod abundance data from the CalVET samples were power transformed to stabilize the variance, the mean and 95% confidence intervals for each month were computed for each of the major taxa, and the results were converted back to the arithmetic values for plotting. The confidence intervals were quite broad (Fig. A-5) indicating substantial patchiness in zooplankton distribution. Nonetheless, some general trends emerged. The mean abundance of *Neocalanus* species during April and May showed a general decline such that confidence intervals between 1998 and 2000 did not overlap. Mean *Neocalanus* abundance during spring of 1999 was intermediate and not significantly different from either 1998 or 2000. Mean abundance of the smaller species (*Pseudocalanus* spp., *Oithona similis*) was highest in spring of 2000 (Fig. A-5). *Pseudocalanus* abundance was particularly low in April and May of 1999, such that the confidence intervals between 1999 and 2000 did not overlap. A general linear model was run to compare the effects of temperature, salinity, year and month on the abundance of the major copepod species along the Seward Line between 1997 and 2000 (Table A-4). Species in the analysis included *Neocalanus cristatus, Neocalanus plumchrus-flemingeri, Calanus marshallae, Calanus pacificus, Eucalanus bungii, Mesocalanus tenuicornis, Metridia pacifica, Pseudocalanus* spp., *Oithona similis* and calanoid nauplii. The major covariate influencing copepod abundance was water column salinity. The mean water column temperature above the thermocline was of secondary influence. The predominant influence of salinity on shelf circulation has been demonstrated by physical data and circulation models (Royer, 1998; Williams, 2003).

Although the abundance of *M. tenuicornis* and *C. pacificus* showed a distinct positive relationship with temperature, obvious relationships between temperature and abundance of the other species were not observed. *M. tenuicornis* and *C. pacificus* were very minor contributors to abundance and biomass. The mean of water mass properties in the upper 100 m for May of each year was computed to characterize interannual differences that may have been influencing the above trends in species abundance (Table A-5). The mean temperature in the upper mixed layer in 1999 was significantly lower than in 1998 and 2000. The mean salinity in 1998 was significantly lower than in 1999 and 2000, and there was a general trend of increasing intensity of the seasonal pycnocline from 1998 through 2000.

A-5. Discussion

The seasonal pattern of zooplankton abundance and biomass on the GOA shelf is characterized by two major events: a biomass peak and an abundance peak. The highest zooplankton biomass over the shelf is observed during May, when the populations of stage V *Neocalanus* species are greatest. The *Neocalanus* species dominate the biomass due to their large size. *N. cristatus*, for example, reach lengths of up to 7 mm with an average wet weight of 13 mg. *N. plumchrus* and *N. felmingeri* are around 4 mm long with an average wet weight of about 3 mg. The *Neocalanus* undergo an ontogenetic migration to depths of 300 to 600 m starting in May and progressing through late summer (Tsuda et al. 1999; Kobari and Ikeda, 2001a; Kobari and Ikeda, 2001b); they are therefore largely absent from the shelf and surface layers of the slope waters from August until the following spring. Copepod populations are overwhelmingly dominated by the smaller copepod species (*Oithona similis* and *Pseudocalanus* spp.), which reach peak abundances in July. These seasonal patterns of abundance and biomass are similar to those reported for Prince William Sound (Cooney et al., 2001) and Shelikof Strait in 1985 (Incze et al., 1996), where the biomass in May is dominated by *N. plumchrus-flemingeri* and the populations are dominated by *Pseudocalanus* spp. When converted to units of carbon, the mean copepod biomass for upper 100 m of the GLOBEC study area in May, 1998 - 2000, was about 2,918 mg C m^{-2} with a maximum and minimum of 9356 and 749 mg C m^{-2} respectively. Copepod biomass for Shelikof Strait in 1986 - 1989 was estimated to be 2 to 13 g C m^{-2} (Incze et al, 1996). Mesozooplankton biomass in open ocean waters of the northeast subarctic Pacific in May 1996 was about 5 -20 mg C m^{-3} in the upper 150 m (Goldblatt et al., 1999). The above comparisons suggest the potential for substantial spatial and temporal variations in the maximum annual copepod biomass in the Gulf of Alaska and adjacent shelf.

The Hirst-Lampitt regressions relating copepod production to body size and temperature consist of three main equations, one for broadcast spawners, one for sack spawners and one for both sack and broadcast spawners combined (Hirst and Lampitt, 1998). The results of production estimates using these regressions can be highly sensitive to the particular equation applied. If the combined regression equation for both broadcast and sack spawners is used for the GOA shelf data, the annual production estimate is about 54 g C m^{-2} y^{-1}, with *Pseudocalanus* and *Oithona* accounting for about 85% of the total. If separate equations for the sack and broadcast spawners are applied to their respective taxa, then the annual production estimate is 6 g C m^{-2} y^{-1}, with *Pseudocalanus* and *Oithona* accounting for only about 28% of the total (see Results section). This large discrepancy between production estimates is due to the non-linear relationship between production and body size in the equations for broadcast spawners, and for broadcast and sack spawners combined. As the animals become smaller, the size correction in the regression equations increasingly dominates, resulting in very high production estimates if the biomass is dominated by small animals. The production equation for sack spawners is independent of body size. Its use for *Pseudocalanus* and *Oithona* removed the body size correction from a large proportion of the small copepod component, thus markedly lowering the overall production estimate for the GOA shelf.

Zooplankton production in Port Valdez, a fjord in Prince William Sound, was estimated at 38-51 g C m^{-2} y^{-1}, assuming a 30% gross growth efficiency, a primary production rate of 150-200 g C m^{-2} y^{-1}, and 85% of the annual carbon production is consumed by zooplankton grazers (Cooney and Coyle, 1988). Although the Valdez zooplankton production estimate is similar to that generated for copepods on the GOA shelf when using the combined regression equation, it excludes the potential influence of microzooplankton grazers, which might substantially reduce the proportion of annual phytoplankton production going directly to mesozooplankton grazers. It therefore probably overestimates the total annual mesozooplankton production in Port Valdez. On the other hand, the copepod production computed for the GOA shelf, using separate regressions for sack and broadcast spawners, probably underestimates total zooplankton production because it excludes the contribution of euphausiids, pteropods, larvaceans and microzooplankton. The above values of 6 and 54 g C m^{-2} y^{-1} are therefore probably reasonable upper and lower limits for zooplankton production on the GOA shelf. Ongoing GLOBEC process studies should help clarify the production relationships in this region.

The unusually low *Pseudocalanus* populations in 1999 relative to 2000 may have been related to the significantly lower water temperatures during 1999 relative to other years. The lower temperatures may have suppressed spring-time reproduction, particularly in neritic taxa, whose reproductive rates are related to ambient shelf water temperatures. Reproduction by the interzonal copepods, which occurs at greater depth, would not have been influenced by the unusually cold temperatures on the shelf. There is at least some evidence that *Pseudocalanus* populations are strongly influenced by survival from the previous winter (Colebrook, 1985), which may also be temperature related. Other factors influencing populations on the shelf would include predation and food availability.

Although the *Neocalanus* species most often occur in oceanic environments, Prince William Sound also sustains a large population of *N. flemingeri* (Cooney et al., 2001). Populations of *N. flemingeri* overwinter in the northwestern regions of the sound, where bottom depths are over 700 m. Substantial populations of late stage copepodids are observed in the upper mixed layer in April and May, and provide an important food source for a variety of fish species (Willette, 1996; Sturdevant et al., 1996). Model simulations indicate that a portion of the resident *Neocalanus* population is swept into Montague Strait (Wang et al., 2001), where they are presumable advected out of the sound and westward along the coast by the Alaska Coastal Current. Therefore, some portion of the *N. flemingeri* populations observed on the shelf in April and May originate in Prince William Sound. Transport of copepods from the shelf into and out of Prince William Sound is also indicated by stable isotope measurements (Kline, 1999).

A number of studies have attempted to link zooplankton variability in the North Pacific to climate anomalies (Conversi and Hameed, 1997; Hameed and Conversi, 1995; Brodeur and Ware, 1992; McGowan et al., 1998). The most detailed have examined long-term data sets from the British Columbia and Oregon coasts (Mackas et al., 2001; Peterson, 1999). Essentially, mean abundances and biomass were computed and significant anomalies from the long term averages were identified and related to climate anomalies. While anomalies in zooplankton biomass were observed off the British Columbia coast, the major anomalies were expressed as changes in species composition. Specifically, the boreal-continental shelf copepods (*Calanus marshallae, Pseudocalanus mimus* and *Acartia longiremis*) off British Columbia declined throughout the 1990s but increased in 1999 (Mackas et al., 2001). At the same time, species with southern affinities (*Ctenocalanus vanus, Paracalanus parvus, Clausocalanus* spp. and *Mesocalanus tenuicornis*) all increased. During the same period, temperatures increased by about 1-2°C with strong but brief declines in salinity during El Niño events (Mackas et al., 2001). We observed significantly warmer temperatures and lower salinity on the GOA shelf during spring of 1998, the end of the last El Niño. In addition, the concentrations of *M. tenuicornis* and *C. pacificus* were significantly higher in 1998 than in subsequent years. *P. parvus* were observed in a small bay in Prince William Sound in 1997 (Foy, 2000). The other species with southern affinities have not been reported in the northern GOA. *M. tenuicornis* has been reported previously from Prince William Sound (Cooney and Coyle, 1985).

The climatological-oceanographic anomalies observed off British Columbia (Mackas et al, 2001) are apparently basin-wide phenomena. The El Niño event of 1997-98 was experienced on the Seward Line (northern Gulf of Alaska shelf) as a period of distinctly higher temperatures and lower salinity during spring of 1998. During summer of 1997 unusually warm, calm conditions were observed in the southeastern Bering Sea (Overland et al, 2001, Stabeno et al, 2001). The warm conditions were accompanied by anomalous ecological events, including a coccolithophorid bloom (Stockwell et al, 2001; Sukhanova and Flint, 1998), high mortality of shearwaters (Baduini et al, 2001) and salmon returns below predicted numbers (Napp and Hunt, 2001). The reversal to colder conditions observed off British Columbia in 1999 (Mackas et al, 2001) was experienced in the southeastern Bering Sea as a period of unusually cold temperatures and extensive spring ice cover, accompanied by significantly lower copepod abundance and production during spring (Coyle and Pinchuk, 2002). The absence of substantial numbers of calanoid species with southern affinities in the northern Gulf of Alaska, even during periods of warming such as experienced during the 1990s, is probably due to the large geographical distance between the northern GOA coast and the faunal boundary separating zooplankton communities in the California Current from those in the North Pacific subarctic gyre.

Climate anomalies on the northern GOA shelf will probably be expressed as changes in the relative abundances of the major zooplankton taxa comprising the northern boreal zooplankton community, or as changes in the timing of seasonal peaks in population or biomass. Long term observations in the north Pacific subarctic gyre suggest that the timing of the annual copepod biomass peak may change by weeks to months (Mackas et al, 1998), which may in turn influence energy transfer in the ecosystem (Anderson and Piatt, 1999). The GOA shelf is very dynamic; strong currents, frequent storms and intense eddies often mix oceanic and coastal waters (Okkonen et al, 2001), producing substantial spatial variation in the species composition and relative abundance of the major zooplankton taxa. The resulting spatial variation generates broad confidence intervals in monthly mean population and biomass estimates. The 95% confidence interval can be as high as two and three times the respective mean, depending on the taxon. The above suggests that means must differ by as much as three times before statistically significant differences can be detected. The broad confidence intervals are a result of the highly patchy distribution of zooplankton related to the complicated dynamics influencing water masses on the shelf (Okkonen et al, 2001; Royer, 1998). The critical periods for assessing zooplankton on the GOA shelf during the production season, are March and October, which set the start and end points, May, which sets the biomass peak, and July which sets the abundance peaks. As data from the ongoing LTOP studies continue to accumulate, significant departures from the long term means of abundance and biomass can be detected and related to specific climatic conditions.

A-6. Acknowledgments

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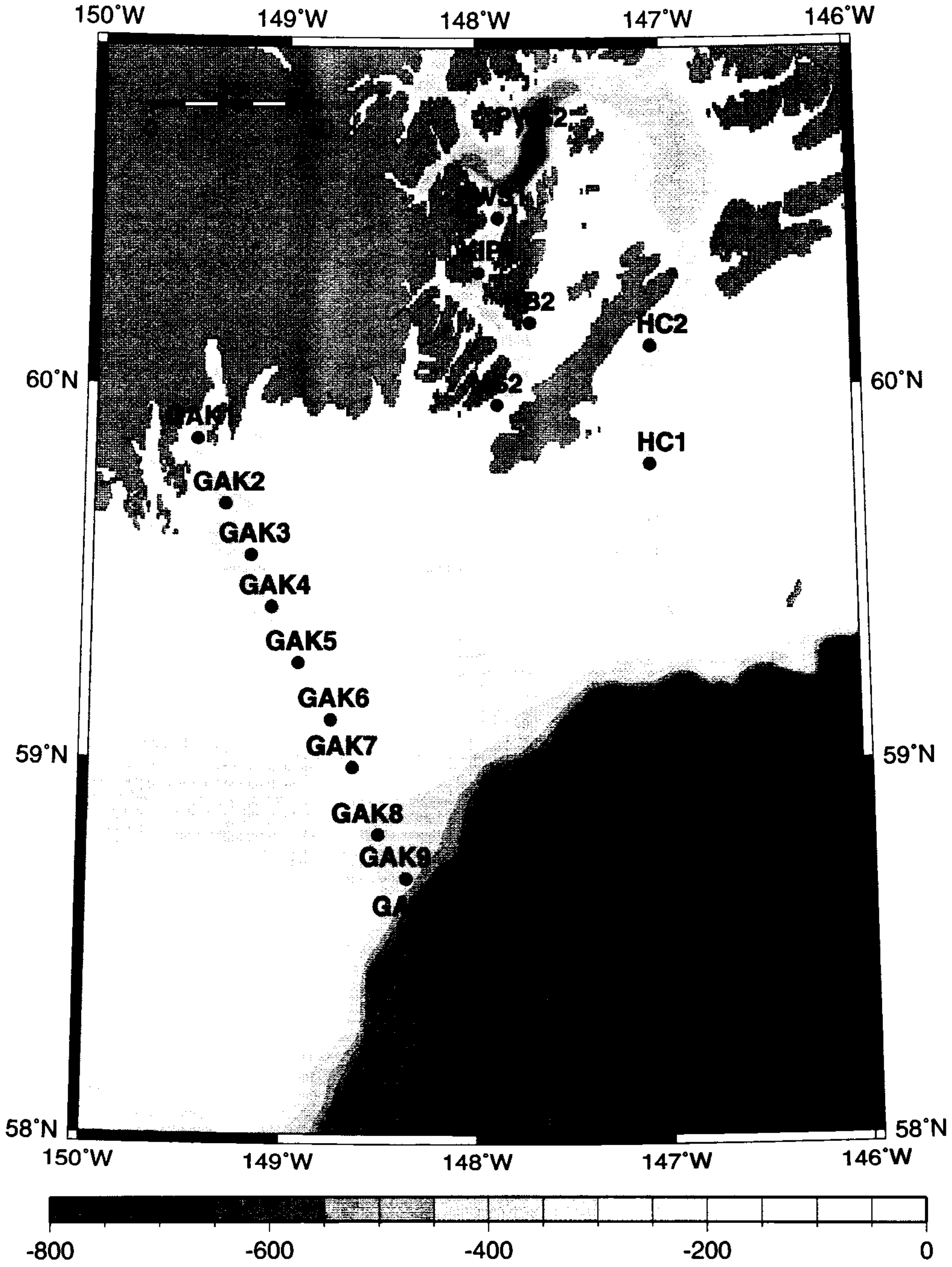

Fig. A-1. Station locations for the northern Gulf of Alaska GLOBEC LTOP project.

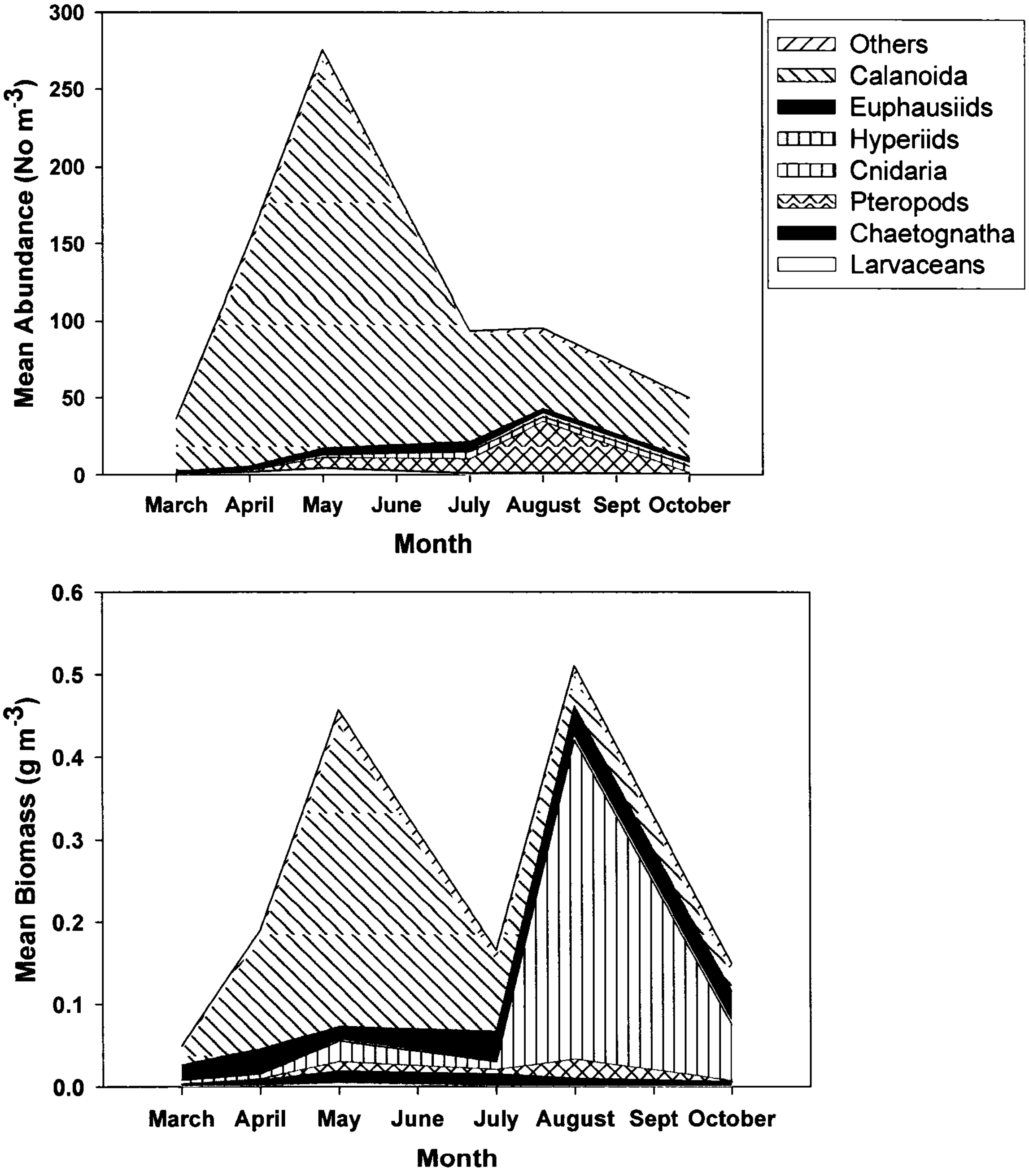

Fig. A-2. Monthly mean abundance and biomass of the major zooplankton taxa on the Seward Line for 1998 through 2000. A: Abundance; B. Biomass

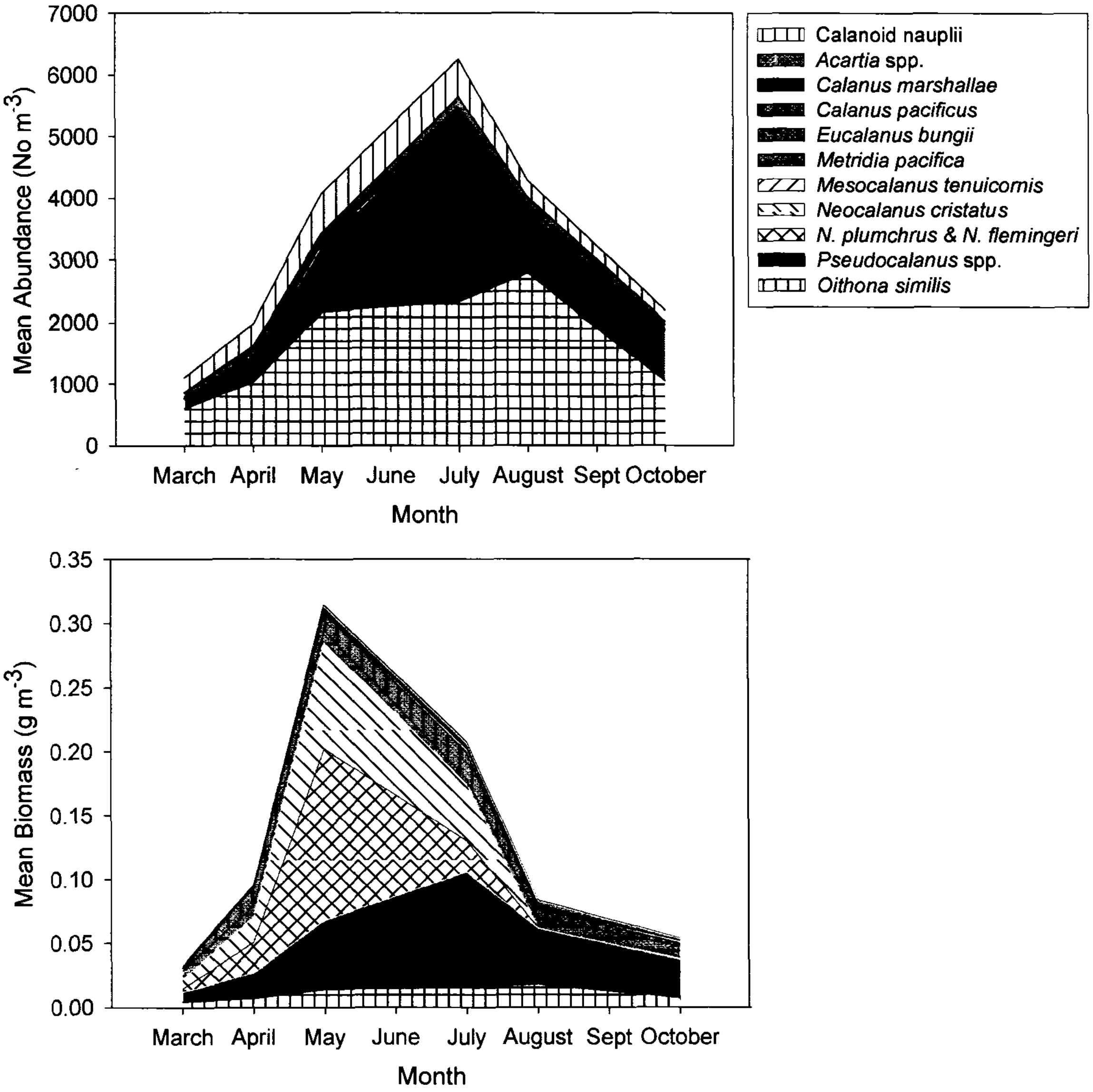

Fig. A-3. Monthly mean abundance and biomass of the major copepod taxa on the Seward Line for 1998 through 2000. A: Abundance; B. Biomass.

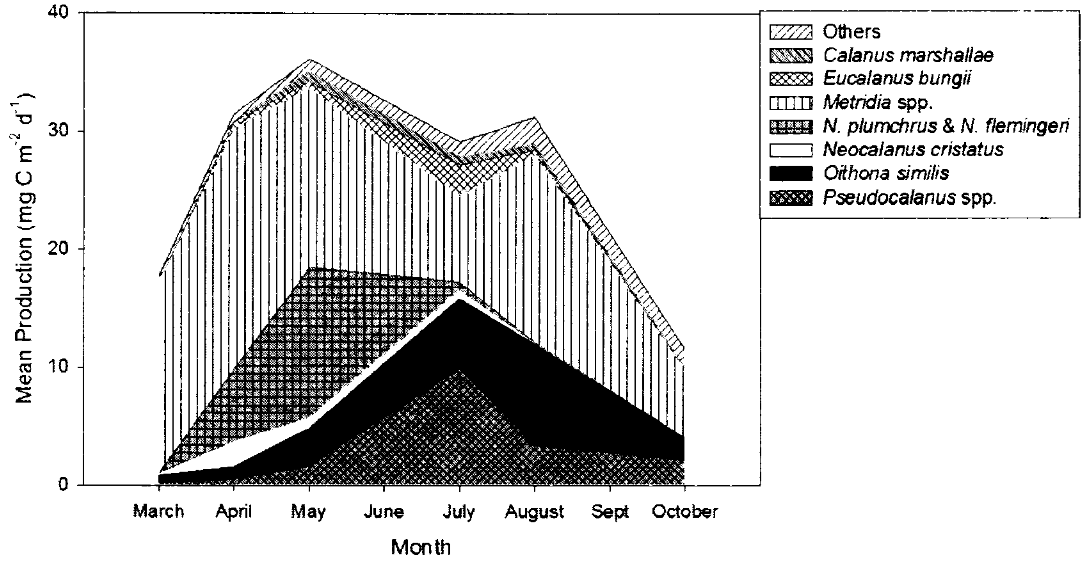

Fig. A-4. Average monthly copepod production on the Seward Line, northern Gulf of Alaska shelf, 1998 through 2000.

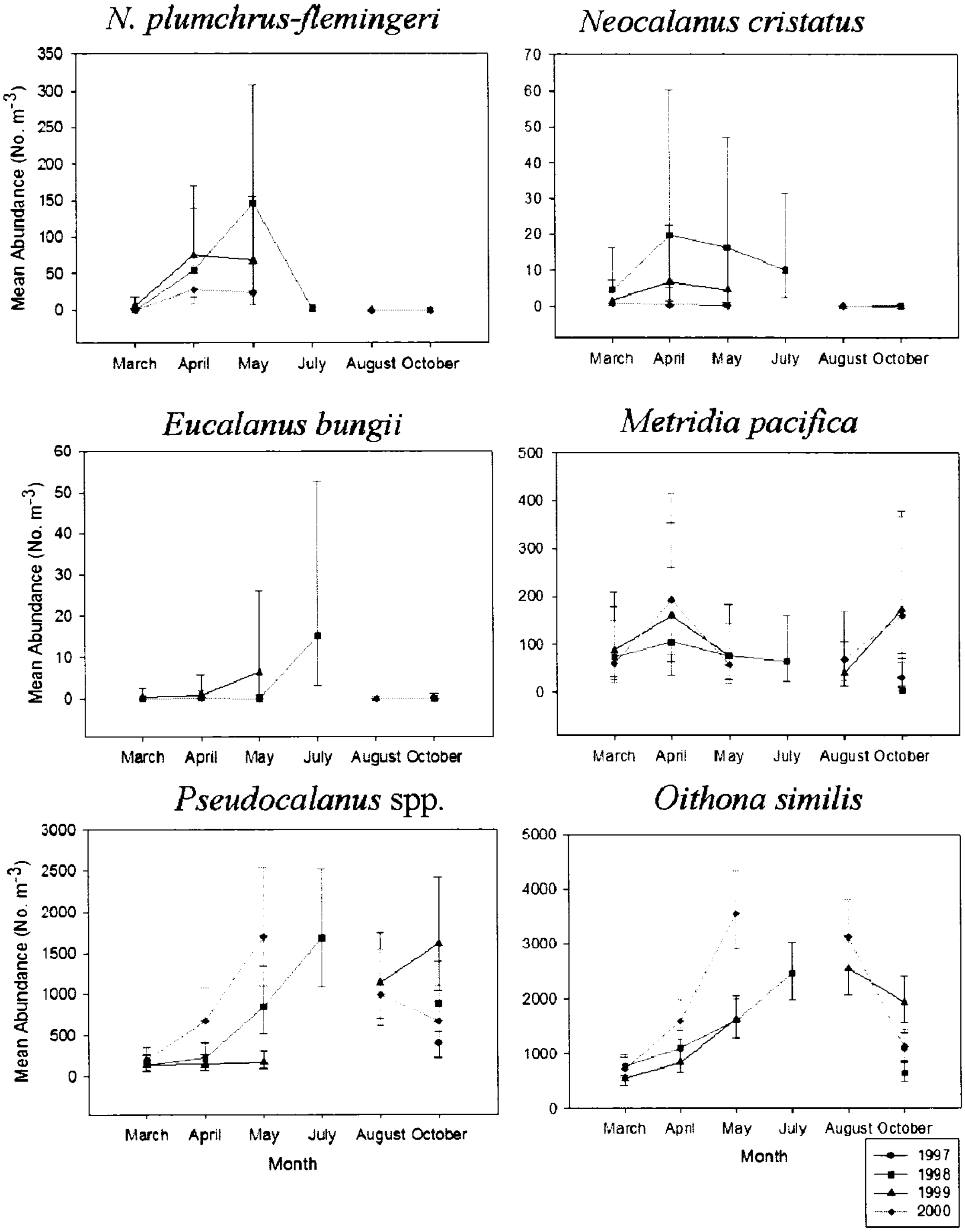

Fig. A-5. Mean monthly abundance and 95% confidence intervals of major copepod taxa from CalVET tows taken off the northern Gulf of Alaska coast from October 1997 through October 2000.

Table A-1. Month and year for GLOBEC LTOP cruises in the northern Gulf of Alaska.

Year	Mar	Apr	May	July	Aug	Oct
1997						HX201
1998	HX203	HX205	HX208	HX211		HX213
1999	HX217	HX218	HX219		HX223	HX225
2000	HX228	HX230	HX231		HX234	HX237

Table A-2. Taxa and stage of calanoids analyzed from CalVET and MOCNESS samples. All animals with wet weights greater than 0.3 mg were taken from the MOCNESS nets, smaller animals were taken from the CalVETS.

Taxa	Gear Type and Stages	
	CalVET	MOCNESS
Acartia spp.	All Stages	
Aetideidae (Adults)	I-IV	V, Adults
Calanus marshallae	I-III	IV, V, Adults
Calanus pacificus	I-IV	V, Adults
Candacia columbiae	I-III	IV, V, Adults
Centropages abdominalis	All Stages	
Clausocalanus spp.	All Stages	
Epilabidoceros amphitrites	I-III	IV, V, Adults
Eucalanus bungii	I-III	IV, V, Adults
Euchaeta elongata	I-II	III - V, Adults
Eurytemora spp.	All Stages	
Heterorhabdus spp.	I-III	IV, V, Adults
Heterostylites spp.	I-IV	V, Adults
Lucicutia spp.	I-IV	V, Adults
Mesocalanus tenuicornis	All Stages	
Metridia okhotensis	I-IV	V, Adults
Metridia pacifica	I-V, Males	Females
Microcalanus spp.	All Stages	
Neocalanus cristatus	I-II	III-V, Adults
Neocalanus plumchrus-flemingeri	I-III	IV, V, Adults
Oithona spp,	All Stages	
Oncaea spp.	All Stages	
Paracalanus spp.	All Stages	
Pleuromamma spp.	I-IV	V, Adults
Pseudocalanus spp.	All Stages	
Racovitzanus antarcticus	All Stages	
Scolecithricella spp.	All Stages	
Tortanus discaudata	All Stages	

Table A-3. Average annual copepod production on the Gulf of Alaska shelf between March and October, 1998 through 2000.

Taxa	Production ($\mathrm{mg\ C\ m^{-2}\ yr^{-1}}$)
Pseudocalanus spp.	757
Oithona similis	926
Neocalanus cristatus	156
Neocalanus plumchrus/flemingeri	794
Metridia spp.	2809
Eucalanus bungii	182
Calanus marshallae	106
Others	276
Total	6008

Table A-4. Multivariate test of the significance of year, month, upper mixed water column temperature (Upper Mixed Temp) and mean water column salinity (Mean Sal) by year and month on the abundance of the major copepod species sampled by CalVET nets along the Seward Line from 1998 through 2000.

	Test	Value	F	Effect df	Error df	p
Upper Mixed Temp	Wilks	0.873126	1.956091	13	175.000	0.027026
Mean Sal	Wilks	0.603388	8.848375	13	175.000	0.000000
Year*Month	Wilks	0.182349	3.792362	91	1099.386	0.000000

Table A-5. Mean salinity, temperature, thermocline and halocline intensity along the Seward Line during May, 1998 – 2000.

	Year			
Variable	1998	1999	2000	Bonferroni test
Salinity	31.93	32.36	32.31	1998 < 1999 = 2000
Temperature	6.88	5.68	6.58	1999 < 1998 = 2000
Thermocline Intensity	0.087	0.111	0.169	1999=1998<2000=1999
Halocline Intensity	0.057	0.030	0.037	No Differences

APPENDIX B

Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior[5]

B-1 Abstract

The cross-shelf distribution of major zooplankton species was examined on the northern Gulf of Alaska (GOA) shelf during the production season for four years, between October 1997 and October 2001. The zooplankton community on the northern GOA shelf consisted of oceanic and neritic species of the North Pacific subarctic species complex. Cross shelf distribution of the major zooplankton species was influenced by their depth preferences, vertical migration behavior, salinity-temperature preferences and by cross-shelf water-mass distribution and movement. The neritic community, dominated by *Pseudocalanus* spp., *Metridia pacifica* and *Calanus marshallae*, had highest abundances on the inner shelf, in the Alaska Coastal Current and the adjacent fjords in late spring and early summer. The oceanic community, which contained primarily *Neocalanus cristatus* and *Eucalanus bungii*, was observed in the Alaska Stream and adjacent waters near the shelf break. A mid-shelf transition zone contained a mixture of oceanic and neritic species. Prince William Sound (PWS) contained a unique species complex of large mesopelagic copepods, amphipods and shrimp. *Neocalanus flemingeri* and *Oithona similis* were abundant in all four regions during spring and early summer. The transition zone commonly crossed much of the shelf between the shelf break and the ACC, but satellite images and CTD data indicate that occasionally a narrow shelf-break front can form, in which case distinct zooplankton species groups are observed on either side of the front. Satellite data also revealed numerous large and small eddies, which probably contribute to cross-shelf mixing in the transition zone.

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[5] Coyle, K.O., Pinchuk A.I. 2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. Deep-Sea Research II 52: 217-245

B-2. Introduction

As human populations expand, the potential for anthropogenic impact on ecosystems through climate change has attracted growing interest and concern. Although climatic influences on ecosystems can be subtle and difficult to document, a growing body of evidence indicates that climate cycles can markedly influence marine populations (Conversi and Hameed, 1997; Hameed and Conversi, 1995; Brodeur and Ware, 1992; McGowan et al., 1998). In the northern Gulf of Alaska (GOA), a substantial shift from a crustacean to a fin-fish fishery in the late 1970s (Anderson and Piatt, 1999; Albers and Anderson, 1985; Hollowed et al., 1994; Thompson and Zenger, 1994) coincided with changes in several climate indices (Trenberth and Hurrell, 1994; Mantua et al., 1997). Subsequent ecosystem changes followed in the 1980s with declines in marine mammal and seabird populations (Merrick et al., 1987; Hatch and Sanger, 1992; Springer, 1998). Although temporal correlations between shifts in climate indices, and fisheries and wild-life resources suggest causal relationships, mechanistic links between climate and the ecosystem response are not obvious. GOA GLOBEC (Global Ocean Ecosystems Dynamics) is a multidisciplanary research effort seeking to clarify the causal links between climate and the ecosystem. Since major climate indices shift on time scales of decades to centuries, long-term observations are necessary to capture specific ecosystem changes related to climate shifts and to identify and document the mechanisms driving the changes. The GLOBEC Long Term Observation program (LTOP) is an initial step in the long-term data acquisition effort in the northern GOA. The zooplankton component of LTOP is gathering data to clarify zooplankton distribution and abundance relative to season and physical oceanographic properties influenced by climate. This paper documents cross-shelf zooplankton distribution relative to oceanographic conditions during the production season. For this analysis, we define the production season as the period between March and October (Coyle and Pinchuk, 2003).

Zooplankton on the northern GOA shelf are a mixture of oceanic and neritic species common in the subarctic North Pacific (Cooney, 1986a; 1986b, Incze et al., 1996; Napp et al. 1996). Large interzonal copepods of the genera *Neocalanus* and *Eucalanus* dominate zooplankton biomass on the GOA shelf in spring and early summer (Incze et al., 1996; Coyle and Pinchuk, 2003; Cooney et al., 2001a). The *Neocalanus* species complete their foraging cycle and begin migrating to overwinter depths in the mesopelagic zone in May and June (Tsuda et al. 1999; Kobari and Ikeda, 2001a, b). Their contribution to zooplankton biomass in the upper mixed layer therefore declines and they are largely absent from shelf water by July and August (Cooney et al., 2001a; Coyle and Pinchuk, 2003). The neritic copepod species include *Pseudocalanus* spp., *Calanus marshallae*, *Centropages abdominalis* and *Acartia* spp. Of the smaller species, *Metridia pacifica, Pseudocalanus* and *Oithona similis* dominate copepod populations. Their highest populations are observed in mid summer (Coyle and Pinchuk, 2003).

Although copepods dominate mesozooplankton biomass during spring and abundance throughout the production season, larger micronektonic species are common and can be important components in the diets of fish and other large predators (Boldt and Haldorson, 2003; Coyle and Paul, 1992; Albers and Anderson, 1985). The most abundant micronekton species on the northern GOA shelf include euphausiids, hyperiid and gammaridean amphipods, and some shrimp species (Incze et al., 1996, Sugisaki et al., 1998). Our analysis therefore includes the dominant euphausiids of the genera *Thysanoessa* and *Euphausia*, the hyperiid genus *Parathemisto*, the gammarid species *Cyphocaris challengeri* and the shrimp *Pasiphaea pacifica.*

The northern Gulf of Alaska has a rugged mountainous coast with numerous bays, inlets and fjords. The shelf in the study area, offshore of the Kenai Peninsula on the cental 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 to 50 km of 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 cross-shelf transport of water masses, influencing the species composition and distribution of zooplankton along the shelf.

Prince William Sound (PWS) is a large fjord system to the northeast of the Seward Line (Fig. B-1). Knight Island Passage, in the western side of the sound, contains one of the deepest areas on the shelf, with maximum depths in excess of 700 m. PWS is an important nursery area and habitat for a number of ecologically and commercially important fish species, including capelin, herring, salmon and pollock (Pearcy, 2001). Many of the juvenile pink salmon taken on the Seward Line by the fish component of GLOBEC originate in the sound (Boldt, per. comm., see also: Farley and Munk, 1997). PWS is also an important habitat for a number of seabird and marine mammal species (Ostrand et al., 1998; Maliscalco et al., 2001). In addition, it is an important local source of fresh water influencing circulation on the shelf. It therefore influences both the ecology and physical properties in the study area and is important to our understanding and interpretation of the Seward Line data set.

B-3. Methods

Zooplankton samples, conductivity-temperature-depth (CTD) and fluorescence profiles were taken along the Seward Line and in Prince William Sound (Fig. B-1) from October 1997 through October 2001 (Table B-1). CTD and fluorescence profiles were taken with a Seabird model 911 Plus with conductivity, temperature and fluorescence sensors. Large zooplankton and micronekton were collected with a 1-m^2 MOCNESS (Wiebe et al. 1976) with 500 μm mesh nets. The MOCNESS was equipped with a flowmeter positioned outside the mouth of the net. Additional sensors included Seabird 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. The small zooplankton component was sampled with a 25 cm diameter CalVET system (CalCOFI Vertical Egg Tow; Smith et al., 1985) having 150 μm mesh nets. Each net was equipped with General Oceanics flowmeters in the mouth of the nets to monitor volume filtered.

The net was fished vertically from 100 m depth to the surface. The samples were preserved in a 10% formalin seawater solution for later analysis.

The zooplankton samples were processed as follows: each sample was poured into a sorting tray and large organisms, primarily shrimp and jellyfish, were removed and enumerated. The sample was then sequentially split using a Folsom splitter until the smallest subsample contained about 100 specimens of the most abundant taxa. All taxa in the smallest subsamples were identified, staged, enumerated and weighed. Each larger subsample was examined to identify, enumerate and weigh the larger, less abundant taxa. The CalVET samples were subsampled with a Stempel pipet to produce subsamples with about 100 specimens of the most abundant taxa. Blotted wet weights of all specimens of each taxa and stage were taken as outlined in earlier papers (Coyle and Pinchuk, 2003; Coyle et al, 1990). All animals in the samples were identified to the lowest taxonomic category possible. Copepodid stages were identified and recorded.

Only adult and occasionally stage V *Acartia* were identified to species. Earlier copepodids were identified as *Acartia* spp. The specimens identified to species were *A. longiremis* and *A. hudsonica*. *Pseudocalanus* were not identified to species but referred to as *Pseudocalanus* spp. Species likely to occur in the northern Gulf of Alaska include *P. minutus, P. moultani, P. newmani* and *P. mimus.* Species previously identified from Shelikof Strait include all of the above except *P. moultani* (Siefert, 1994). Copepodid stages IV through VI of the *Neocalanus plumchrus - N. flemingeri* species complex were routinely identified to species. Earlier stages were referred to as *Neocalanus plumchrus-flemingeri.* The two species were pooled for statistical analysis.

The data were uploaded to a Microsoft Access data base, and analysis was done with standard statistics software. Analysis included a total of 1862 MOCNESS samples and 330 CalVET 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.

Multidimensional scaling (MDS) was applied in conjunction with the Bray-Curtis dissimilarity index to the ten most abundant taxa in each MOCNESS sample to discriminate community differences. The data from October 1997 to October 2001 were stratified by region and month to determine the seasonal pattern of cross-shelf distribution of the major zooplankton taxa on the northern GOA shelf. The regions included the Outer Region, Transition Zone, Inner Shelf and Prince William Sound. The Outer Region consisted of Stations GAK10 through GAK13, which are at or just offshore of the continental slope and generally influenced by the Alaska Stream. The Inner Shelf region consisted of Stations GAK1 through GAK4, which are influenced by the ACC during the production season. The Transitional region consisted of Stations GAK5 through GAK9 and Prince William Sound stations included the three stations in Knight Island Passage (PWS1, PWS2, KIP2) and Montague Strait (MS2, HB2). The abundance data from the MOCNESS and CalVET tows were power transformed to stabilize the variance and a MANOVA was run to look for relationships between month and region.

Physical properties influencing zooplankton 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; σt = 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, 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). Analysis of variance was used to test for significant differences in mean physical properties by station and month. Canonical correlation was run on both CalVET and MOCNESS abundance data to detect relationships between the physical properties and abundance of the major zooplankton taxa.

Satellite data (Sea-Viewing Wide Field-of-View Sensor; SeaWIFS) were provided by Dave Musgrave (Institute of Marine Science, University of Alaska).

B-4. Results

B-4.1 Station groupings by dominant taxa

Multidimensional scaling revealed four major patterns of station distribution on two-dimensional scale plots generated using the ten most abundant taxa in each of the MOCNESS nets (Fig. B-2). Examples in Fig. B-2 were selected because satellite images were available to illustrate the mesoscale distribution of surface fluorescence and associated water properties for each major pattern. The most common pattern (Fig. B-2D, Table B-2) consisted of two station groupings, with shelf stations and PWS stations forming separate groups (stress values between 0.2 and 0.1). The outer and inner stations on the transect line occurred at opposite ends of the shelf group, with mid-shelf stations scattered between. A second common pattern consisted of a scatter of stations with no distinct groupings (Fig. B-2A, Table B-2), in which case the outer and inner stations again occurred at the opposite ends of the plot, with the mid-shelf stations scattered between (stress > 0.2). Occasionally the shelf stations were clustered in distinct groups (Fig. B-2B, C, Table B-2) (stress < 0.09). Temperature, salinity and fluorescence profiles along the Seward Line revealed that shelf station groupings were usually associated with particular water masses, as indicted primarily by salinity (Figs. B-3-6). Fluorescence profiles and satellite color images indicated that water masses were commonly associated with distinctly different chlorophyll concentrations present over wide regions of the shelf and adjacent ocean. Examples from May and July, depicting conditions for MDS patterns in Fig. B-2, are detailed below.

B-4.2 Cross shelf distribution of zooplankton and physical properties

The cross shelf distribution of physical properties and zooplankton for MDS patterns A and D (Table B-2) is illustrated by data taken in May 1998 and May 2000 (Fig. B-3 and B-4). Although oceanic species were more abundant on the outer end of the line and shelf species on the inner end, much of the transect consisted of a mixture of taxa; obvious regions with distinct zooplankton communities were not observed. The zooplankton community was dominated by *Neocalanus plumchrus* and *N. flemingeri* across the entire shelf in May 1998 (Fig. B-3A). *Metridia pacifica* was most abundant on the inner shelf, but was common across the shelf to 180 km. *Neocalanus cristatus* was present across the shelf in substantial concentrations to within 30 km of the coast. Temperatures > 7°C were observed in the upper 20-40 m over much of the shelf (Fig. B-3C). A shelf-break salinity front was not observed (Fig. B-3E). The region of low salinity within 10 km of the coast is a characteristic of the ACC and a common feature of salinity profiles on the northern Gulf of Alaska coast (Weingartner et al., 2005). A SeaWiFS satellite image during the cruise revealed no distinctive pattern of chlorophyll distribution (Fig. B-3D). Elevated chlorophyll concentrations at 50-60 km were associated with a localized upwelling as indicated by the salinity profile (Fig. B-3E and F).

Eddies can be an important feature of shelf circulation. Intense eddy activity occurred in May, 2000 (Fig. B-4), when MDS pattern D was observed (Fig. B-2, Table B-2). The SeaWIFS image in late May revealed a number of large and small eddies propagating along the shelf (Fig. B-4D). Streams of oceanic water were being advected shoreward and mixing with shelf water, particularly evident offshore of Prince William Sound. Additional eddies were observed near the coast to the west of the Seward line and offshore of Resurrection Bay. The eddy off Resurrection Bay is a common feature, which appears to be related to deflection of the coastal current by bathymetric changes to the west of the Seward Line (Weingartner, pers. comm.). The intense eddy activity was revealed in the salinity and temperature profiles as distinct doming and depression of the isohalines and isothermals along the transect line at 200, 120, 70 and 20 km (Fig. B-4C and E). The cross shelf distribution of zooplankton suggests substantial differences in abundance associated with the various eddies (Fig. B-4A). *Metridia* and *Calanus marshallae* were more abundant on the shelf out to the shelf break at 150 km, while *Eucalanus bungii* were more abundant in the oceanic regime. The *Neocalanus* species comprised a relatively constant percentage of the total abundance across the entire shelf (Fig. B-4B).

During July, 1998, distinct zooplankton communities were observed, as illustrated by MDS pattern B (Fig. B-2B). In July the seasonal thermocline was present across the entire shelf (Fig. B-5C). Oceanic water, as indicated by elevated salinity, was present from the outer end of the transect into the shelf break front at 150 km; ACC water as indicated by lower surface-layer salinity, was observed from the inner end of the transect out to station GAK4 (Fig. B-5E). The outer-shelf station group in the MDS plot (Fig. B-2B) consisted of stations occurring in oceanic water. Shelf water, characterized by salinity < 32, occurred on the inner shelf between 150 and 20 km. The inner station group (Fig. B-2B) occurred over the shelf. Stations GAK8 and GAK9, transitional in the MDS plot, were located in the frontal zone. A SeaWiFS image of the shelf during the cruise revealed a distinct region of elevated chlorophyll on the shelf, a transition zone near the shelf break, and a region of lower chlorophyll in oceanic waters off the shelf (Fig. B-5D). A fluorescence profile along the Seward Line confirmed the chlorophyll distribution indicated by the satellite image (Fig. B-5F). Oceanic species, *Neocalanus cristatus, N. plumchrus, N. flemingeri* and *Eucalanus bungii*, dominated the zooplankton community on the outer shelf (Fig. B-5A and B). A distinct transition in species composition was observed in the frontal region at 150 km. The zooplankton species composition in coastal waters was dominated by *Metridia pacifica*, *Calanus marshallae,* and the pteropod *Limacina helicina.*

Elevated chlorophyll concentrations were also observed on the offshore side of the shelf-break front in May 1999 (Fig. B-6), when three distinct station groupings occurred (Fig. B-2C). A SeaWiFS image revealed elevated chlorophyll concentrations in oceanic waters and a distinct transition to lower concentrations at the shelf break front (Fig. B-6D). A fluorescence profile along the Seward Line confirmed the satellite observation (Fig. B-6F). A distinct shelf-break front was observed near 150 km, as characterized by a transition between regions with salinity above and below 32.4 (Fig. B-6E). The inner shelf copepod community during May 1999 was dominated by *Metridia pacifica* out to the shelf break and *Calanus marshallae* shoreward of 50 km (Fig. B-6A and B). *Neocalanus plumchrus- flemingeri* were a dominant percentage of the community along the entire transect (Fig. B-6B), but their overall abundance was much higher on the inner shelf (Fig. B-6A). *Neocalanus cristatus* and *E. bungii* comprised a higher percentage of abundance off shore of 130 km. A thermocline was beginning to develop in the upper 40 m on the outer and inner shelf (Fig. B-6C).

The cross-shelf distribution of water properties and zooplankton was characterized by dividing the shelf into four separate zones. The Outer Zone (stations GAK10 – GAK13) included the oceanic region from the shelf-break front near 150 km to the end of the line (Figs. B-5E and B-6E). The Inner Zone (stations GAK1 – GAK4) consisted of those stations commonly influenced by the ACC, particularly in summer and fall (e.g. Fig. B-5E). The Transitional Zone included stations between the Inner and Outer Zones (GAK5 – GAK9). Stations in PWS (PWS1, PWS2, KIP2, MS2, HB2) were placed in a separate zone, due to their geographical separation from the Seward Line and their unique salinity characteristics as outlined below.

Upper mixed-layer temperatures (temperature above the thermocline) exhibited a strong seasonal signal (Fig. B-7A); however, cross-shelf differences were insignificant. Sub-thermocline temperatures (temperature between the thermocline and 100 m depth, the approximate depth of the permanent halocline) had a seasonal signal of lower magnitude than surface temperatures (Fig. B-7B). Confidence intervals broadly overlapped, except in August and October, when Inner Zone temperatures were significantly warmer than in the Transitional and Outer zones. Salinity above the pycnocline exhibited the greatest cross-shelf differences (Fig. B-7C). Mean salinity in PWS and the Inner Zone were significantly lower than in the Outer Zone in March, but gradually declining differences in cross-shelf salinity resulted in overlap of the error bars between the Inner and Outer zones by May. However, as the season progressed, declining salinity in PWS and the Inner Zone resulted in increasingly greater differences between upper water-column salinities in PWS, the Inner Zone and rest of the shelf, with greatest differences in August and October (Fig. B-7C). Salinity between the pycnocline and 100 m depth showed consistent cross-shelf differences (Fig. B-7D). Significant differences in sub-pycnocline salinity were observed in all regions on the shelf from March to May, with overlapping confidence intervals only between Inner and PWS regions. Later in the season, significant differences in Outer and Transitional zone salinities disappeared, but differences between the Inner Zone and other shelf regions remained highly significant, while declining salinities in PWS in August and September magnified the differences between the sound and all of the shelf zones (Fig. B-7D).

Water column profiles of mean temperature and salinity for all years (1997-2001) by region during March, July and October characterize the extreme conditions of late winter, fall, and mid summer at opposite ends of the study grid. The winter condition in PWS has surface temperature and salinity minimums, and a gradual increase with depth (Fig. B-8A). In contrast, the outer region has a subsurface temperature minimum and a distinct halocline below 80 m (Fig. B-8B). Surface temperature maxima of around 13°C are observed at both ends of the study grid by mid summer (Fig. B-8C and D). However, in PWS a distinct shallow brackish layer developed in the upper 15-20 m due to freshwater runoff. By fall, minimum salinity occurred in the upper 20-30 m in PWS, but a surface temperature depression is observed, as winter cooling and mixing begins to restore the winter condition (Fig. B-8E). Minimum surface salinity is observed in the outer region during fall, but winter cooling and mixing has begun to erode the surface temperature maxima observed in July (Fig. B-8F). The Inner Shelf temperature-salinity profiles are similar to the PWS condition, but with more moderate extremes of temperature and salinity. Profiles from the transitional region reflect cross-shelf mixing between the ACC and the outer region of the study area.

B-4.3. Zooplankton distribution by month, region and depth

MANOVA analyses by month and regions revealed distinct trends in the cross shelf distribution of major taxa. The mean abundances were generated by pooling data from individual months by region and year (1997 through 2001). Analyses were done for the major calanoids, euphausiids and other micronekton.

Mean abundance of the major calanoid species varied by region and season. Confidence intervals for *Pseudocalanus*, *Metridia* spp., and *Calanus marshallae* tended to overlap in March, particularly for regions outside Prince William Sound (Fig. B-9 C-F), but during April-July mean abundance of the above species was higher on the Inner Shelf and in Prince William Sound than in the Outer and Transitional regions. During August and October the confidence intervals between regions overlapped and significant differences in means were largely absent. The abundance of the oceanic copepod species *Neocalanus cristatus* and *Eucalanus bungii* were higher in the Outer Region relative to Prince William Sound and the Inner Shelf (Fig. B-9 B and D), especially before August. *Neocalanus plumchrus-flemingeri* showed a significant difference in mean abundance by region only during April, when populations in Prince William Sound were significantly higher than in the Transitional and Outer zones (Fig. B-9A). The variability in *Neocalanus* abundance on the inner shelf is partially the result of down-stream effects of ACC flushing through parts of PWS (Niebauer et al., 1994). *Oithona similis* (data not shown) was widely distributed across the shelf, with overlapping confidence intervals in the inner, transitional and outer zones.

A number of species were consistently more abundant in Prince William Sound than at the shelf stations (Fig. B-10). They include pelagic Ostracods, *Pasiphaea pacifica*, *Pareuchaeta elongata, Parathemisto libellula*, *Cyphocaris challengeri* and *Metridia okhotensis*. The shrimp *P. pacifica*, pelagic ostracods and *P. elongata* were also occasionally observed in the oceanic regime, but were rare or absent from the shelf environment (Figs. B-10 A, B and E). *Parathemisto libellula*, *M. okhotensis* and *C. challengeri* were confined primarily to PWS (Figs. B-10 C, D and F) and were rarely observed outside the sound. Four species of euphausiids, which occurred in substantial quantities in the study area, were *Thysanoessa inermis*, *T. spinifera*, *T. longipes* and *Euphausia pacifica* (Fig. B-11). *T. inermis* were consistently abundant in the inner shelf and in PWS, especially by the end of summer. *T. spinifera* showed a similar trend, although in August and October it was present over the whole study area. *T. longipes* occurred primarily in PWS. In contrast, *E. pacifica* was consistently more abundant in the outer domain, dominating the euphausiid population in March, and was practically absent from PWS for most of the production season except October.

The mean nighttime vertical distribution of the major zooplankton, for all years, regions and months, differed by species (Figs. B-12-14). The most widely distributed species, *Neocalanus plumchrus-flemingeri* and *Metridia pacifica*, had highest abundance in the upper mixed layer (Figs. B-12A and C). In contrast, *N. cristatus* and *E. bungii*, which were more abundant in the outer and transitional regions, had significantly lower abundance in the surface layer relative to the pycnocline layer (20 - 40 m, Figs. B-12B and D). *Pareuchaeta elongata, Pasiphaea pacifica*, ostracods, *Cyphocaris challengeri* and *Parathemisto libellula*, all of which were confined primarily to PWS, avoided the upper 40 m, even at night, and had a distinct trend toward higher abundance with depth (Figs. B-12F, B-13A-C, F). Although *Metridia okhotensis* occurred primarily in PWS, it did not have a distinct depth distribution at night (Fig. B-13D). *Calanus marshalle*, which occurred primarily in PWS and the inner shelf, had higher abundance in the upper 40 m (Fig. B-12E), and *Parathemisto pacifica*, common to the shelf and in PWS, showed no depth preferences (Fig. B-13E). Of the euphausiids, *Euphausia pacifica*, *Thysanoessa spinifera* and *T. inermis* had significantly higher nighttime distributions in the upper 20 m relative to deeper layers (Fig. B-14A-C). The nighttime depth distribution of *T. longipes*, which was confined primarily to PWS, did not show a significant trend (Fig. B-14D).

B-4.4. Correlation of species abundance to physical parameters

Canonical correlation revealed significant relationships between the physical properties and abundance of the major zooplankton taxa in both MOCNESS and CalVET tows (Fig. B-15). Comparison of pooled data with monthly data indicated that the influence of physical properties on the zooplankton abundance varied by month. Physical properties explained between 20% and 63% of the redundancy (a measure of the amount of variance in abundance explained by the physical data), depending on gear type and season (Table B-3). The redundancy in CalVET data increased from April through July but declined in August and October. Note that correlations for CalVET data in August were not significant. The redundancy in MOCNESS data peaked in July and August, with a subsequent decline in October. When the data for all months were pooled, physical variables could account for 23-28% of the variance for MOCNESS and CalVET data. The above suggests that the seasonal component substantially influences correlations between species abundance and physical properties. The declines in explained variance in August and October conform to declines in differences between regions observed in the species abundance data (Figs. B-9-11).

The influence of physical variables on individual taxa can be inferred from comparison of correlations between the physical variables and species abundance (Table B-4). *Neocalanus* were negatively correlated to temperature, due to their higher abundance in the upper 100 m during April and May, when temperatures are low. *Neocalanus cristatus* and *Eucalanus bungii* were positively correlated to salinity, reflecting their preference for off-shore sub-thermocline water masses, while *N. plumchrus-flemingeri* showed little correlation to salinity, reflecting its ubiquitous distribution in upper layers throughout the study area (Table B-4). *Metridia okhotensis*, *M. pacifica*, *C. marshallae*, *Pasaphaea pacifica*, *Parathemisto libellula* and *Cyphocaris challengeri* were negatively correlated to salinity, due to their preference for the inner shelf and PWS habitats. *Pareuchaeta elongata* and ostracods were weakly correlated to physical properties, probably due to their occurrence in both the offshore and PWS habitats (Fig. B-10B and E). *Parathemisto pacifica* was positively correlated to temperature due to its higher abundances during summer and fall. Of the small copepods from CalVET net samples, *Oithona similis* was positively correlated to upper mixed layer temperature, but weakly correlated to the other variables, indicating a preference for the upper mixed layer during summer in all regions. *Pseudocalanus* and *Acartia* were positively correlated to temperature and the stability coefficient, but negatively correlated to salinity, reflecting their preference for warm, stratified shelf conditions. Note that some of the absolute values for the monthly correlations between abundance and salinity exceeded 0.7-0.8 for *N. cristatus, M. okhotensis, C. marshallae*, *E. bungii*, and *Pasaphaea pacifica*, suggesting a strong relationship between salinity and the cross-shelf distribution for these species. Temperature correlations for the *Neocalanus* species and *Parathemisto pacifica* (Table B-4) disappear in data from individual months, indicating that temperature correlations are driven primarily by seasonal life-history effects.

B-5. Discussion

The seasonal cross-shelf distribution patterns of major zooplankton species were generated from data collected over four years from October 1997 through October 2001. They are therefore a very robust measure of consistent mean distributions occurring throughout the production season. The observed distributions are undoubtedly the result of both physical forcing and biological factors.

The major physical features in the northern GOA are influenced by persistent climatic patterns. During much of winter and early spring, climate on the northern Gulf of Alaska shelf is dominated by the Aleutian Low, which generates storms that drive cyclonic circulation, onshore surface transport and downwelling (Royer, 1982). The storms, blocked by the coastal mountains, produce large amounts of precipitation, much of which is stored as snow and ice on the coastal range during winter. Freshwater discharge and cyclonic wind stress generates the ACC, a swift westward-flowing low-salinity current (Royer, 1981, Johnson et al., 1988; Stabeno et al., 1995; Weingartner et al., 2005). Reduced discharge and onshore Ekman transport confines the ACC to a narrow region in the vicinity of station GAK1 during winter. Much of the remainder of the shelf is dominated by the prevailing onshore transport of water masses containing a random mixture of overwintering zooplankton species.

As the storm activity subsides during spring and early summer, the wind-driven onshore Ekman transport relaxes, solar radiation melts the snow pack, increasing the discharge and elevating surface temperatures. The increased discharge and slackening winds result in a broadening and shallowing of the ACC, which then occupies a larger portion of the shelf environment (Weingartner et al., 2005; Williams, 2003). The abundance of neritic species, such as *C. marshallae* and *Pseudocalanus*, increase in ACC waters from April through July. PWS and the inner shelf had consistently higher concentrations of *Metridia*, *C. marshallae* and *Pseudocalanus* than the transitional and offshore regions during spring and summer. This distributional pattern is consistent with observations in Shelikof Strait (1985-1992), where copepod abundance was also consistently higher in the ACC than in the surrounding shelf water (Napp et al., 1996). As the ACC and its associated frontal zone expands and mixes across the shelf during summer, more of the Seward Line stations will be influenced by the neritic water masses and associated species complex, thus submerging differences observed between mean abundance in inner and offshore stations. By August the differences in mean abundance of neritic species in onshore and offshore waters are no longer statistically significant.

Vertical distribution may also affect the cross-shelf distribution of copepod species. *Metridia* undergo diurnal vertical migrations (Batchelder, 1985). During the longer nights of winter and early spring, they probably spend more time in surface waters, which are mixed across the shelf by winter storms. The cross-shelf mixing erases any significant cross-shelf differences in abundance, as indicated by the overlapping error bars in March (Fig. B-9C). As day-length increases, *Metridia pacifica* spend a greater portion of their diurnal cycle in the deep daytime habitat. As winds relax and discharge increases in summer, the along-shelf transport weakens, resulting in a net onshore transport of sub-halocline water over the shelf (Weingartner et al., 2005). *Metridia* are probably transported onshore with bottom waters and aggregate on the inner shelf during spring and early summer. As day length declines in late summer, the *Metridia* spend a greater period of time in surface waters, which are apparently mixed offshore by frontal meanders and eddies. Eddies, sometimes up to 150 km in diameter, are a common feature along the northern GOA shelf (Okkonen, et al., 2001) and satellite data clearly demonstrate the potential for eddies to generate cross-shelf transport on the northern GOA shelf (Okkonen et al., 2003). By August significant differences between mean onshore and offshore abundances of *M. pacifica* are no longer observed.

The oceanic species *N. cristatus* and *E. bungii* were consistently more abundant in offshore and middle shelf locations than on the inner shelf and in PWS. They tended to predominate between the halocline and thermocline (20-80 m depth) and are apparently less inclined to onshore movement by surface currents. The cross-shelf salinity gradient, which is strongest in spring and early summer, suggests the potential presence of the barrier to the onshore transport of animals residing between the permanent halocline at 80-100 m depth and the seasonal thermocline at 30-20 m depth. *N. cristatus* occur primarily in the pycnocline layer in the upper 30 m in the western Bering Sea (Coyle, 1998), but both *N. cristatus* and *E. bungii* occur between the seasonal thermocline and the permanent halocline (45 to 150 m depth) in the North Pacific gyre (Mackas, 1993). It is thought that both species actively avoid the turbulent mixing zone above the seasonal thermocline (Mackas, 1993).

The mean abundance of *Neocalanus plumchrus-flemingeri* did not show significant regional differences except in April, when PWS populations were consistently higher than those in other regions on the Seward Line. The higher April populations in PWS are probably the result of physics, the bathymetry and the ontogenetic migration behavior of this species group. Depths in excess of 500 m occur in Knight Island Passage, in the northwest region of PWS (Fig. B-1). These deep areas are apparently a good overwintering habitat for *N. flemingeri*, as indicated by the dense populations at these depths in winter and early spring (Cooney et al., 2001a). At least some portion of the populations observed in the upper 100 m of PWS in April probably originated from reproduction in late winter and early spring by overwintering *Neocalanus* populations in Knight Island Passage. Long-term observation at hatcheries in western PWS have documented up to five fold interannual differences in maximum plankton settled volume (Cooney et. al., 2001b). These differences were positively correlated to the Bakun

Upwelling Index (BUI) computed from forecast sea-level pressure fields for the northern GOA. The correlation was interpreted as an indication that low BUI values (strong cyclonic wind stress) promote flushing of PWS zooplankton out of the sound by an accelerated and intruding ACC (Cooney et al., 2001b; Niebauer et al., 1994). In addition, chlorophyll distribution from satellite data and GLOBEC measurements suggest that the spring bloom occurs earlier in PWS than on the GOA shelf, probably due to earlier stratification caused by calmer conditions and surface freshening in PWS relative to the gulf (Weingartner et al., 2002, 2005). The resulting elevated phytoplankton concentrations in PWS probably generate favorable conditions for more rapid growth and development of *Neocalanus* copepodids. Thus, the magnitude of early spring differences in mean *Neocalanus* abundance between PWS and shelf regions is likely to vary annually in relation to the intensity and frequency of storm activity and runoff.

The timing and intensity of the spring *Neocalanus* biomass peak in PWS apparently influences the populations of a number of higher trophic-level species. Juvenile pink salmon (*Onchorynchus gorbuscha*) are known to feed heavily on large and small copepods in April and May (Willette et al., 2001). Studies indicate that wild pink salmon fry have evolved to enter PWS about the time of the large calanoid bloom (Cooney et al., 1995). In addition, hatchery fry released during the zooplankton biomass peak have enhanced survival over fish released before and after the peak (Cooney et al., 1995). The year class strength of herring populations may also be linked to food availability during their early life history. Energetic studies indicate that zero-class herring store lipid, which provides energy for winter survival to the beginning of the following year's production season with little margin for error (Paul and Paul, 1998). A failure or delay in spring copepod production could result in high mortality of overwintering populations. Thus, climatic conditions influencing the abundance of *Neocalanus* in PWS in April may impact on the survival and year-class strength of both herring and salmon. The timing of the spring *Neocalanus* biomass peak is thought to influence the abundance of other apex predators and has been presented as a mechanism linking climate to ecological regime shifts on the GOA shelf (Anderson and Piatt, 1999).

Mixing in the nearshore environment is apparently sufficient to eliminate the differences in mean *Neocalanus* populations between PWS and Seward Line stations by May. Between May and July the *Neocalanus* begin their ontogenetic migration out of the surface waters. Those animals on the shelf probably enter the bottom layer below the halocline, which is moving shoreward. They are therefore likely to concentrate in the submarine canyons which cross the shelf. Bottom water renewal in the coastal fjords would then reseed deep layers with overwintering *Neocalanus*, adding to reproductive populations for the following production cycle. Stable isotope data indicate that at least some portion of the over wintering population in PWS originated from outside the sound (Kline, 1999).

Many of the species with elevated abundance in PWS are diurnal vertical migrators with daytime depth preferences in the mesopelagic zone. They are therefore less likely to be flushed from the sound by surface advection and storms. *Parathemisto libellula* is an Arctic species and on the Pacific coast it is restricted to fjords, where deep temperatures are < 8°C. The juveniles and adults have a daytime depth of 200-300 m (Wing, 1976). *Cyphocaris challengeri* occurs at 200-500 m depth in the North Pacific during the day, but is observed in the upper 100 m at night, and it is most common where temperatures are less than 10°C and salinity is less than 34.4 (Yamada and Ikeda, 2000; Birstein and Vinogradov, 1964). *Pareuchaeta elongata* has a day-time depth of 75-175 m in Puget Sound (Bollens and Frost, 1991) and 200-500 m in the North Pacific (Brodskiy, 1950). Although it is reported in surface layers at night (Bollens and Frost, 1991), it was predominantly below the surface layers in the GOA samples. *Metridia okhotensis* is a bathypelagic copepod found in abundance in the North Pacific coastal zone between 50-200 m depth (Brodskiy, 1950, 1977, Gardner and Szabo, 1982). *Pasiphaea pacifica* is common in the epipelagic zone along the Pacific coast from California to the Sea of Okhotsk (Butler, 1980). In PWS it is commonly parasitized by the cryptoniscid isopod *Holophryxus alaskensis*, whose intermediate host is *P. elongata* (Coyle and Mueller, 1981). The elevated abundance of both host species in PWS makes it a good habitat for the parasite. All of the above species share a common vertical distribution in the mesopelagic zone below 200 m depth during the day, and a tendency to avoid the upper mixed layer at night. The prevailing onshore movement of bottom water during summer probably transports them into the sound, where they are retained in the unusually deep fjords of PWS.

The cross-shelf distribution of the major euphausiid species also conforms to their habitat preferences. *Thysanoessa inermis* form dense feeding and spawning aggregations on or near continental shelves (Drobysheva, 1985; Kulka and Corey, 1978; Hanamura et al, 1989; Brinton et al, 2000). In northern GOA they were present primarily on the inner shelf and in PWS, both unusually deep shelf habitats. *T. spinifera* occurs in coastal waters (Tanasichuk, 1998, Brinton et al. 2000) but can be found offshore as well (Mauchlin and Fisher, 1969), as indicated by its presence on the outer end of the Seward Line. *T. longipes* occurs along the North Pacific coast from California to Japan, but is virtually absent from open ocean (Ponomareva, 1963, Afanasiev, 1982, Zhuravlev, 1977). In this study *T. longipes* was almost completely restricted to PWS in the deeper regions of Knight Island Passage. In contrast to the *Thysanoessa* species, *E. pacifica* was most abundant on the outer shelf and probably originates from the Alaska Current. It is restricted to the North Pacific, where it is abundant in the North Pacific Gyre and adjacent marginal seas (Mauchlin and Fisher, 1969; Yoon et al., 2000; Ponomareva, 1963 Zhuravlev, 1977). Its presence in PWS in the fall may be related to deep-water renewal in the sound.

In many respects, the northern GOA shelf is similar to that offshore of British Columbia (BC). Both areas have a deep shelf with submarine canyons and a low salinity, buoyancy-driven coastal current. In addition, many of the dominant zooplankton taxa on the GOA shelf are also dominant on the BC coast (Mackas, 1992). Nevertheless, the regions differ in several important ways. Station groupings based on zooplankton species composition and abundance on the BC shelf were distinctive and fairly consistent (Mackas, 1992), whereas groupings on the GOA shelf were seasonal, occurring primarily in May through July, but largely absent by August and October. Summer upwelling on the BC coast is intense and consistent throughout much of the summer, leading to continuous high nutrient concentrations and summer phytoplankton production (Mackas, 1992). Summer upwelling on the northern GOA shelf is episodic and weak or absent (Royer, 1998). Summer declines in shelf species on the BC coast result from upwelling and dilution (Mackas, 1992). Summer zooplankton population declines on the GOA shelf are probably influenced by cross shelf mixing of Alaska Coastal Current water, in addition to biological effects such as predation, food limitation and life history strategies. Much of the deep flow on the BC coast comes from the California Undercurrent, which transports California Current species northward onto the BC shelf (Mackas, 1992), where they can form an important component of the zooplankton community during warm periods and El Nino events (Mackas et al., 2001). The shelf break flow on the northern GOA coast is dominated by the Alaska Current and Alaskan Stream, which contains the subarctic oceanic zooplankton assemblage (Cooney, 1986b); California Current species are rare or totally absent (Coyle and Pinchuk, 2003). The coastal subarctic species assemblage is also observed on the Oregon coast in the summer, where it is transported by prevailing southward coastal flow (Morgan et al., 2003). The offshore zooplankton assemblage off Oregon is dominated by California Current species, which are probably transported northward by the Davidson Current during winter (Morgan et al., 2003).

B-6. Summary

Zooplankton on the northern GOA shelf consisted of a mixture of oceanic and neritic species. Cross shelf distribution of the major zooplankton species was influenced by their depth preferences, vertical migration behavior, salinity-temperature preferences and by cross shelf water mass distribution and movement. The three main water masses observed on the GOA shelf included: 1) ACC water, a low-salinity, upper water-column feature occurring in PWS and the inner shelf; 2) a transitional zone, separated from the ACC by a distinct salinity front and with gradually increasing salinity from the seaward boundary of the ACC front out to the shelf break; 3) oceanic water mass, influence by the Alaska Current, flowing westward along the continental slope. The vertical structure consisted of an upper mixed layer, an intermediate layer between the base of the seasonal thermocline and the halocline, and a sub-halocline layer, which is slowly advected shoreward during much of the production season (March through October). Zooplankton distribution was characterized by four broad categories, composed of species with characteristic depth preferences, vertical migration behavior and salinity-temperature preferences. They include: 1) Broadly distributed species, which occur primarily in the upper mixed layer day and night, including *Neocalanus plumchrus-flemingeri* and *Oithona similis*. 2) Mesopelagic species, which remained below the seasonal thermocline, even at night (*Cyphocaris challengeri*, ostracods, *Pareuchaeta elongata*, *Parathemisto libellula*) or species randomly distributed vertically in the upper 100 m at night (*Metridia okhotensis*, *Thysanoessa longipes*), but which reside below the halocline during the day; these species were confined primarily to PWS. 3) Species, which reside below the halocline during the day but in the upper mixed layer at night (*Metridia pacifica*, *Thysanoessa spinifera*, *T. inermis*), tended to have elevated abundance on the inner shelf or in PWS, with the exception of *Euphausia pacifica*, which was more abundant on the outer shelf during spring. 4) Species, with maximum abundance between the seasonal thermocline and halocline tended to have a cross-shelf abundance gradient, with *Neocalanus cristatus* and *Eucalanus bungii* more abundant on the outer shelf and *Calanus marshallae* and *Pseudocalanus* more abundant on the inner shelf. Cross-shelf differences in abundance of animals in categories 3 and 4 are seasonal, with significant differences occurring primarily in late spring and early summer. Satellite images indicate that eddies are probably an important contributor to cross-shelf mixing in the transitional zone.

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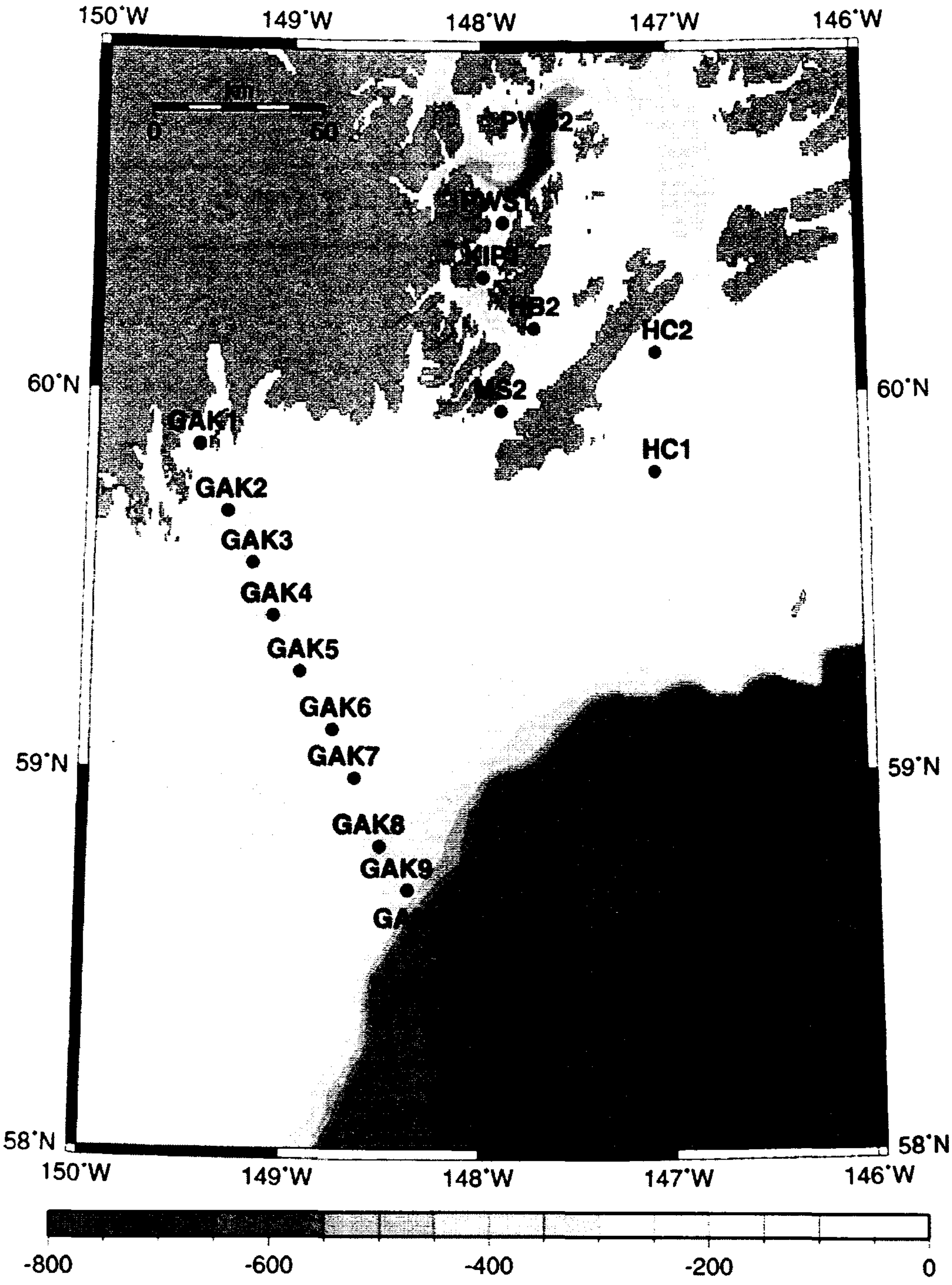


Fig. B-1. Station locations for the northern Gulf of Alaska GLOBEC LTOP project.

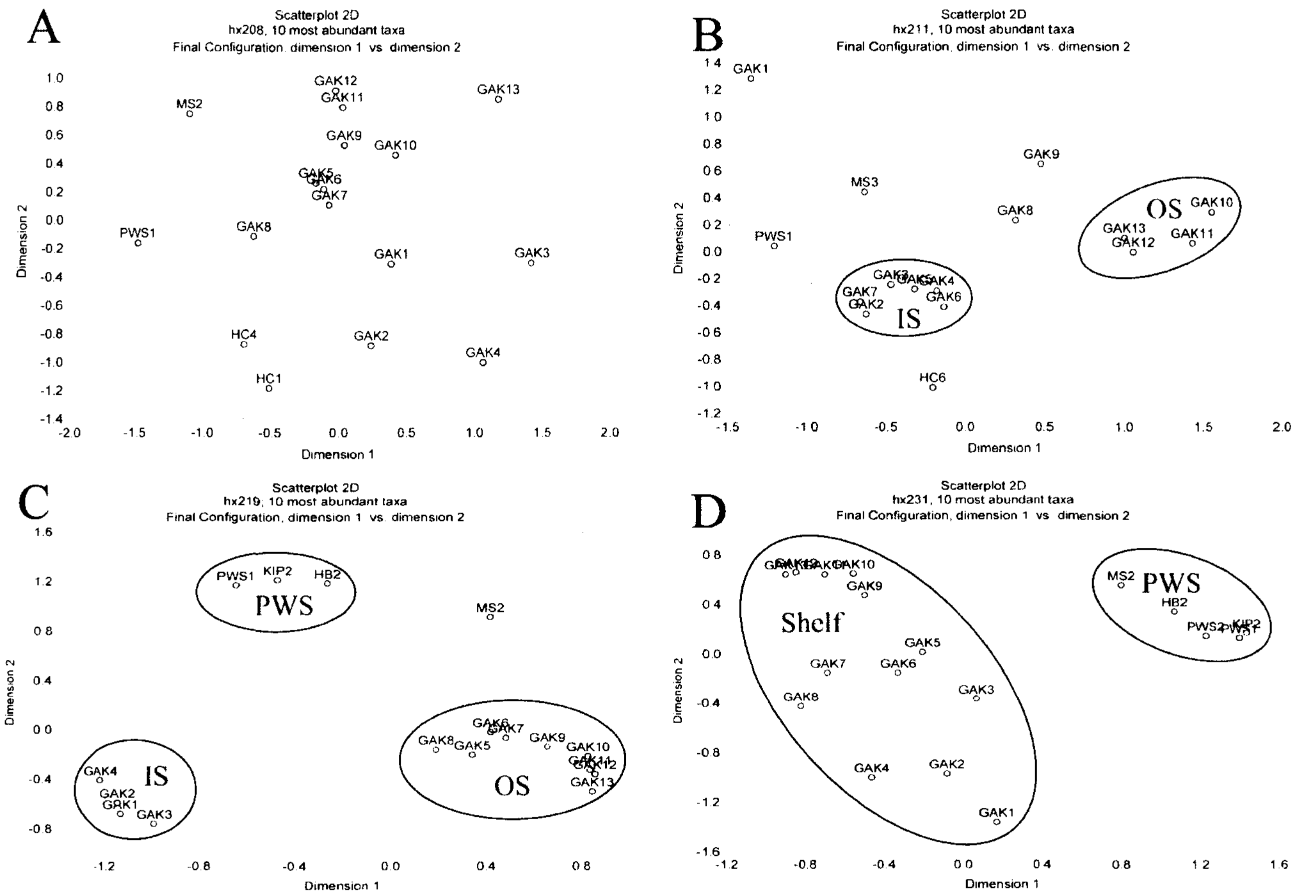


Fig. B-2. Multidimensional scaling plot of the station groupings computed from the ten most abundant taxa in MOCNESS nets from the northern GOA: A. May 1998, B July 1998; C. May 1999. D. 2000. OS = outer shelf; IS = inner shelf; PWS = Prince William Sound.

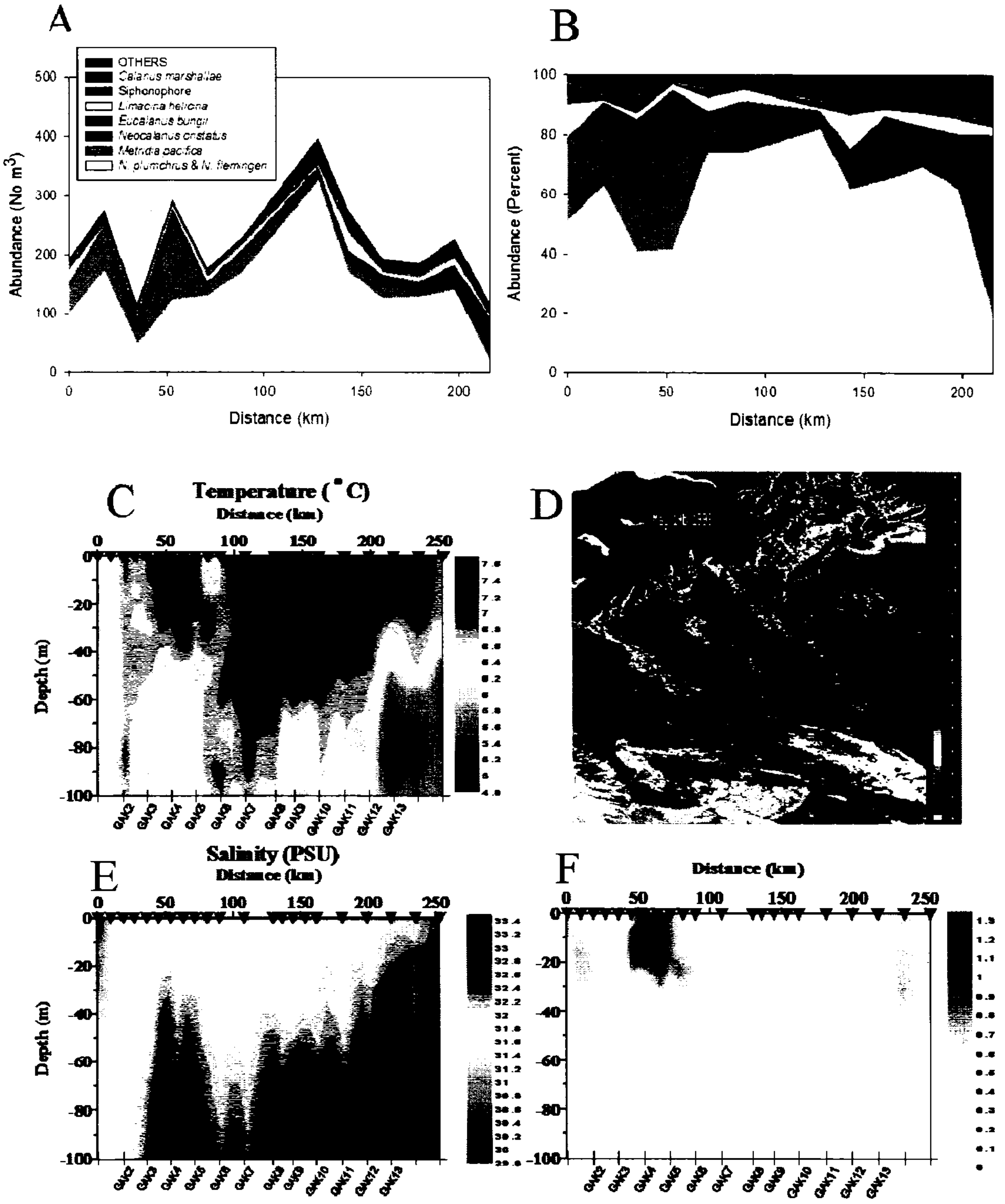


Fig. B-3. Water properties and zooplankton abundance along the Seward Line in May, 1998. A. Abundance from MOCNESS tows; B. Percent Abundance, taxa list same as in A; C. Temperature profile; D. SeaWIFS satellite image of chlorophyll distribution; E. Salinity profile; F. Fluorescence profile. Filled triangles indicate station locations.

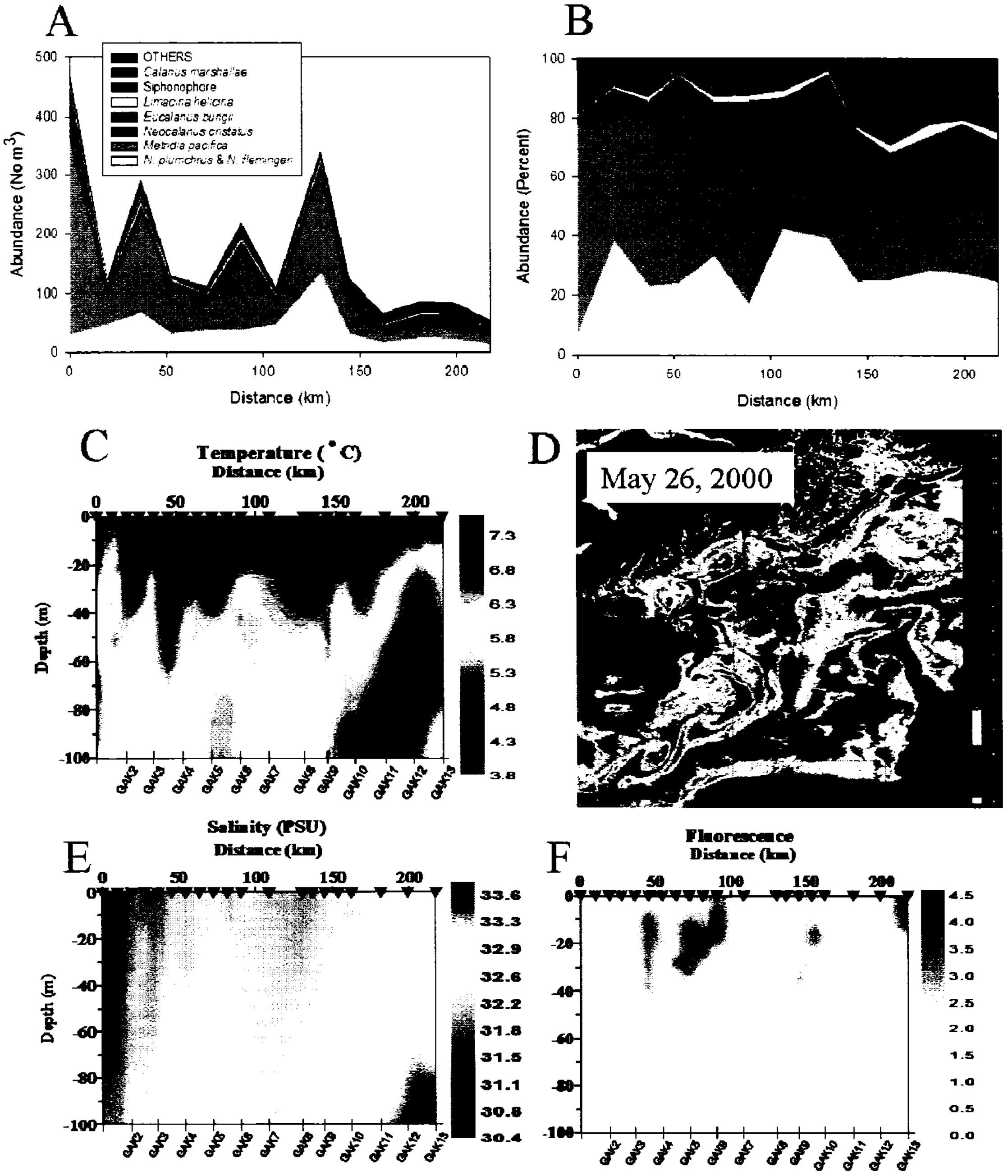


Fig. B-4. Water properties and zooplankton abundance along the Seward Line in May, 2000. A. Abundance from MOCNESS tows; B. Percent Abundance, taxa list same as in A; C. Temperature profiles; D. SeaWIFS satellite image of chlorophyll distribution; E. Salinity profile; F. Fluorescence profile. Filled triangles indicate station locations.

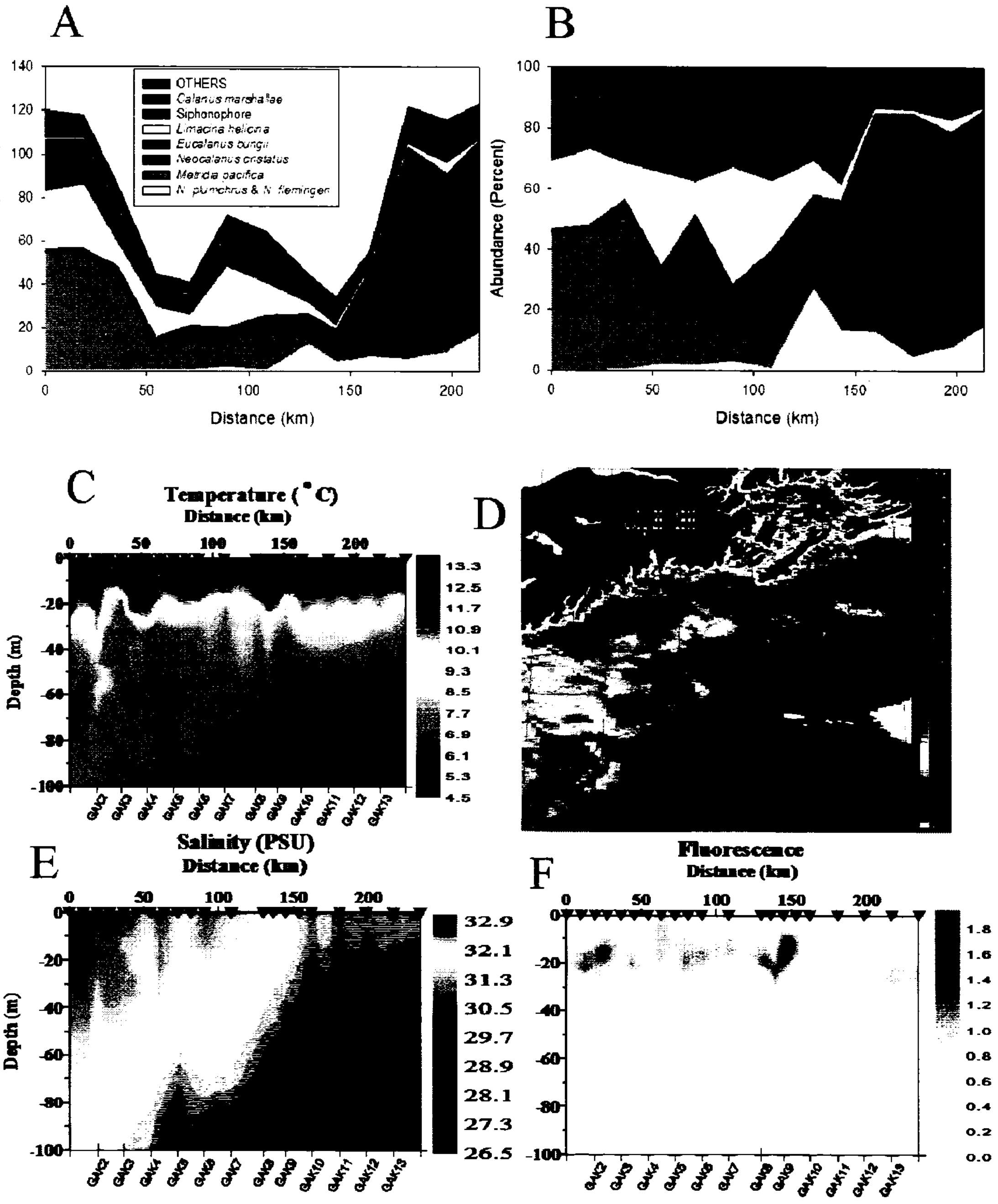


Fig. B-5. Water properties and zooplankton abundance along the Seward Line in July, 1998. A. Abundance from MOCNESS tows; B. Percent Abundance, taxa list same as in A; C. Temperature profile; D. SeaWIFS satellite image of chlorophyll distribution; E. Salinity profile; F. Fluorescence profile. Filled triangles indicate station locations.

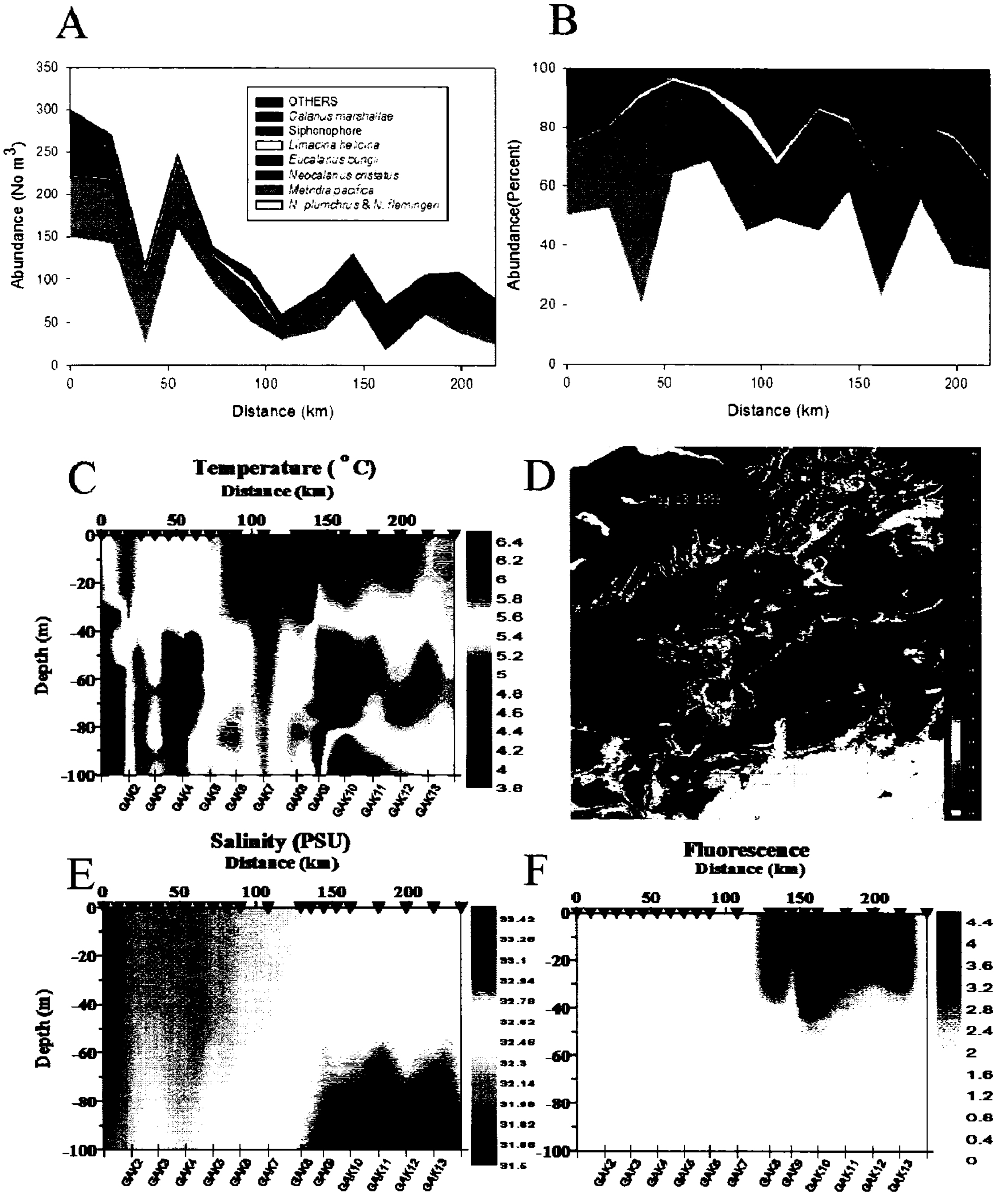


Fig. B-6. Water properties and zooplankton abundance along the Seward Line in May, 1999. A. Abundance from MOCNESS tows; B. Percent Abundance, taxa list same as in A; C. Temperature profile; D. SeaWIFS satellite image of chlorophyll distribution; E. Salinity profile; F. Fluorescence profile. Filled triangles indicate station locations.

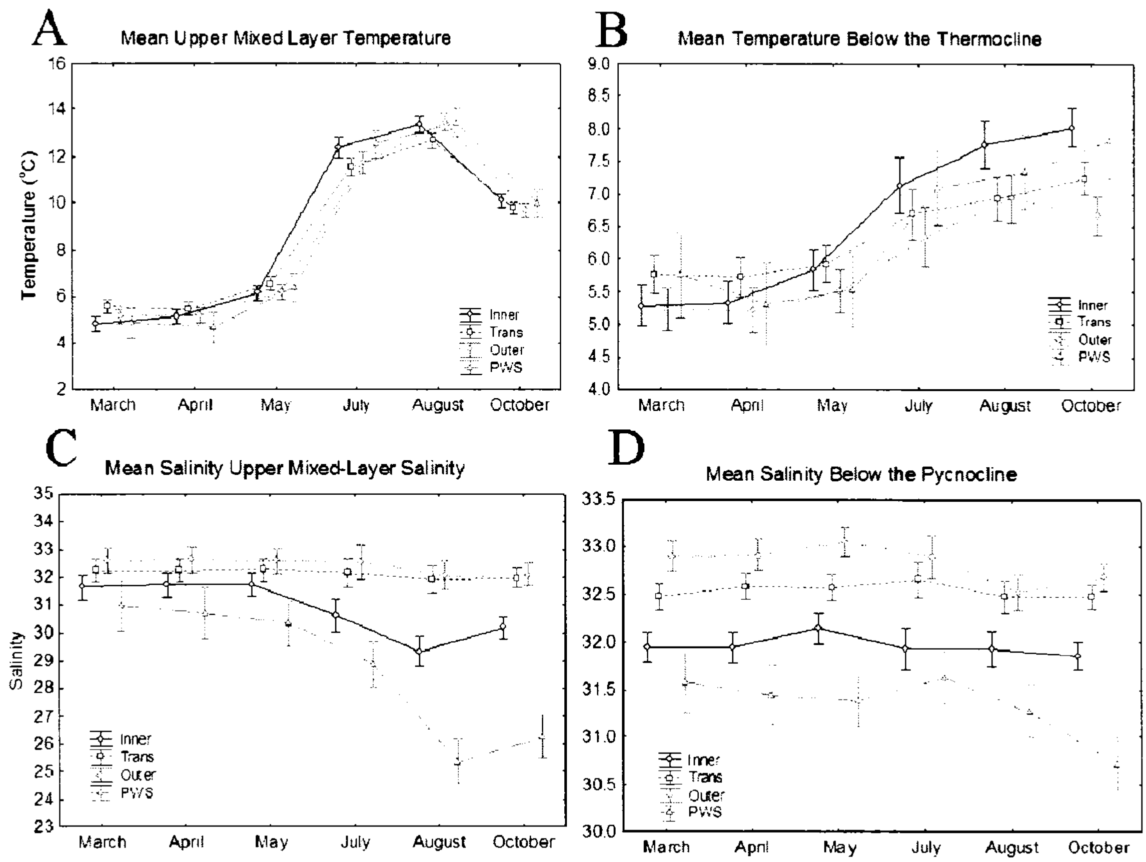


Fig. B-7 (A-D). Mean physical properties on the northern Gulf of Alaska shelf by region and month. Outer = Outer Region (GAK10 – GAK13), Trans = Transition Zone (GAK5-GAK9), Inner = Inner Shelf (GAK1-GAK4). PWS = Prince William Sound. Error bars are 95% confidence intervals.

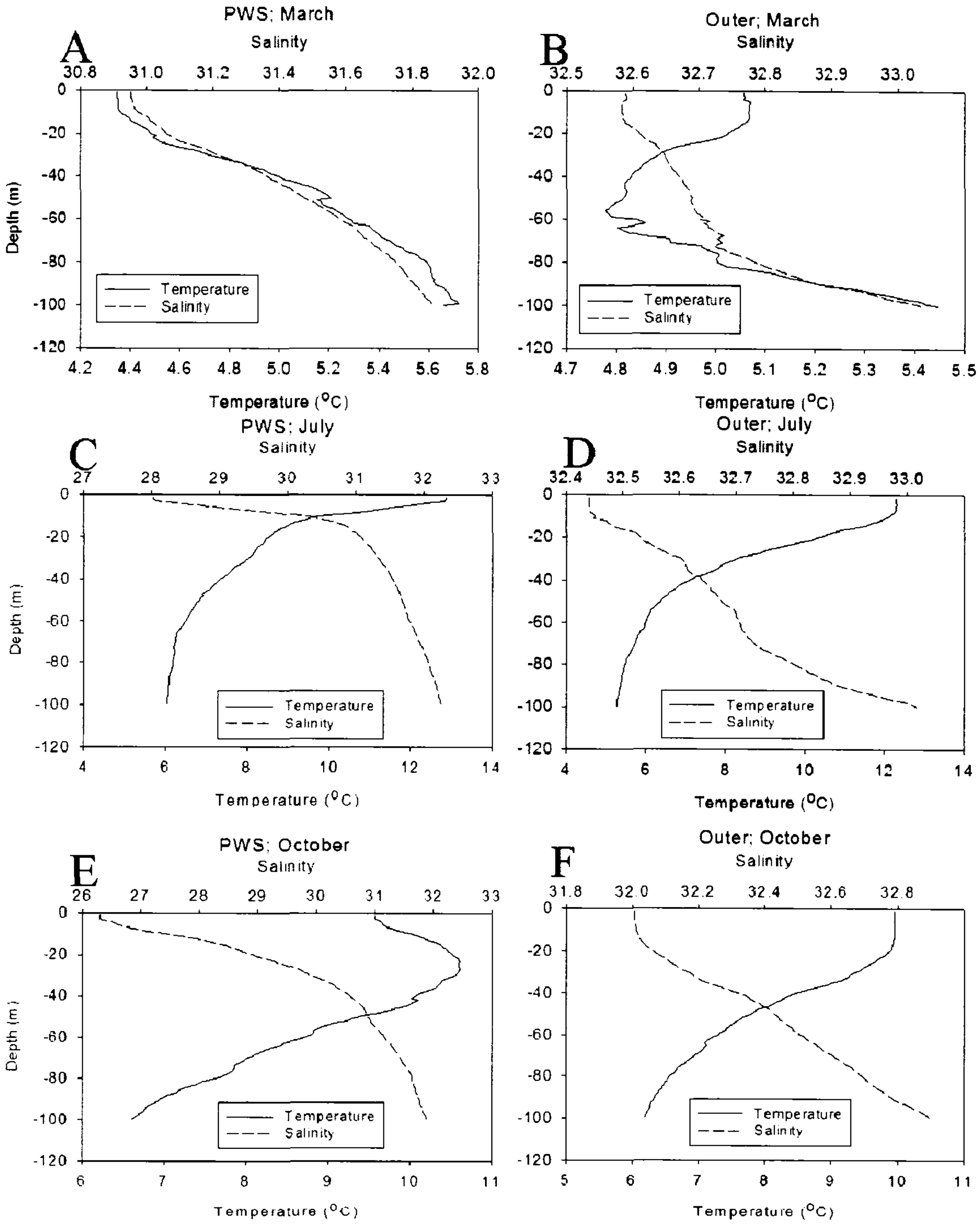


Fig. B-8 (A-F). Mean water-column profiles of temperature and salinity by month and region on the northern GOA shelf, 1997 – 2001. Outer = Outer Region (GAK10 – GAK13); Trans = Transition Zone (GAK5-GAK9); Inner = Inner Shelf (GAK1-GAK4). PWS = Prince William Sound.

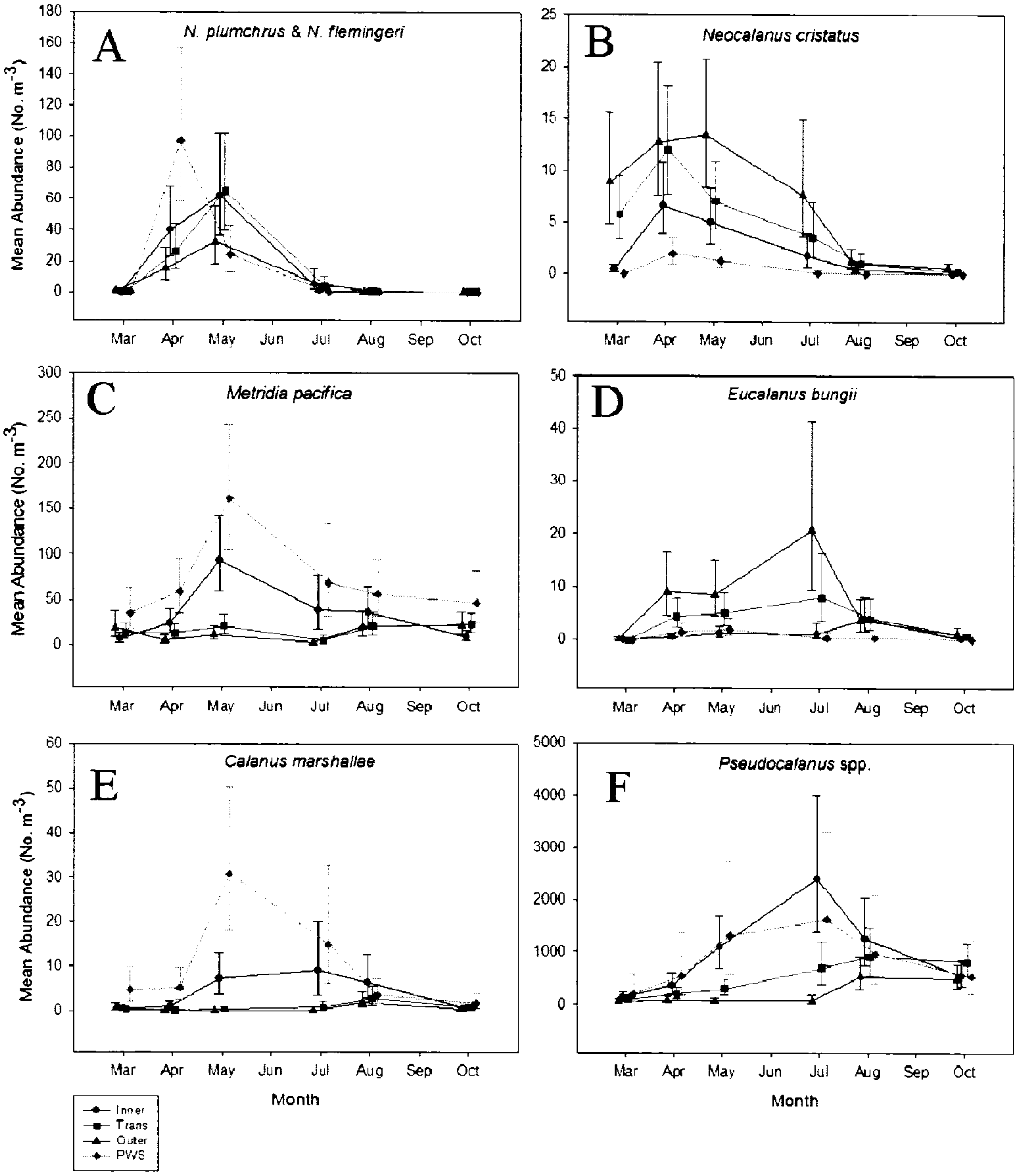


Fig. B-9 (A-F). Mean abundance of major copepod taxa on the northern GOA shelf by region and month. Outer = Outer Region (GAK10 – GAK13); Trans = Transition Zone (GAK5-GAK9); Inner = Inner Shelf (GAK1-GAK4). PWS = Prince William Sound. MOCNESS tows (A-E); CalVET tow (F). Error bars are 95% confidence intervals.

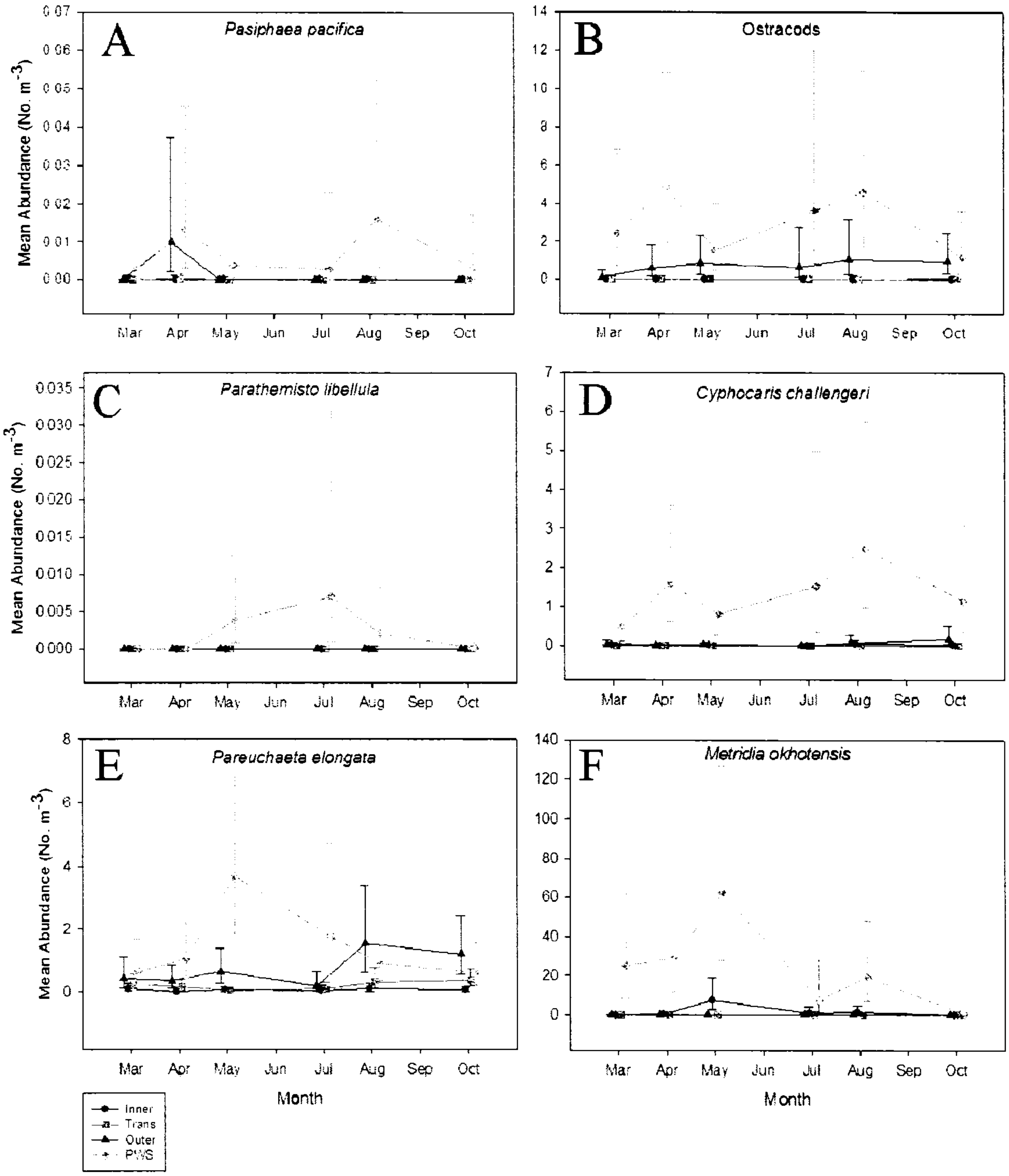


Fig. B-10 (A-F). Mean abundance of major zooplankton taxa on the northern GOA shelf by region and month from MOCNESS tows. Outer = Outer Region (GAK10 – GAK13); Trans = Transition Zone (GAK5-GAK9); Inner = Inner Shelf (GAK1-GAK4). PWS = Prince William Sound. Error bars are 95% confidence intervals.

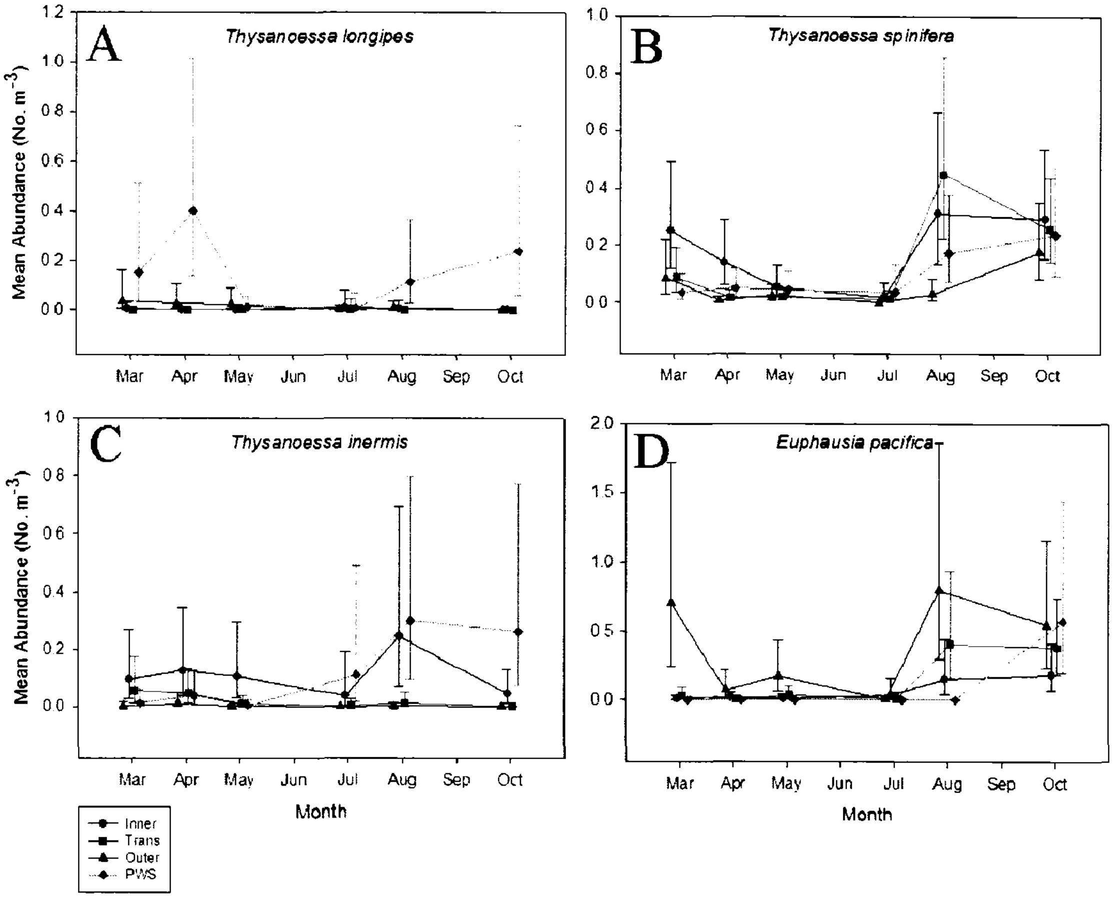


Fig. B-11 (A-D). Mean abundance of major euphausiid species on the northern GOA shelf by region and month from MOCNESS tows. Outer = Outer Region (GAK10 – GAK13); Trans = Transition Zone (GAK5-GAK9); Inner = Inner Shelf (GAK1-GAK4). PWS = Prince William Sound. Error bars are 95% confidence intervals.

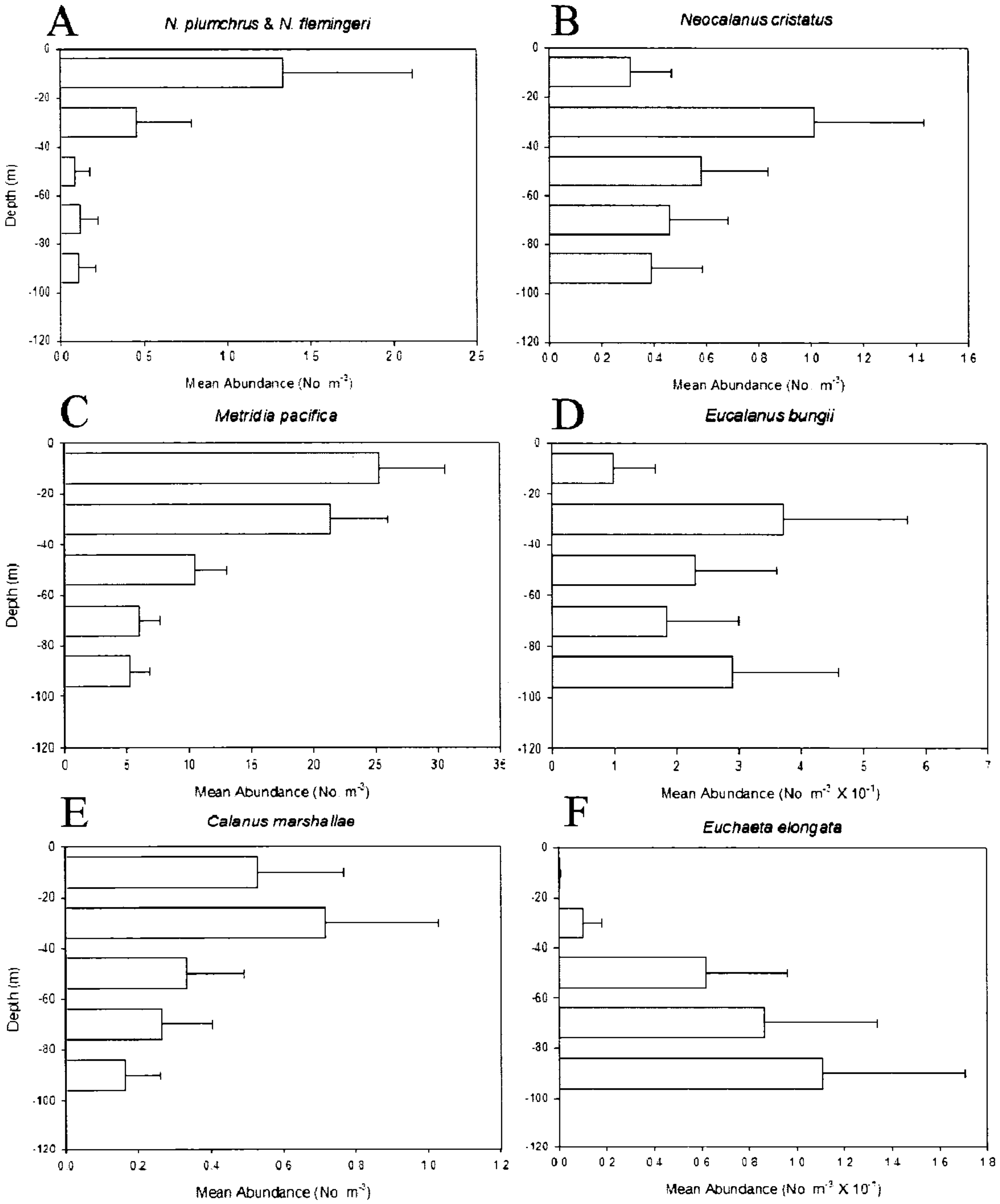


Fig. B-12 (A-F). Mean depth distribution (1997 – 2001, all regions and months) of the dominant copepods on the GOA shelf.

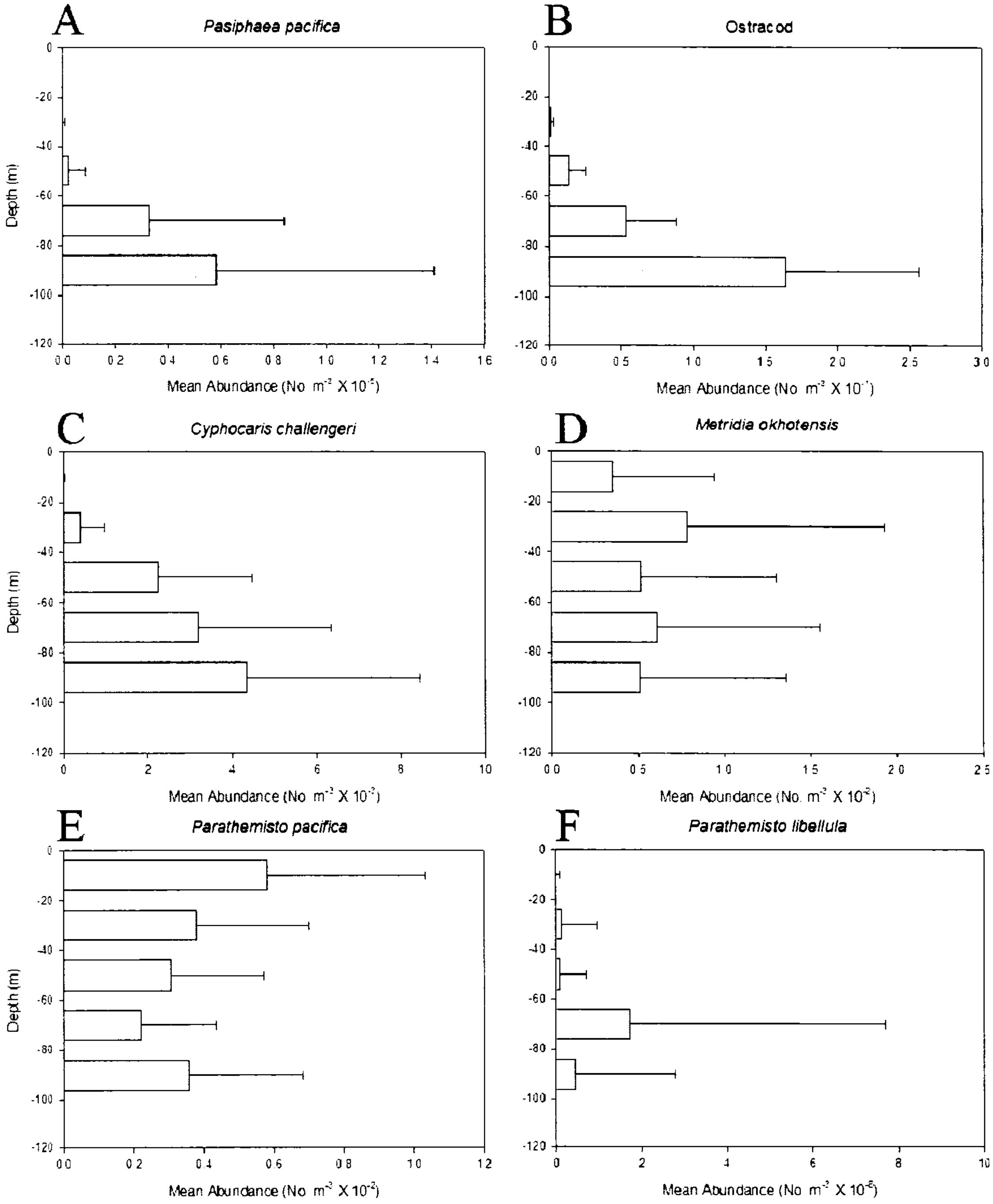


Fig. B-13 (A-F). Mean depth distribution (1997 – 2001, all regions and months) of the dominant micronekton on the GOA shelf.

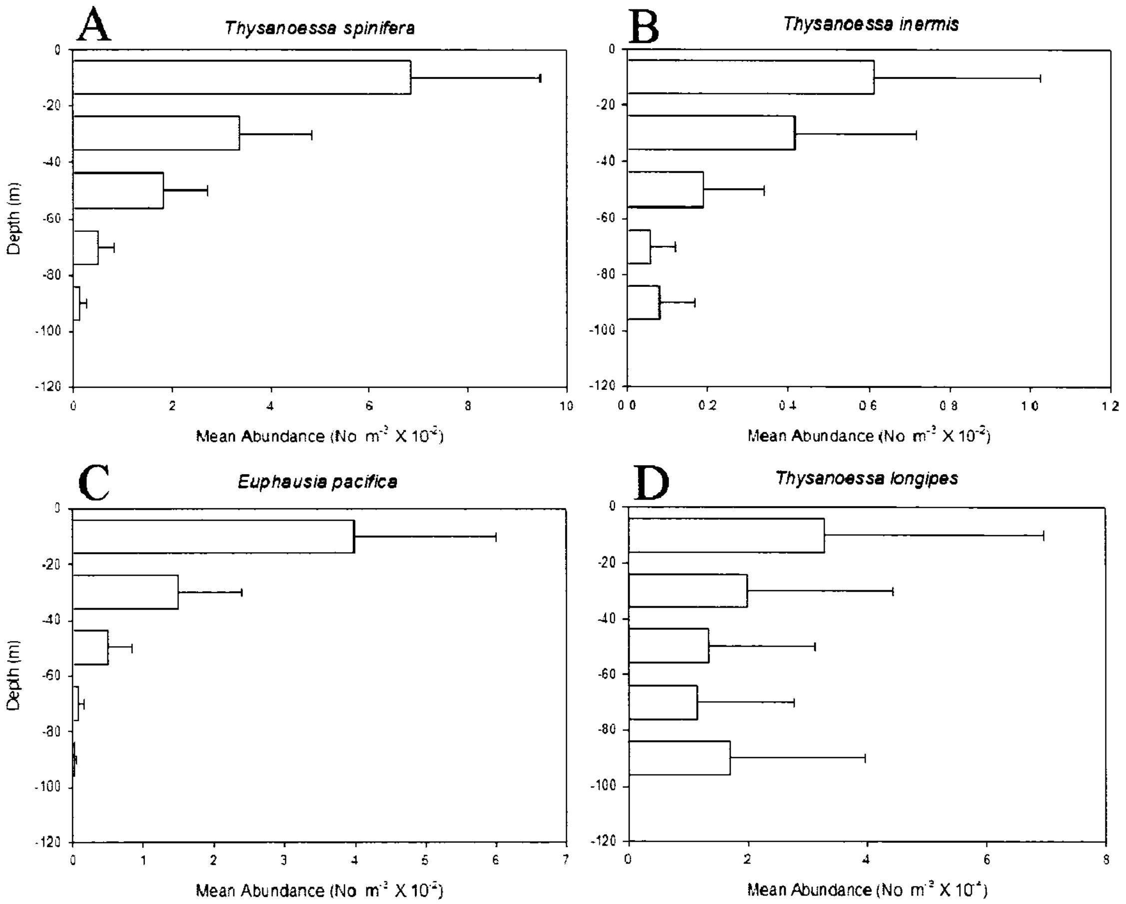
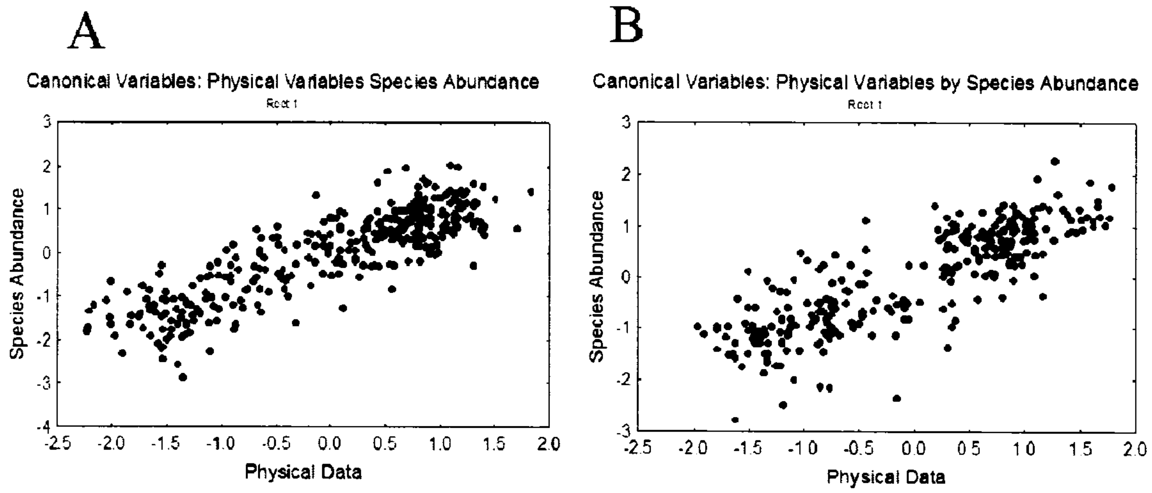


Fig. B-14 (A-D). Mean depth distribution (1997 – 2001, all regions and months) of the dominant euphausiids on the GOA shelf.



Canonical Variables: Physical Variables Species Abundance

Canonical Variables: Physical Variables by Species Abundance

Fig. B-15. Physical and species-abundance canonical variables for MOCNESS (A) and CalVET (B) tows from the northern GOA, October 1997 – October 2001.

Table B-1. Month and year for GLOBEC LTOP cruises in the northern GOA.

	Month					
Year	Mar	Apr	May	July	Aug	Oct
1997						X
1998	X	X	X	X		X
1999	X	X	X		X	X
2000	X	X	X		X	X
2001	X	X	X	X	X	X

Table B-2. Multidimensional scaling patterns of stations on the northern GOA coast during 1998 through 2001. Letters indicate patterns as shown in Fig. 2.

Year	Month					
	Mar	Apr	May	Jul	Aug	Oct
1998		D	A	B		A
1999	D	D	C		A	A
2000	D	D	D		D	C
2001	D	D	C	D	D	D

Table B-3. Canonical correlation relating physical oceanographic properties to abundance of major taxa in MOCNESS and CalVET tows taken on the GOA shelf, 1997-2001.

Month	Canonical R	No. of Cases	Total Redundancy	Probablilty	Tow Type
Mar	0.948	54	40.1%	0.000000	MOCNESS
Apr	0.962	64	40.3%	0.000000	MOCNESS
May	0.957	66	41.7%	0.000000	MOCNESS
Jul	0.979	33	63.4%	0.0000009	MOCNESS
Aug	0.973	52	46.2%	0.000000	MOCNESS
Oct	0.931	73	38.5%	0.000000	MOCNESS
Total	0.857	342	27.6%	0.000000	MOCNESS
Mar	0.922	52	31.9%	0.000000	CalVET
Apr	0.848	50	28.3%	0.0000943	CalVET
May	0.891	52	45.5%	0.000000	CalVET
Jul	0.950	28	58.0%	0.0000776	CalVET
Aug	0.794	38	20.2%	0.1853283	CalVET
Oct	0.714	64	22.5%	0.0000177	CalVET
Total	0.842	284	23.8%	0.000000	CalVET

Physical Variables: Temperature above the thermocline, temperature below the thermocline, stability coefficient, temperature above the halocline, temperature below the halocline.

Species CalVET: *Oithona similis*, *Pseudocalanus* spp., *Neocalanus plumchrus-flemingeri*, *Neocalanus cristatus*, *Metridia* spp., *Eucalanus bungii*, *Calanus marshallae*, *Acartia* spp., calanoid nauplii.

Species MOCNESS: *Neocalanus plumchrus-flemingeri*, *Neocalanus cristatus*, *Metridia pacifica*, *Metridia okhotensis*, *Pareuchaeta elongata*, *Eucalanus bungii*, *Calanus marshallae*, *Euphausia pacifica*, *Thysanoessa spinifera*, *Thysanoessa inermis*, *Thysanoessa longipes*, pelagic ostracods, *Pasiphaea pacifica*, *Parathemisto libellula*, *Parathemisto pacifica*, *Cyphocaris challengeri*, *Limacina helicina*, larvaceans.

Table B-4. Correlation of physical variables with species abundance.

Taxa	Upper Mixed Temp	Lower Mixed Temp	Mean Temp	Stability Coeff	Upper Mixed Sal	Lower Mixed Sal	Mean Sal
Neocalanus plumchrus/flemingeri (MOC)	-0.447	-0.497	-0.541	-0.344	0.211	0.140	0.172
Neocalanus cristatus (MOC)	-0.404	-0.473	-0.511	-0.580	0.610	0.638	0.669
Metridia pacifica (MOC)	0.0217	-0.008	-0.031	0.081	-0.183	-0.340	-0.313
Metridia okhotensis (MOC)	-0.051	-0.123	-0.176	0.124	-0.329	-0.549	-0.518
Pareuchaeta elongata (MOC)	0.105	-0.027	0.005	0.123	-0.095	-0.050	-0.067
Eucalanus bungii (MOC)	0.180	-0.059	0.013	-0.020	0.277	0.419	0.398
Calanus marshallae (MOC)	0.139	0.106	0.068	0.148	-0.243	-0.498	-0.450
Pasiphaea pacifica (MOC)	-0.218	-0.225	-0.263	0.133	-0.359	-0.392	-0.401
Ostracods (MOC)	0.049	-0.060	-0.050	0.188	-0.226	-0.163	-0.186
Parathemisto libellula (MOC)	0.153	0.064	0.024	0.261	-0.374	-0.394	-0.413
Parathemisto pacifica (MOC)	0.526	0.404	0.471	0.340	-0.139	0.020	-0.010
Cyphocaris challengeri (MOC)	0.091	0.023	0.037	0.351	-0.436	-0.437	-0.463
Thysanoessa spinifera (MOC)	0.131	0.192	0.217	0.199	-0.180	-0.189	-0.194
Thysanoessa inermis (MOC)	-0.050	-0.023	-0.062	0.115	-0.268	-0.276	-0.292
Thysanoessa longipes (MOC)	-0.137	-0.256	-0.260	0.133	-0.227	-0.229	-0.242
Euphausia pacifica (MOC)	0.255	0.266	0.356	0.138	0.091	0.261	0.223
Oithona similis (CalVET Tows)	0.411	0.254	0.298	0.282	-0.085	-0.031	-0.009
Pseudocalanus spp. (CalVET Tows)	0.470	0.449	0.479	0.433	-0.389	-0.423	-0.408
Acartia spp. (CalVET Tows)	0.475	0.341	0.394	0.371	-0.276	-0.318	-0.279

MOCNESS tows from the northern GOA, 1998 through 2001. Temp = temperature (°C), Sal = salinity, Stability Coeff = stability coefficient, MOC = MOCNESS