

# Interannual abundance patterns of copepods during an ENSO event in Icy Strait, southeastern Alaska

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Interannual copepod abundance (number  $m^{-3}$ ) and sea surface temperatures (SST, 2-m depth) were examined from four stations in Icy Strait, southeastern Alaska, monthly from May to September, 1997–2002. SST was generally lowest in May ( $\cong 7^{\circ}C$ ), increased rapidly to a summer peak ( $\cong 12^{\circ}C$ ), and declined again by September. SST was relatively high in the El Niño year, 1998, and was low during a regional cold event, 2002, compared to other years. Overall, copepods constituted 18.8% of the total biomass and 88.2% of zooplankton abundance, and included >34 species. The common copepod species were grouped into two size classes by total length (TL), those >2.5 mm (11.4% biomass, 24.2% abundance) and those <2.5 mm (7.4% biomass, 64.0% abundance). In order of dominance, large species included *Metridia ochotensis*, *Calanus marshallae*, *M. pacificus*, and *Neocalanus* spp. and small species included *Pseudocalanus* spp., *Acartia longiremis*, and *Centropages abdominalis*. Overall, the small species were more abundant than the large species. Densities of large copepods were relatively low compared to those of small copepods during El Niño (1998) and a cold year (2002), suggesting that large copepods with long lifespans are more sensitive to ocean climate fluctuation.

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## Introduction

Climate variability affects the productivity and foodweb dynamics of marine ecosystems. Fish population responses to variation in the physical and biological conditions and processes in the North Pacific Ocean have been well documented, while fewer zooplankton responses have been reported (e.g. Batchelder and Powell, 2002). In the North Pacific Ocean, zooplankton development timing, species composition and diversity, and biomass responses to climate change have been observed (Brodeur and Ware, 1992; Roemmich and McGowan, 1995; Brodeur *et al.*, 1996; McGowan *et al.*, 1996; Mackas *et al.*, 1998, 2001; Napp *et al.*, 2002; Baier and Napp, 2003). Furthermore, because physiological processes can depend on body size (Frost, 1980), copepod species or life stages with different body sizes may respond differently to climate changes.

However, in southeastern Alaska little is known about how the annual abundance patterns of copepod species with different body sizes correlate with drastic climate changes such as El Niño–Southern Oscillation (ENSO) events (Paul *et al.*, 1990; Coyle and Paul, 1992), or how such shifts might affect the production of their fish predators.

ENSO is a coupled ocean–atmosphere phenomenon that has a worldwide impact on climate and causes interannual variability in macroscale interactions between ocean and atmosphere (Philander, 1989; Fiedler, 2002). El Niño and La Niña represent opposite extremes of large climate changes that follow seasonal changes in the Pacific Ocean. El Niño events are largely characterized by warm temperature anomalies in the central to eastern equatorial Pacific, waning towards the poles, whereas La Niña events are reversed from the atmospheric and oceanic conditions in El Niño events. The ENSO is irregular, reversing every

3–7 years, with episodes lasting 8–15 months (Fiedler, 2002). Compared to La Niña conditions, El Niño events are accompanied by decreases in ocean mixed layer depths (stratification patterns), and more rapid depletion of nutrient levels, as well as increased temperatures (Whitney and Welch, 2002); however, the duration and strength of these changes vary among events and their effects vary by area (Francis *et al.*, 1998; NOAA El Niño theme page, <http://www.pmel.noaa.gov/tao/elnino/la-nina-story.htm>; NOAA Climate Prediction Center and Climate Data Center websites, <http://www.cpc.ncep.noaa.gov/> and <http://www.ncdc.noaa.gov/>).

Production of commercial fish species has been affected by climate changes in the North Pacific region over past decades and centuries (Francis and Sibley, 1991; Beamish and Bouillon, 1993; Francis and Hare, 1994; Mantua *et al.*, 1997; Anderson and Piatt, 1999; Finney *et al.*, 2000). Fluctuations in Pacific salmon (*Oncorhynchus* spp.) stocks have been linked to local, regional, and global weather patterns and to fluctuations in their prey (e.g. Martin and Fitzwater, 1988; Gargett, 1997; Sugimoto and Tadokoro, 1997; Finney *et al.*, 2000; Gargett *et al.*, 2001). Distinguishing the effects of local and remote processes, as well as top–down and bottom–up processes, however, is often difficult (Roessler and Chelton, 1987). Furthermore, because the intensity of ENSO events varies, the strength of biotic responses to environmental change can also be expected to vary (Francis *et al.*, 1998).

Understanding the effects of climate variability on marine ecosystems requires consistent sampling in long time-series to investigate low-frequency periodicity of changes, but few such monitoring programmes have been maintained (Ware and Thomson, 2000; Fiedler, 2002). In the North Pacific, Ocean Station P (50°N 145°W), representing a Subarctic oceanic ecosystem, was sampled for zooplankton continuously from 1956 to 1980 and irregularly since then. An area of the eastern boundary current, the CalCOFI grid, has been sampled since the late 1940s. With these sample series, researchers have attempted to use trends in zooplankton biomass to indicate changes in productivity in offshore and coastal oceanic systems. For example, Francis (1993) reported that interdecadal variation in salmon production in these two oceanic domains is inversely correlated. However, other studies found no correlation between physical oceanographic characteristics and the abundance of zooplankton, such as the euphausiid prey of commercial fish species off the coast British Columbia, Canada (Tanasichuk, 2002), or zooplankton concentrations during the 1997–1998 El Niño event that occurred during a 41-year time-series in the southeastern Bering Sea (Napp *et al.*, 2002). Thus, different taxonomic groups and trophic levels may be affected differently by ENSO or other oceanographic events (Francis *et al.*, 1998). Little has been published about biotic effects of climate change in southeastern Alaska, a region in the northeastern Pacific Ocean with high salmon production. However, long-term records of sea surface temperature

(SST) in Auke Bay, southeastern Alaska, are available (Bruce *et al.*, 1977; Wing and Pella, 1998), and typical water column profiles were reported (Murphy and Orsi, 1999). Numerous multi-year zooplankton studies in the region have reported interannual differences in production and biological processes (e.g. Coyle *et al.*, 1990; Napp *et al.*, 1996; Mackas *et al.*, 2001).

Zooplankton are utilized by many fish species in Alaskan waters (e.g. Sturdevant *et al.*, 1999), including salmon. Juvenile salmon are abundant, high level planktivores in Alaskan surface waters during the day (Bailey *et al.*, 1975; Ware and McFarlane, 1989; Orsi *et al.*, 1997, 1998, 1999, 2000a, b, 2001a, b, 2002, 2003a, b), while vertically migrating planktivores such as juvenile walleye pollock (*Theragra chalcogramma*), eulachon (*Thaleichthys pacificus*), and Pacific herring (*Clupea pallasii*) predominate in trawl catches at night (Haldorson *et al.*, 1997; Stokesbury *et al.*, 2000; Orsi *et al.*, 2000a, b, 2001a, b, 2002, 2003a, b). These planktivores consume multiple size categories of prey (Bailey *et al.*, 1975; Coyle and Paul, 1992; Landingham *et al.*, 1998; Sturdevant *et al.*, 1999; Willette *et al.*, 1999; Cooney *et al.*, 2001a). In southeastern Alaska, juvenile pink (*O. gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon feed on calanoid copepods throughout the spring into the summer (Bailey *et al.*, 1975; Landingham and Mothershead, 1988; Murphy *et al.*, 1988; Landingham *et al.*, 1998; Sturdevant *et al.*, 2002, 2004), while maturing pollock, Pacific herring, chinook (*O. tshawytscha*) salmon, and coho (*O. kisutch*) salmon utilize fewer calanoids and more macroplankton and planktivorous fish (e.g. Brodeur and Percy, 1990; Landingham *et al.*, 1998; Willette *et al.*, 1999). Production of piscivores may be trophically linked to the effects of climate change through larval/juvenile fish, which depend on an appropriately timed copepod abundance (e.g. Paul *et al.*, 1991; Napp *et al.*, 1996; Grover *et al.*, 2002).

In our study, we compare size and abundance of copepods to seasonal and annual temperature patterns in southeastern Alaska. This article examines a 6-year time-series on copepods in two adult size categories (<2.5 mm and >2.5 mm) and their individual species because physiological rate differ for copepods with such size differences (Allan, 1974; Lynch, 1977). The interannual abundance, size, and type of prey available to juvenile salmon such as copepods, could be significantly impacted by ENSO and other climate events.

## Materials and methods

### Southeast Coastal Monitoring (SECM) Project

Increasing information concerning relationships between Pacific salmon production and annual climate variation has renewed interest in processes governing year-class strength in salmon. However, actual links between salmon production and variability in oceanographic processes caused

by climate variations are poorly understood due to inadequate time-series data. A coastal monitoring study in northern southeastern Alaska, known as the SouthEast Coastal Monitoring (SECM) project, was initiated in 1997 to develop an understanding of the relationship between annual time-series of environmental data and stock-specific information on Pacific salmon. Monthly oceanographic sampling, zooplankton sampling, and fish sampling by surface trawl have been conducted along four transects annually in late spring–summer by Auke Bay Laboratory, National Marine Fisheries Service, NOAA, using the research vessel “John N. Cobb”. In general, the field data collected include fish species composition and catch per unit effort, water column salinity–temperature profiles, 2 m temperatures, surface water samples for nutrient and chlorophyll analysis, ambient light levels, and several types of zooplankton samples (Orsi *et al.*, 1998, 1999, 2000a, b, 2001a, b, 2002, 2003a, b).

### Study site

The SECM study area is a fjord system surrounded by snowfields, glaciers, and densely forested mountains in the Alexander Archipelago of northern southeastern Alaska (Figure 1). We examined data from a 12-km long transect in the SECM study area, the four stations crossing Icy Strait, located approximately 50 km west of Juneau, AK. Stations on the transect are situated 3.2–6.4 nm from shore between 58°13′N 135°31′W and 58°16′N 135°24′W (Orsi *et al.*, 1998, 1999, 2000a, b, 2001a, b, 2002, 2003a, b).

The southernmost station on the transect, ISA (Figure 1), is 70 m deep, while the others are 200–250 m in depth; the typical tidal range in Icy Strait is about 4 m. Spring snow, glacial melts, and heavy precipitation cause large influxes of freshwater to the Strait, especially from Glacier Bay, located to the north. Icy Strait links the inside passages of southeastern Alaska to the Gulf of Alaska and is the primary migration corridor for Pacific salmon in the region. Thus, both wild and hatchery-produced juvenile salmon spend 2–3 months in the area during the spring and summer months feeding on zooplankton, including large and small copepods (Jaenicke and Celewycz, 1994; Landingham *et al.*, 1998; Orsi *et al.*, 1998, 1999, 2000a, b, 2001a, b, 2002, 2003a, b; Sturdevant *et al.*, 2002).

Zooplankton and oceanographic data were collected from May to September 1997–2001 and from May to August in 2002, during the last 10–11 days of each month. All sampling occurred during daylight, between 07:00 and 20:00 hours. The physical environment was sampled with a Sea-Bird SBE 19 Seacat CTD, to 200 m or within 10 m of the bottom at shallow stations. However, in this article, we report only on SST and salinity measured at 2-m depth with the vessel’s onboard thermosalinograph (Sea-Bird SBE 21). Typical CTD profiles were reported in Murphy *et al.* (1999). At each station, we deployed a 60-cm diameter bongo net (505 and 333  $\mu$ m meshes) once in double oblique fashion, to a depth of 200 m or within 20 m of bottom (ISA). We report here on samples collected with the 333- $\mu$ m mesh net. The bongo was deployed and retrieved at a 45° wire angle with a descent rate of 1.0 m s<sup>-1</sup> and an

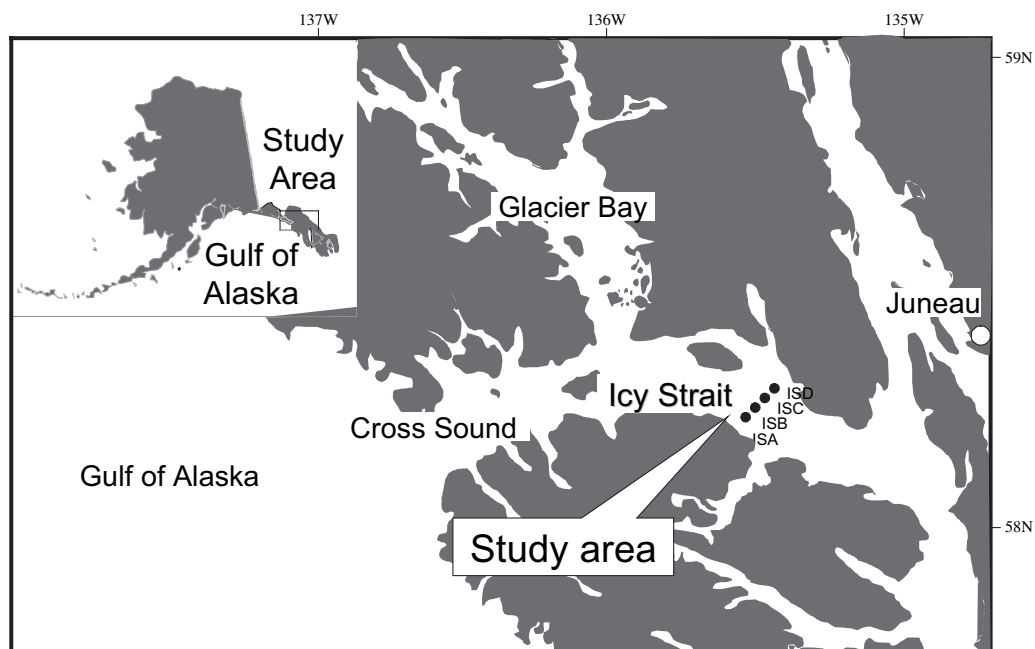


Figure 1. Southeast Coastal Monitoring (SECM) project sampling stations in Icy Strait, southeastern Alaska.

ascent rate of  $0.5 \text{ m s}^{-1}$ , with a 30-s pause at maximum depth. A Bendix bathythermograph was used to record the maximum sampling depths; General Oceanics model 2031 or Rigosha flow meters were placed inside the bongo nets. Large gelatinous taxa were removed before plankton samples were preserved in 5% buffered formalin aboard the ship and transported to the laboratory.

In the laboratory, displacement volume (DV, ml) of total plankton, used as a proxy for biomass, was estimated by subtraction: samples were brought to a constant volume (500 ml) by adding water, then were sieved through 243- $\mu\text{m}$  mesh until liquid no longer dripped into the container below (a few hours). DV was estimated by subtracting the volume of decanted liquid from the sample-liquid starting volume. DV was then converted to standing stock ( $\text{ml m}^{-3}$ ) by dividing by the volume of water filtered per sample. In addition, the total sample was scanned in a dissecting tray to estimate the volumetric composition of major taxonomic groups; the percentages were applied to the total DV to estimate per cent biomass by taxonomic group. Detailed species composition was determined by splitting samples with a Folsom splitter (usually 8–9 splits, or a 1/256–1/512 fraction) to achieve a total count of 300–500 individuals under the microscope. All copepod species and other taxa in the splits were identified and enumerated by species and stages, if possible. The common copepod species occurring every year were grouped into two size groups by total length (TL), those  $> 2.5 \text{ mm}$  (large) and those  $< 2.5 \text{ mm}$  (small).

Species counts were expanded for each sample and density ( $\text{number m}^{-3}$ ) was calculated using the filtered volumes. The estimated abundance and biomass of large and small copepods and of all other zooplankton combined were compared, as well as the individual copepod species within large and small size groups. For seasonal summaries, means and standard errors (s.e.) were computed across stations ( $n=4$ ) by month ( $n=5$ , except  $n=4$  in 2002) for each year ( $n=6$ ). For interannual comparisons, means and standard errors were computed from monthly means ( $n=4$ ) each year; only 4 months were used because no sample was taken in September 2002. The densities were untransformed for all analyses. Percentage abundances were calculated in two ways, (a) by dividing large and small copepod group densities by the total sample density, and (b) by dividing copepod species by its group density. Because SST data from the study area were limited to the 5 months in which copepod data were collected each year, we used SST data collected daily each year in nearby Auke Bay ( $58^{\circ}22' \text{N}$ ,  $134^{\circ}44' \text{W}$ ; data from Dr B. Wing, Auke Bay Laboratory, AFSC, NMFS, NOAA, 11305 Glacier Hwy., Juneau, Alaska 99801-8626; Wing and Pella, 1998) to extend our information on local oceanographic conditions for comparisons with interannual densities of copepod groups and species in Icy Strait. Similarity of SSTs from the Icy Strait transect and nearby Auke Bay was compared using linear regression analysis. Based on their high correlation ( $r^2=0.893$ ), each full year of Auke Bay temperature data was then used to characterize annual

environmental conditions. To do this, temperatures were converted to degree-days by summing daily measurements for the 365-day period between 1 September in the year preceding zooplankton sampling and 31 August in the year of zooplankton sampling; this calendar was used because most organisms present at a given time result from past episodes. We examined the variation in interannual densities of copepod species within size groups using pie graphs, including species whose abundance was  $> 2 \text{ m}^{-3}$ . To analyse interannual variation more quantitatively, we used the Bray–Curtis Similarity Index (BCSI; Boesch and Swartz, 1977). BCSI was applied to mean densities of three copepod groups: all dominant copepods, dominant large copepods [*Metridia ochotensis*, *Calanus marshallae*, *M. pacificus* and *Neocalanus* spp. (*N. plumchrus* and *N. flemingeri*)], and dominant small copepods (*Pseudocalanus* spp., *Acartia longiremis*, and *Centropages abdominalis*). BCSI values range from 0, indicating no similarity, to 1.0, indicating complete similarity.

## Results

Hydrographic measures exhibited a consistent, seasonal pattern each year (Figure 2). A total of 116 SST and 116 psu data points were included in our analysis of hydrographic measures in Icy Strait. Mean SST was generally lowest in May (approximately  $7\text{--}8^{\circ}\text{C}$ ), increased rapidly over the summer (peak approximately  $12\text{--}13^{\circ}\text{C}$ ), and declined again by September ( $8\text{--}9^{\circ}\text{C}$ ). Mean salinity was highest in May ( $30\text{--}31 \text{ psu}$ ), and declined over the summer to approximately  $21\text{--}22 \text{ psu}$ , then began to increase by September. The water column was weakly stratified in May, became strongly stratified in June through August, and stratification then weakened again in September (unpublished data on file, Auke Bay Laboratory). These typical patterns have been reported previously for the region (Bruce *et al.*, 1977; Coyle and Paul, 1992; Wing and Pella, 1998; Murphy and Orsi, 1999; Orsi *et al.*, 1998, 1999, 2000a, b, 2001a, b, 2002, 2003a, b).

Interannual variations in minimum and peak values were superimposed on seasonal hydrographic patterns during the study period. Interannual comparisons of surface temperatures showed warm summers in 1997 and 1998, the years with highest peaks in SST ( $> 13^{\circ}\text{C}$ ); conversely, a regional cold event (peak SST of  $9.7^{\circ}\text{C}$ ) was recorded in 2002 (Figure 2). Similarly, degree-days for the full years were highest ( $3255^{\circ}\text{C}$ ) in 1998 and lowest ( $2773^{\circ}\text{C}$ ) in 2002.

Zooplankton biomass (standing stock,  $\text{ml m}^{-3}$ ) varied interannually in Icy Strait, although consistent seasonal patterns were observed (Figure 3). Monthly mean standing stock for May–August ( $n=4$  per month) ranged from 0.25 to  $1.29 \text{ ml m}^{-3}$  during the sampling period; annual mean standing stock ( $n=4$  months) was lowest ( $0.44 \text{ ml m}^{-3}$ ; s.e. = 0.08) in 1998 and highest ( $0.89 \text{ ml m}^{-3}$ ; s.e. = 0.19) in 2001. Calanoid copepods constituted 18.8% of the total

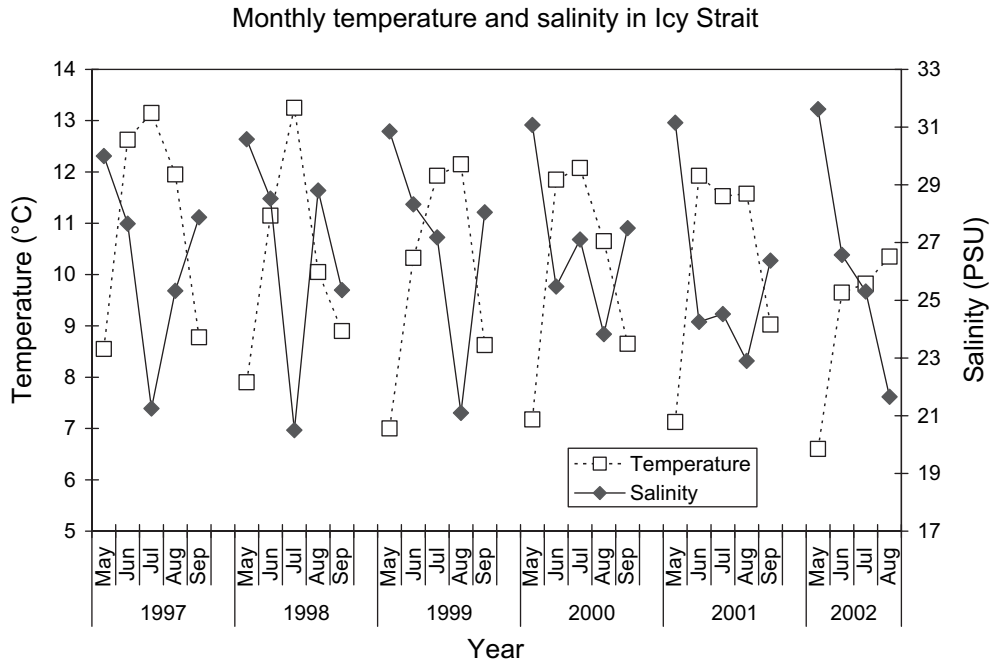


Figure 2. Salinity (psu) and sea surface temperature (°C) in Icy Strait, southeastern Alaska, from May to August, 1997–2002.

biomass and 88.2% of the total abundance of zooplankton across the entire period. The large calanoid copepods constituted 11.4% of zooplankton biomass and 24.2% of zooplankton abundance; small copepods constituted 7.4% of zooplankton biomass and 64.0% of zooplankton abundance. More than 34 copepod species were recorded (Table 1). Large species included *Euchaeta elongata*, *Calanus marshallae*, *C. pacificus*, *Eucalanus bungii*, *Metridia pacifica*, *M. ochotensis*, *Neocalanus cristatus*, and *Neocalanus* spp., a mixture of *N. flemingeri* and

*N. plumchrus*. The small species were represented by *Pseudocalanus* spp., *Centropages abdominalis*, *Oithona* spp., *Microcalanus pygmaeus*, and *Acartia longiremis*. The non-calanoid zooplankters ranged from 8.0% to 15.2% of total zooplankton density each year, and principally comprised *Oikopleura* sp., euphausiids, cladocerans, barnacle nauplii, and chaetognaths.

Seasonal and annual patterns in copepod density and percent density were observed in Icy Strait. Annual mean copepod density varied by approximately a factor of 2

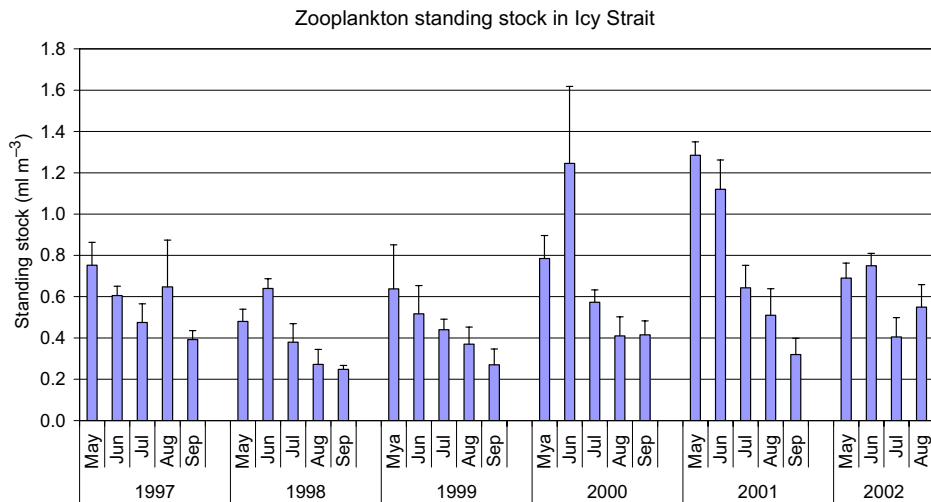


Figure 3. Monthly zooplankton standing stock (ml m<sup>-3</sup>) in Icy Strait, southeastern Alaska, from May to August, 1997–2002. Values are means and standard errors of four samples per month.

Table 1. Large (>2.5 mm TL) and small (<2.5 mm TL) copepod species occurring in Icy Strait, southeastern Alaska, from 1997 to 2002.

Large copepod species (>2.5 mm TL)	Small copepod species (<2.5 mm TL)
Aetideidae spp.	<i>Centropages abdominalis</i> *
<i>Calanus marshallae</i> *	<i>Acartia longiremis</i> *
<i>C. pacificus</i> *	<i>A. clausi</i> *
<i>Candacia columbiae</i>	<i>Chiridius gracilis</i>
<i>Chiridius polaris</i>	<i>Oithona</i> spp.*
<i>Epilabidocera longipedata</i>	<i>Oncaea</i> sp.
<i>Eucalanus bungii</i> *	<i>Pseudocalanus</i> spp.*
<i>Euchaeta californica</i>	<i>Tortanus discaudatus</i>
<i>E. elongata</i> *	<i>Microcalanus pygmaeus</i> *
<i>E. spinosa</i>	
<i>Gaetanus intermedia</i>	
<i>G. pileatus</i>	
<i>Heterorhabdus tanneri</i>	
<i>H. robustoides</i>	
<i>Heterostylites major</i>	
<i>Lophothrix frontalis</i>	
<i>Metridia ochotensis</i> *	
<i>M. pacifica</i> *	
<i>Neocalanus cristatus</i> *	
<i>Neocalanus</i> spp.	
( <i>N. flemingeri</i> and <i>N. plumchrus</i> )*	
<i>Pleuromamma scutullata</i>	

\*Indicates species studied in detail in the article.

over the 6 years, and averaged  $952.2 \text{ m}^{-3}$  (s.e. = 76.5) for the period. Minimal copepod densities ( $711.7 \text{ m}^{-3}$  and  $792.6 \text{ m}^{-3}$ ) were observed in 1998, a warm El Niño year, and in 2002, a regionally cold year; maximal copepod densities ( $1155.1$  and  $1175.9 \text{ m}^{-3}$ ) were observed in 2000 and 2001, years with typical annual temperatures that preceded a regional cold year (Table 2; Figure 4). Annual mean densities of large and small copepods followed similar patterns, although the small species were numerically dominant every year (Figure 4); the mean annual density of large copepods was  $321.9 \text{ m}^{-3}$  (s.e. = 44.4), while the mean annual density of small copepods was  $630.1$  (s.e. = 36.6). Nonetheless, the small species were relatively more abundant in the warm, El Niño year, while the large species were relatively more abundant in years with typical annual temperatures (Figure 4). In general, copepod abundance peaked in June–July each year, with large copepod peak abundance occurring earlier than small copepod peak abundance (Figures 5 and 6), and some interannual variation in the timing.

Copepod species abundance also varied by year, and was generally lower in the warm El Niño year (1998) and the regional cold year (2002; Table 2; Figure 7). Among large copepods, *M. ochotensis* dominated in all seasons and years, constituting 70–84% of all large copepods (Figure 7). The annual mean density of *M. ochotensis* was

anomalously low ( $125.1 \text{ m}^{-3}$  and  $142.7 \text{ m}^{-3}$ ) in 1998, a warm El Niño year, and in 2002, a regional cold event; it was highest ( $368.4 \text{ m}^{-3}$ ) in 2000, a year with typical annual temperatures (Table 2; Figure 7). *C. marshallae* (primarily copepodites) and *M. pacifica* were the next most abundant large copepods, constituting 2–19% of all large copepods; however, they exhibited different interannual patterns. The annual mean density of *C. marshallae* was lowest ( $4.6 \text{ m}^{-3}$ ) in 1998 and highest ( $73.4 \text{ m}^{-3}$  and  $78.6 \text{ m}^{-3}$ ) in 2001 (Table 2); conversely, annual mean density of *M. pacifica* was lowest ( $12.2 \text{ m}^{-3}$  and  $9.8 \text{ m}^{-3}$ ) in 1998 and 2001 and highest ( $43.1 \text{ m}^{-3}$  and  $38.4 \text{ m}^{-3}$ ) in 1999 and 2002 (Table 2). Interannual density differences for the remaining large copepod species were smaller than for *Metridia* spp. and *C. marshallae*. *N. cristatus* density was consistently  $<0.1 \text{ m}^{-3}$  (Table 2). Most *N. cristatus* observed were copepodite V. The abundance of *Neocalanus* spp. (including *N. plumchrus* and *N. flemingeri*) was relatively low ( $2.5 \text{ m}^{-3}$  and  $1.5 \text{ m}^{-3}$ ) in 1998 and 2002 and relatively high ( $5.2 \text{ m}^{-3}$  and  $4.8 \text{ m}^{-3}$ ) in 2000 and 2001. The mean density of *E. elongata* was lowest ( $0.6 \text{ m}^{-3}$ ) in 1998 and highest ( $1.4 \text{ m}^{-3}$ ) in 2000. The abundance of *E. bungii* was lowest ( $0.3 \text{ m}^{-3}$ ) in 1998 and highest ( $4.9$  and  $4.6 \text{ m}^{-3}$ ) in 2001 and 2002 (Table 2).

Interannual abundance patterns of small copepod species were generally similar to those of large copepods (Table 2; Figure 7). *Pseudocalanus* spp. dominated throughout the study period, constituting 84–94% of all small copepods. The density of *Pseudocalanus* spp. was relatively low ( $<533 \text{ m}^{-3}$ ) in 1997–1998 and 2002, and was relatively high ( $696.7 \text{ m}^{-3}$ ) in 2001. *A. longiremis* density was relatively low ( $18.2 \text{ m}^{-3}$  and  $15.8 \text{ m}^{-3}$ ) in 1998 and 2002 and relatively high ( $33.8 \text{ m}^{-3}$ ) in 2000 (Table 2). The interannual abundance pattern for *C. abdominalis* differed from patterns for *Pseudocalanus* spp. and *A. longiremis*, with a minimum value ( $4.8 \text{ m}^{-3}$ ) in 1999 and a peak ( $51.8 \text{ m}^{-3}$ ) in 2000. The densities of *M. pygmaeus* and *Oithona* spp. were low compared to the other small species throughout the sampling period. *M. pygmaeus* mean density was particularly low ( $0.4 \text{ m}^{-3}$ ) in 1998 and 2001. *Oithona* spp. density was relatively low ( $0.3 \text{ m}^{-3}$  and  $0.4 \text{ m}^{-3}$ ) in 2001 and 2002, and relatively high ( $1.9 \text{ m}^{-3}$ ) in 1997 (Table 2).

Bray–Curtis Similarity Index (BCSI) measuring community similarity showed relatively high similarity for small copepod abundances between years, while BCSI was relatively low for large copepod abundances, especially between El Niño and a regional cold year and their neighbouring years (Table 3). These results suggest that large copepods are more sensitive to ocean climate changes than are small copepods.

## Discussion

We examined interannual variation of spring–summer copepod density in a small area of the Northeast Pacific in

Table 2. Annual mean density (no. m<sup>-3</sup>) of dominant copepod species in Icy Strait, southeastern Alaska, from May to August, 1997–2002. Values are means and standard errors (s.e.) of four monthly means; s.e. not shown for species with mean densities <2 m<sup>-3</sup> or for pooled other species.

	1997		1998		1999		2000		2001		2002	
	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.
Large copepod species												
<i>Neocalanus</i> spp.	3.0	2.1	2.5	1.7	3.6	2.6	5.2	4.6	4.8	1.7	1.5	0.4
<i>Neocalanus cristatus</i>	0.1	—	0.1	—	0.1	—	0.1	—	0.0	—	0.1	—
<i>Metridia pacifica</i>	25.6	5.6	12.2	5.3	43.1	32.9	23.8	8.5	9.8	3.6	38.4	26.8
<i>Metridia ochotensis</i>	306.4	53.74	125.1	67.0	223.5	93.2	368.4	109.5	326.4	171.4	142.7	38.1
<i>Gaetanus intermedius</i>	1.4	—	0.6	—	0.5	—	1.1	—	1.9	—	1.3	—
<i>Euchaeta elongata</i>	1.1	—	0.9	—	1.3	—	1.4	—	0.6	—	1.1	—
<i>Eucalanus bungii</i>	1.0	—	0.1	—	0.2	—	2.2	—	2.7	—	0.5	—
<i>Calanus marshallae</i>	26.7	16.2	4.6	0.8	15.5	4.9	18.0	7.6	78.6	50.7	73.4	40.0
Others	4.7	—	1.9	—	3.0	—	3.8	—	7.6	—	7.3	—
Subtotal	370.0		148.0		290.8		424.0		432.4		266.3	
Small copepod species												
<i>Acartia clausi</i>	0.0	—	0.3	—	0.3	—	4.8	—	2.0	—	0.9	—
<i>Acartia longiremis</i>	21.4	5.6	18.3	8.6	22.3	3.6	33.8	5.7	23.4	4.0	15.8	1.9
<i>Centropages abdominalis</i>	26.0	13.8	11.5	5.5	4.8	1.3	51.8	34.5	6.6	2.0	11.6	5.4
<i>Microcalanus pygmaeus</i>	1.9	—	0.4	—	1.8	—	1.4	—	0.4	—	1.3	—
<i>Oithona</i> spp.	1.9	—	0.7	—	1.1	—	1.0	—	0.3	—	0.4	—
<i>Pseudocalanus</i> spp.	528.6	74.2	532.7	69.3	595.9	77.9	610.6	41.7	696.7	36.6	493.1	63.0
Others	5.4	—	5.2	—	4.7	—	27.7	—	14.1	—	3.2	—
Subtotal	585.2		569.1		630.9		731.1		743.5		526.3	
Total copepods	955.2		711.7		921.7		1155.1		1175.9		792.6	

relation to global and regional scale climate shifts including an El Niño event. Interannual—interdecadal variations in zooplankton biomass, chlorophyll concentration, and physical environment in the Subarctic Pacific and Bering Sea have been closely linked to local weather patterns (Sugimoto and Tadokoro, 1997; Francis *et al.*, 1998; Whitney and Welch, 2002). The copepod community composition in our study was typical for reports from the Northeast Pacific (e.g. Coyle *et al.*, 1990; Goldblatt *et al.*, 1999; Napp *et al.*, 1996, 2002). Recent studies have documented El Niño and La Niña events from the 1990s to the present (see NOAA websites above), but effects are not consistent among study areas, particularly in high latitudes. Our data from southeastern Alaska indicate the strong El Niño occurring from the summer of 1997 to the spring of 1998, but do not indicate the weaker El Niño occurring in 2002, both of which were indicated by the Southern Oscillation Index (SOI) and reported in NOAA climate data (<http://www.ncdc.noaa.gov>). The warm temperatures we observed in 1998 did coincide with a strong El Niño event; however, the extremely cold year in the study region, 2002 did not coincide with a weak El Niño year.

Although we have documented substantial interannual variation in copepod abundance patterns, at present we lack sufficient data from the straits of southeastern Alaska to

distinguish between short-term variations and long-term changes in zooplankton biomass. Local marine production is not static, but exhibits a series of trends similar to those observed in other pelagic ecosystems. In addition, hydrodynamics of the straits in southeastern Alaska are influenced by advection from the Gulf of Alaska (Coyle *et al.*, 1990) and freshwater from numerous rivers, glaciers, and high rainfall, as well as by strong tidal action. Climate events interact with geographical features to influence the timing and volume of snow meltwater and glacial discharge. This may be the source of the extremely cold water we observed in 2002.

Few long-term studies have linked climate change with interannual variation in the densities of different size groups of copepods (Brodeur and Ware, 1992). The present study carried out in a strait in northern southeastern Alaska confirmed that standing stock and densities of both large and small copepods were relatively low during both the warmest and coldest of the 6 years we examined. The densities of large copepod species in Icy Strait were much lower and varied more among years than did those of small copepod species, conditions typical of their populations in Subarctic regions (e.g. Coyle *et al.*, 1990; Goldblatt *et al.*, 1999; Cooney *et al.*, 2001b). Furthermore, we may have underestimated the densities of small species, in particular,

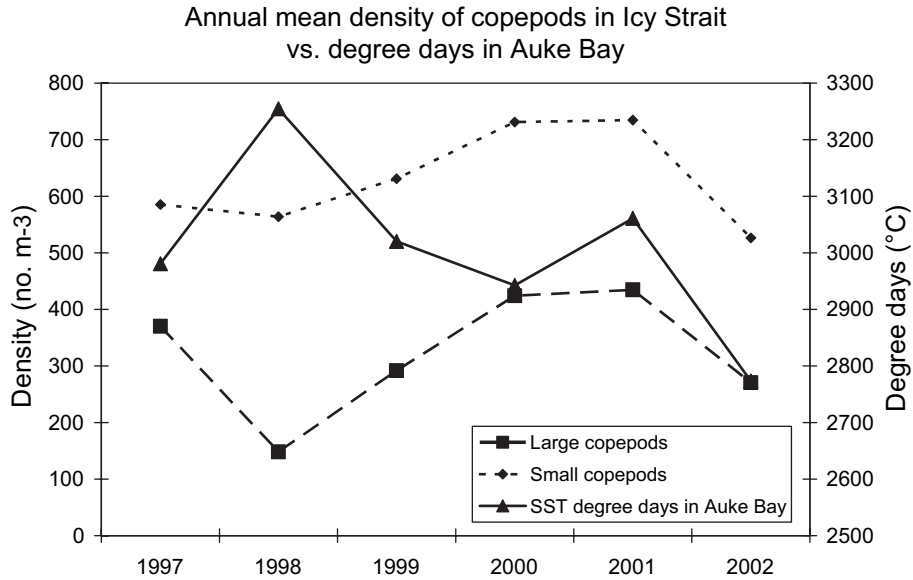


Figure 4. Annual mean density of copepods (mean of four monthly means) in Icy Strait in relation to interannual sea surface temperature degree-days in Auke Bay, southeastern Alaska, from May to August, 1997–2002.

because many copepodites were likely to have passed through the 333- $\mu\text{m}$  mesh (e.g. Sturdevant, 2001). Nonetheless, since the patterns of interannual variation in density of copepod size categories are based on consistent sampling methods, variation in time of the day and weather conditions that could affect environment through tidal stage, clouds, and rain may account for some of the variability in

hydrographic data and in zooplankton densities and standing stock (Brodeur and Ware, 1992).

Copepod life-history strategies may determine the impact of climate change on their abundance. In high latitudes, the phytoplankton bloom is often uncoupled from zooplankton production (Frost, 1987; Paul *et al.*, 1991; Haldorson *et al.*, 1993). Seawater temperature controls reproductive cycles

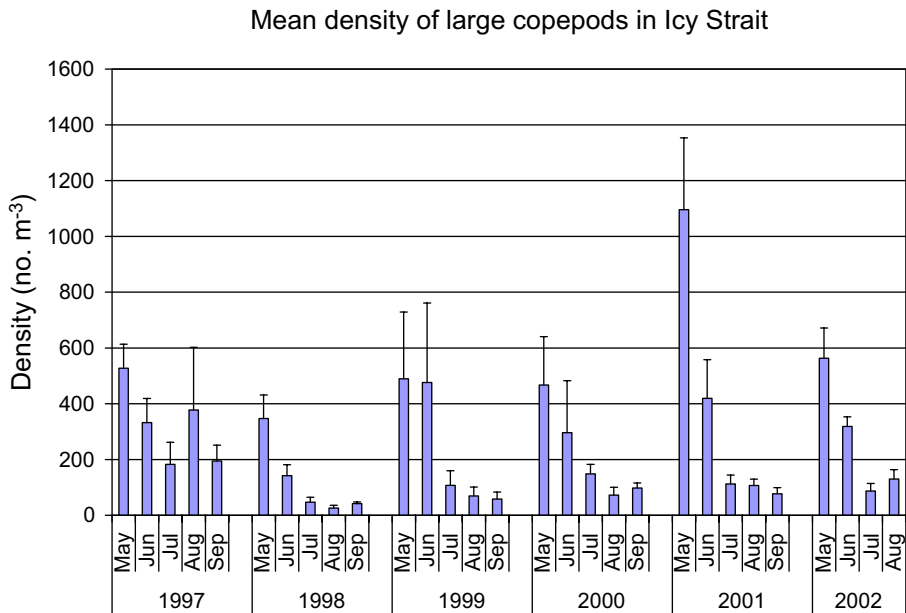


Figure 5. Seasonal densities (no. m<sup>-3</sup>) of large copepods in Icy Strait, southeastern Alaska, from May to August, 1997–2002. Values are means and standard errors for four samples per month in each year.



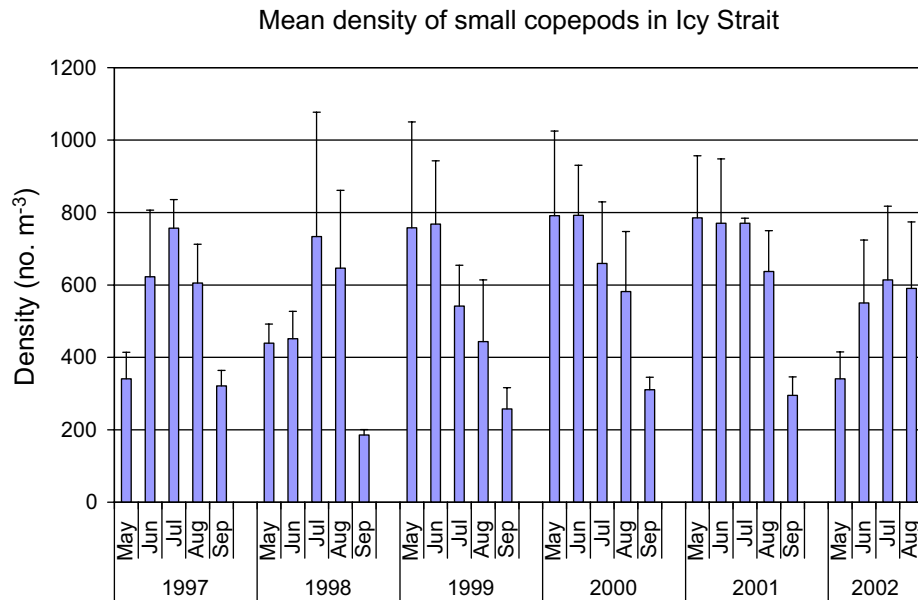


Figure 6. Seasonal densities (no. m<sup>-3</sup>) of small copepods in Icy Strait, southeastern Alaska, from May to August, 1997–2002. Values are means and standard errors for four samples per month in each year.

and generation times of Subarctic copepod species because many copepods enter a resting stage from winter until spring, when they begin to feed and reproduce (Corkett and McLaren, 1978; Conover, 1988). The negative effects of climate change on copepod productivity may be greater for carnivorous species than for omnivorous species and for those with high food requirements because they have no alternate food sources when their prey populations are low.

The reproductive cycles, fecundities, and development rates of marine organisms vary with temperature. For example, the occurrence and duration of *Neocalanus* spp. and *C. marshallae* varied by area (Vidal and Smith, 1986; Coyle et al., 1990; Mackas et al., 1998) and the time of appearance was slightly earlier at Ocean Station P and in Auke Bay than in the Bering Sea (Coyle et al., 1990). Generation time of *Pseudocalanus* spp. and *Acartia* spp. differed with temperature (McLaren, 1978; McLaren and Corkett, 1981). Coyle et al. (1990) concluded that variation in interannual densities of *Oithona* spp. and *Centropages* spp. may result in differential survival of over-wintering stocks.

In our study, annual mean densities of small copepods may have been consistently high for several reasons. The small species are usually distributed in surface waters and tolerate frequent environmental change. Their relatively short lifespans may allow a quick reproductive response, an advantage in dynamically changing environments. Small copepods may also be better grazers on phytoplankton stocks than large copepods (Frost, 1987), many of which are carnivores, although no local studies of grazing rates exist. Small copepods with a shorter, more frequent generation time may adapt to the timing of temperature cues, whereas large species may be less flexible due to their

different life-history strategies (Conover, 1988; Coyle et al., 1990). Small copepods with an abundance of females are also less dependent on high individual fecundity to maintain their populations (Paul et al., 1990). Thus, small copepod species having a shorter lifespan and multiple generations per year may be less affected by climate change than are large copepod species having a relatively long lifespan and one generation per year. However, the relatively low interannual variability exhibited by the most abundant small copepod genus in our study, *Pseudocalanus* spp., may be moderated by the four species present, but difficult to identify, in southeastern Alaska: *P. minutus*, *P. moultoni*, *P. newmani*, and *P. mimus* (Frost 1990). These multiple species have different reproductive and survival strategies that overlap in time.

Among large copepods, the genus *Neocalanus* is a principal herbivore in the open Subarctic ocean. However, the abundance of its life stages varies less than phytoplankton stocks do on both spatial and temporal scales (Parsons and Anderson, 1970; Frost, 1987). Annual phytoplankton biomass at Ocean Station P was relatively constant through the years, while rates of primary production varied seasonally with a spring peak in the upper mixed layer (Frost, 1993; Wong et al., 1995). However, in Auke Bay, Alaska, adjacent to our study area, the date of peak phytoplankton production in April varied by only 5 days in a 5-year period (Zimmerman et al., 1991). Interdecadal variation in the developmental timing of *Neocalanus plumchrus* populations at Ocean Station P tracked large-scale annual and decadal fluctuations in ocean climate, which were reflected in spring SST anomalies in the surface mixed layer where copepodites feed and grow

Interannual density of copepod species

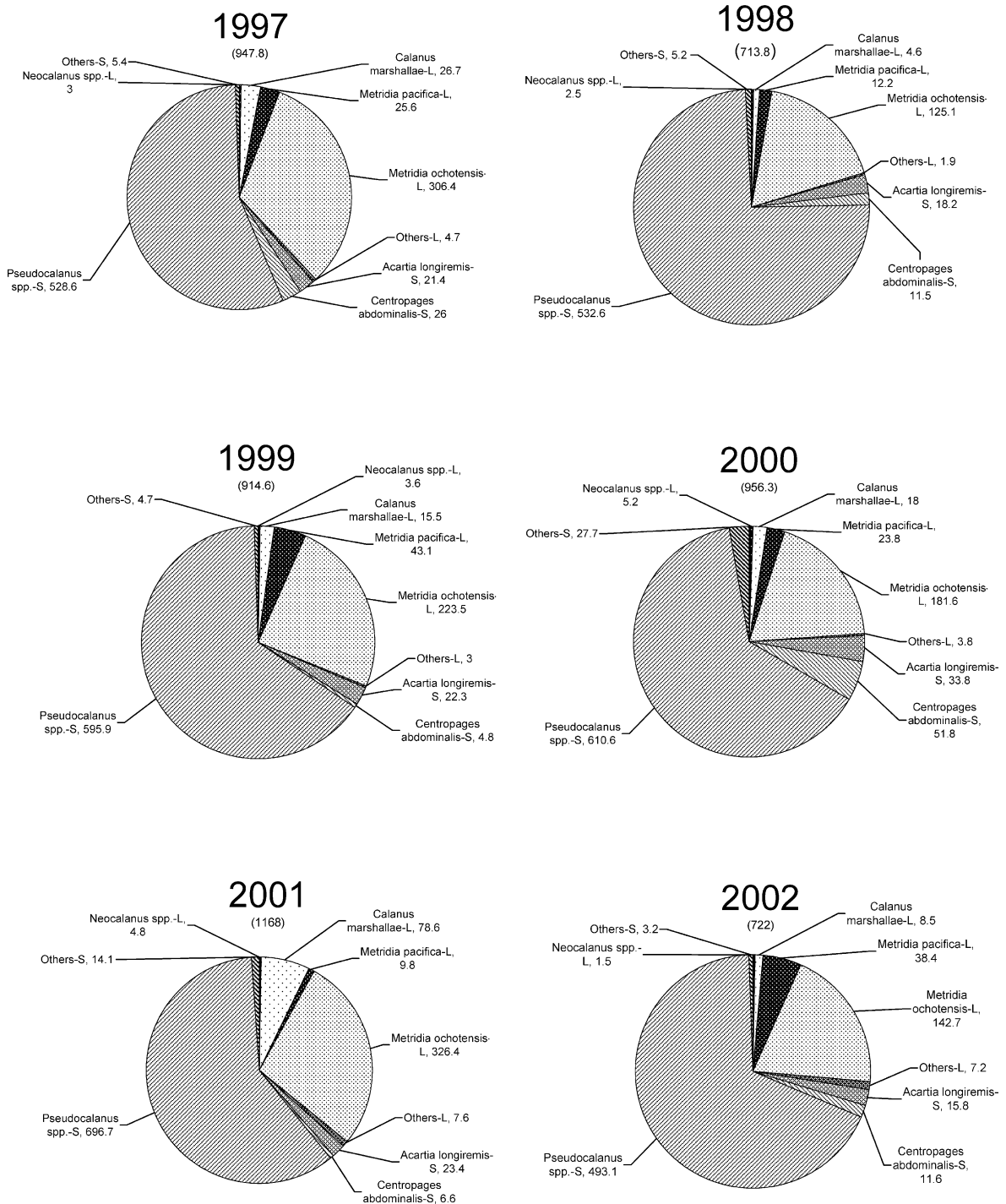


Figure 7. Interannual mean density of copepods in Icy Strait, southeastern Alaska, from May to August, 1997–2002. Abbreviations: L, large copepods (>2.5 mm TL); S, small copepods (<2.5 mm). The numbers after species names indicate their annual mean density ( $\text{no. m}^{-3}$ ); total copepod density is indicated below the year.

Table 3. Interannual Bray–Curtis similarity indices for copepod communities occurring in Icy Strait, southeastern Alaska, from May to August, 1997–2002.

	1997	1998	1999	2000	2001	2002
All copepods						
1997	1	0.851	0.882	0.835	0.861	0.865
1998	0.851	1	0.851	0.829	0.746	0.915
1999	0.882	0.851	1	0.907	0.860	0.875
2000	0.835	0.829	0.907	1	0.814	0.836
2001	0.861	0.746	0.860	0.814	1	0.729
2002	0.865	0.915	0.875	0.836	0.729	1
Dominant large copepods						
1997	1	0.570	0.807	0.727	0.893	0.788
1998	0.570	1	0.632	0.684	0.497	0.833
1999	0.807	0.632	1	0.860	0.758	0.826
2000	0.727	0.684	0.860	1	0.653	0.827
2001	0.893	0.497	0.758	0.653	1	0.558
2002	0.879	0.788	0.826	0.827	0.558	1
Dominant small copepods						
1997	1	0.980	0.925	0.891	0.850	0.948
1998	0.980	1	0.952	0.879	0.860	0.960
1999	0.925	0.952	1	0.929	0.917	0.898
2000	0.891	0.879	0.929	1	0.894	0.840
2001	0.850	0.860	0.917	0.894	1	0.820
2002	0.948	0.960	0.898	0.840	0.820	1

(Mackas *et al.*, 1998). In our study, however, *Neocalanus* spp. was not prominent among large copepod species.

The differences in interannual densities of copepod size groups probably reflect their longer or shorter lifespans. Large species with longer lifespans typically complete one life cycle in a year, while small species produce several generations per year. If El Niño and regional cold events are strong, large copepod species may fail to complete their life cycles in one year and extend into the next (Miller and Terazaki, 1989). Therefore, copepod biomass may be low during El Niño and regional cold events because these climatic changes may have larger effects on large copepods than on small copepods. At present we cannot distinguish the effects of ENSO events from those of other factors that affected copepod densities, such as a regional cold event in southeastern Alaska during an El Niño year.

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