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Interannual and decadal variability in zooplankton communities of the southeast Bering Sea shelf

Jeffrey M. Napp^{a,*}, Christine T. Baier^a, Richard D. Brodeur^b, Kenneth O. Coyle^c, Naonobu Shiga^d, Kathy Mier^a

^aNOAA/NMFS/Alaska Fisheries Science Center, 7600 Sand Point Way, NE, Seattle, WA 98115-0070, USA

^bNOAA/NMFS/Northwest Fisheries Science Center, Hatfield Marine Science Center, Newport, OR 97365-5297, USA

^cInstitute of Marine Science, P.O. Box 757220, University of Alaska, Fairbanks, Fairbanks, AK 99775-7220, USA

^dGraduate School of Fisheries Sciences, Hokkaido University, 3-1-1, Minato-cho, Hakodate, 041 Japan

Abstract

The southeastern Bering Sea shelf ecosystem is an important fishing ground for fin- and shellfish, and is the summer foraging grounds for many planktivorous seabirds and marine mammals. In 1997 and 1998, Northern Hemisphere climate anomalies affected the physical and biological environment of the southeastern Bering Sea shelf. The resulting anomalous conditions provided a valuable opportunity to examine how longer-term climate change might affect this productive ecosystem. We compared historical and recent zooplankton biomass and species composition data for the southeastern Bering Sea shelf to examine whether or not there was a response to the atmosphere–ocean–ice anomalies of 1997 and 1998. Summer zooplankton biomass (1954–1994) over the southeastern shelf did not exhibit a decline as previously reported for oceanic stations. In addition, zooplankton biomass in 1997 and 1998 was not appreciably different from other years in the time series. Spring concentrations of numerically abundant copepods (*Acartia* spp., *Calanus marshallae*, and *Pseudocalanus* spp.), however, were significantly higher during 1994–1998 than 1980–1981; spring concentrations of *Metridia pacifica* and *Neocalanus* spp. were not consistently different between the two time periods. *Neocalanus* spp. was the only taxon to have consistent differences in stage composition between the two time periods—CV copepodites were much more prevalent in May of the 1990s than early 1980s. Since relatively high zooplankton concentrations were observed prior to 1997, we do not attribute the high concentrations observed in the summers of 1997 and 1998 directly to the acute climate anomalies. With the present data it is not possible to distinguish between increased production (control from below) and decreased predation (control from above) to explain the recent increase in concentrations of the species examined.

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1. Introduction

The southeastern Bering Sea shelf is a rich, productive region. Commercially valuable fin- and shellfish, protected marine mammals, seabirds,

and indigenous peoples all rely on high production from the Bering Sea (National Research Council, 1996). High productivity in this marginal sea results from a combination of factors including: a high rate of nutrient supply, long summer day length, and a food web that efficiently transfers pelagic production to both pelagic and benthic communities. The southeastern Bering Sea shelf ecosystem rapidly responds to atmospheric

*Corresponding author. Tel.: +1-206-526-4148; fax: +1-206-526-6723.

E-mail address: jeff.napp@noaa.gov (J.M. Napp).

perturbations in many different ways (Vance et al., 1998; Hunt et al., 1999; Napp and Hunt, 2001).

Long-period shifts in climate affect production and composition of aquatic ecosystems. For example, the North Atlantic Oscillation (NAO; Hurrell and Van Loon, 1997) exhibits variability on the quasi-biennial and quasi-decadal time scales. NAO variability affects both pelagic and benthic communities of oceans and lakes (Heath et al., 1999; Kroencke et al., 1998; Planque and Reid, 1998; Weyhenmeyer et al., 1999). Its influence on the ocean ecosystem is produced, in part, by shifting the path of storm tracks, and by varying wintertime cooling of the ocean surface.

Decadal-scale variability in winter atmospheric conditions is also important for the Northern Pacific Ocean and Eastern Bering Sea (e.g., Trenberth and Hurrell, 1995; Wooster and Hollowed, 1995). Shifts in seasonally averaged storm track lines (identified by the strength and position of the Aleutian Low) affect the atmosphere–ocean coupling of the Northern Pacific Ocean and its fisheries (e.g., Brodeur and Ware, 1995; Hollowed and Wooster, 1995; Mantua et al., 1997; Schumacher et al., in press). In the eastern Bering Sea shelf ecosystem, shifts in both cold and warm season storm-track lines affect the: timing of the spring phytoplankton bloom; amount of primary production that is transported to the benthos; and match–mismatch of prey production for larval fish (Napp et al., 2000; Overland et al., 2001; Stabeno et al., 2001).

Recent anomalies in weather provide an unique opportunity to understand how longer-term climate changes may affect the Bering Sea ecosystem. In 1997 for example, a *decadal* trend in higher atmospheric warm season pressure, plus a *monthly* high pressure system (in May), plus a *seasonal* anomaly in North Pacific atmospheric circulation in response to the 1997/98 El Niño, combined to create anomalously calm, warm, sunny conditions over the Bering Sea (Overland et al., 2001). This resulted in high heat transfer to the surface layer (+4°C anomaly by August; Stabeno et al., 2001). Concomitant with these environmental anomalies was the first documented coccolithophore bloom for the region (Sukhanova and Flint, 1998; Vance et al., 1998); low euphausiid concentrations (Coyle

and Pinchuk, 2002; Stockwell et al., 2001); mass mortality and dietary shifts in a planktivorous seabird (*Puffinus tenuirostris*; Baduini et al., 2001; Hunt et al., 2002a).

This paper reports our initial efforts to synthesize zooplankton data from the eastern Bering Sea shelf. Our goal is to understand the mechanisms responsible for fluctuations in biomass and community structure. We compare two different types of data: historical zooplankton biomass data collected by the Hokkaido University training ship (*Oshoro Maru*) and zooplankton species composition data (concentration) collected by two research programs: Processes and Resources of the Bering Sea shelf (PROBES) and Southeast Bering Sea Carrying Capacity (SEBSCC). Specifically, we examined whether zooplankton biomass and community structure responded to the atmosphere–ocean–ice anomalies of 1997/1998.

2. Methods

2.1. Zooplankton biomass

Summer (1954–1994) estimates of zooplankton biomass (preserved wet weight) were obtained from the Hokkaido University, T/S *Oshoro Maru* time series published in annual data reports (e.g., Anonymous, 2000). Over the length of the time series, sampling in the Bering Sea began as early as 17 June and ended as late as 3 August. Sampling effort and station locations varied considerably over the time series (Fig. 1A and B). In recent years (since 1995), the sample grid pattern for the southeastern Bering Sea shelf has remained more or less constant (Fig. 1C). We included in our statistical analyses only those stations from the southeastern shelf (≤ 200 m water depth) and categorized each station according to the associated hydrographic domain (sensu Coachman, 1986). The Outer Shelf Domain (hereafter referred to as the outer shelf) was where water depth was 200–100 m; Middle Shelf Domain (middle shelf) was stations where the water depth was 100–50 m; Coastal Domain was stations where the water depth was < 50 m. We excluded samples that data reports noted as biased by the predominance of

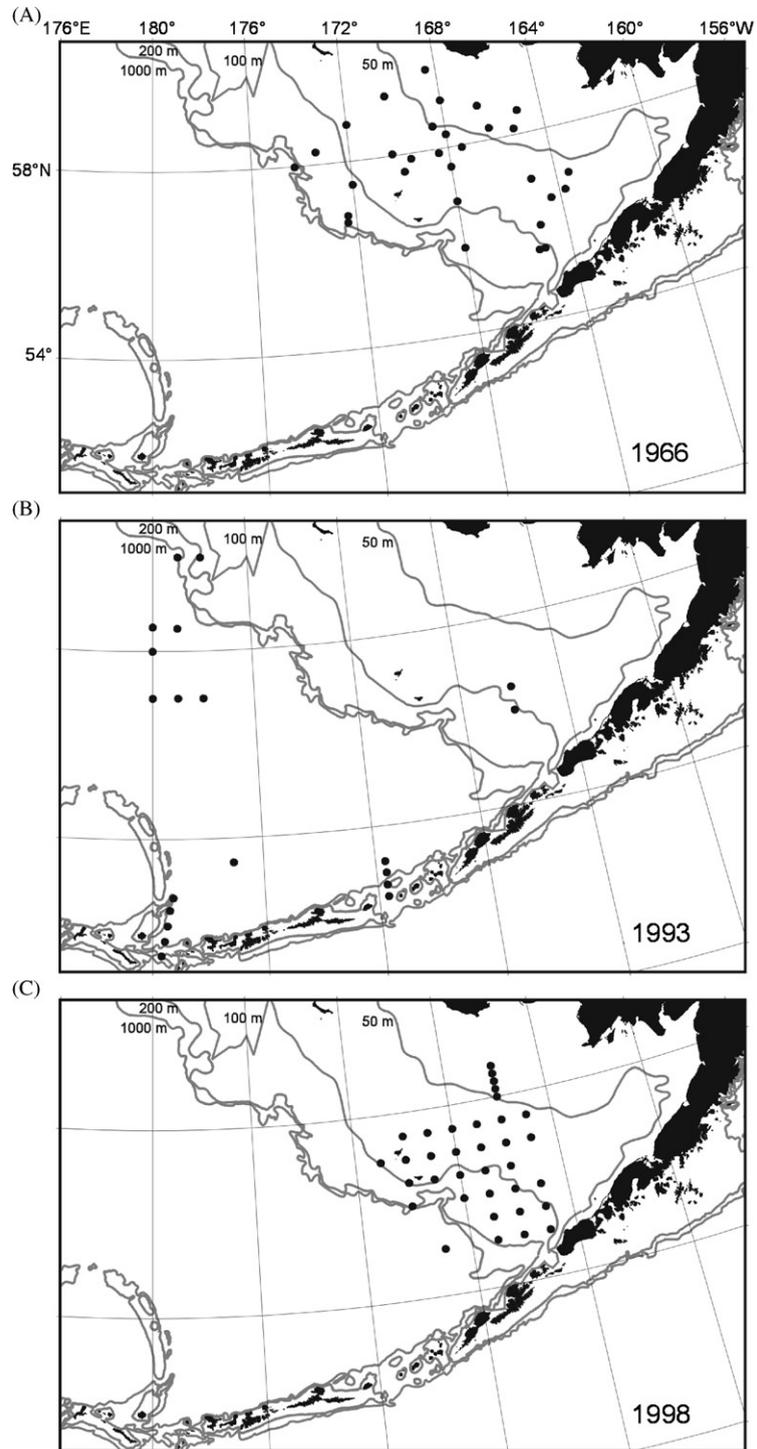


Fig. 1. Examples of station locations for the T/S *Oshoro Maru* summer zooplankton biomass time series: (A) 1966; (B) 1993; (C) 1998. Note that since 1995 the same grid of shelf stations has been occupied each summer.

taxa with high water content (e.g., salps) or calcareous material (coccolithophores).

T/S *Oshoro Maru* samples were collected with 45-cm mouth diameter NORPAC nets (0.33-mm mesh) towed vertically from 150 m or near bottom (estimated by wire angle) to the surface at about 1 m/s. Flow meters mounted inside the net mouth were annually calibrated using vertical tows at several open ocean stations.

2.2. Species concentrations

Concentrations of numerically dominant copepod species were quantified from samples collected 1994–1999 during the last 2 weeks of April and first 2 weeks of May near biophysical moorings on the outer and middle shelf. Mooring 3 (120 m) and Mooring 2 (72 m) were intended to characterize processes in the outer and middle shelf, respectively. Before 1997, stations were in the general vicinity of the moorings; starting in 1997 there

were 4 stations around each mooring and one at the mooring (Fig. 2).

Zooplankton species concentrations were obtained from double-oblique tows of paired (20- and 60-cm mouth diameter) bongo net frames with 0.150- and 0.333-mm mesh, respectively (Incze et al., 1997) to within 5 m of the bottom. Net depth was determined in real time using a SeaCat CTD that telemetered instrument depth to the ship; volume filtered was estimated using calibrated General Oceanics flowmeters mounted inside the net mouths. Samples were preserved in a 5% Formalin:seawater solution, and zooplankton was identified to the lowest taxon (and stage) possible at the Polish Plankton Sorting Center (Szczecin, Poland). The mesh size selected for enumeration of any particular developmental stage was based on the size of the stage and the predicted retention efficiency of the mesh for that stage (Incze et al., 1997).

Zooplankton species data from the same time period (late April and early May) in 1980 and 1981

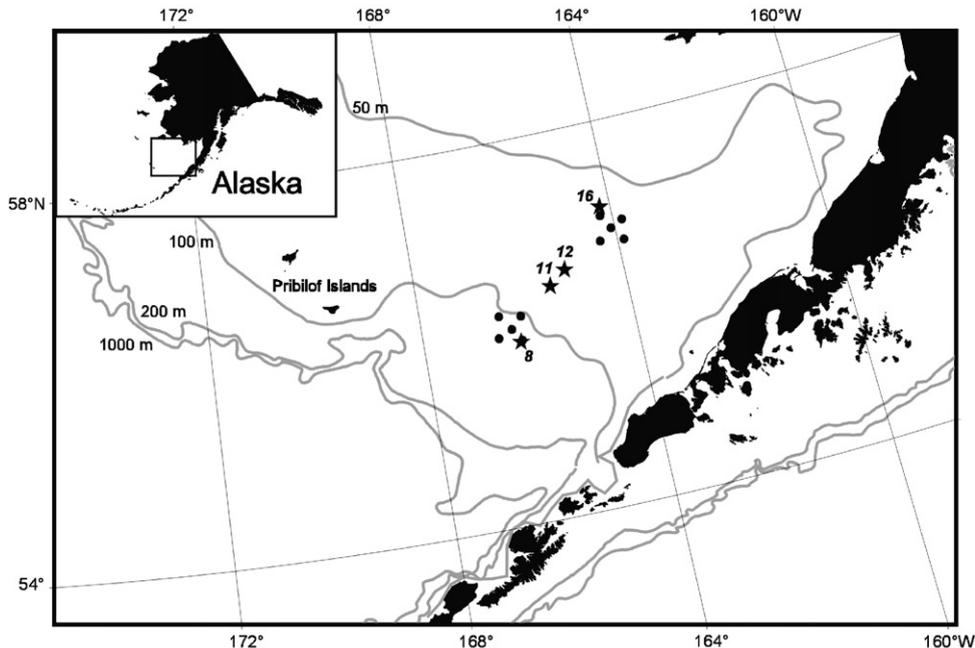


Fig. 2. Eastern Bering Sea and zooplankton species concentration station locations. Southeast Bering Sea Carrying Capacity (SEBSCC) outer and middle shelf monitoring stations indicated by ● and PROBES stations by ★ Included with the PROBES stations are the “Master Station Number” (Smith et al., 1982).

were obtained from PROBES data reports (e.g., Smith et al., 1982). Whenever possible we used the PROBES stations closest to our own (outer shelf, Station 8; middle shelf, Station 16). In 1981 this was not always possible for the middle shelf so data from PROBES Stations 11 and 12 were used as well (Fig. 2). PROBES zooplankton samples were collected with a 1 m² MOCNESS using 149- μ m mesh nets. Species concentrations from depth-stratified MOCNESS tows were numerically integrated to make them comparable to the results from our oblique bongo tows. For this study, we selected taxa and stage combinations from our samples that would match those used by Smith and Vidal (1986; *Acartia* spp., C6 male and female; *Calanus marshallae*, C2–C6 female; *Neocalanus* spp. (*N. plumchrus* and *N. flemingerii*), C2–C5; *Metridia pacifica*, all copepodites; *Pseudocalanus* spp., C2–C6).

2.3. Statistics

Analysis of variance (ANOVA) was performed on both the biomass and concentration data using SYSTAT v 8.0 generalized linear model algorithms to test the null hypothesis that there were no differences among means. When a difference was detected, we performed multiple, pairwise comparisons tests using a Bonferroni correction to identify which means were significantly different.

The T/S *Oshoro Maru* biomass data, which contained no zero entries, were relatively well behaved; i.e. a logarithmic transformation ($\ln X$) of the raw data was sufficient to normalize the distribution and satisfactorily remove heteroscedasticity. Species concentration data, on the other hand, which included zero entries, violated both assumptions of the ANOVA (normality and equality of variances). Sample sizes were unequal and small (<10 in most cases). Logarithmic and 4th root transformations (Clarke and Green, 1988; Downing, 1979; Field et al., 1982) failed to satisfactorily take care of the two problems for all species. Transformations suggested by a Box–Cox analysis (Venables and Ripley, 1997) improved normality, but did not sufficiently stabilize the variances.

Heteroscedasticity is the more critical of the two assumptions for an ANOVA, so a spread vs. level plot was used to determine the best transformation to remove the trend, thus stabilizing the variance for each individual taxon (Wilkinson, 1996). Transformed concentration data were tested for equality of variance using Levene's test (Milliken and Johnson, 1992) following an ANOVA to ensure that the transformation was effective. The transformations used are reported in the figure legends (Figs. 4–7).

3. Results

3.1. Biomass

Visual examination of the T/S *Oshoro Maru* time series for the oceanic eastern Bering Sea (depth >150 m; reported by Sugimoto and Tadokoro, 1997) reveals what appear to be periods of high (late 1960s), moderate (mid-1970–1980s), and low (early 1990s) zooplankton biomass (Fig. 3A). We stratified the shelf data (depth <200 m) by these time periods and the three shelf domains (Outer, Middle, Coastal) to account for spatial and temporal variability. We compared data from those three time periods with shelf biomass data from a fourth time period (1995–1998; Fig. 3B). An ANOVA was unable to detect a significant interaction between time period and shelf domain ($P = 0.48$). The test was also unable to detect a significant difference among the four time periods ($P = 0.13$). There was, however, a significant difference in biomass among the three shelf domains ($P < 0.0006$), with the mean biomass from the Coastal Domain (LS Mean = 1.71) significantly less than that of the middle shelf ($P < 0.0004$; LS Mean 2.10), and slightly less than the outer shelf ($P = 0.11$; LS Mean = 1.96).

Summer shelf zooplankton biomass in 1997 and 1998, the years with anomalous weather patterns, did not appear to be different from the majority of years selected for inspection (Fig. 3B). Years that stand out for their high biomass (and variability) were 1967, 1979, and 1995. Mean biomass in 1968 and 1996 appeared to be lower than most other years.

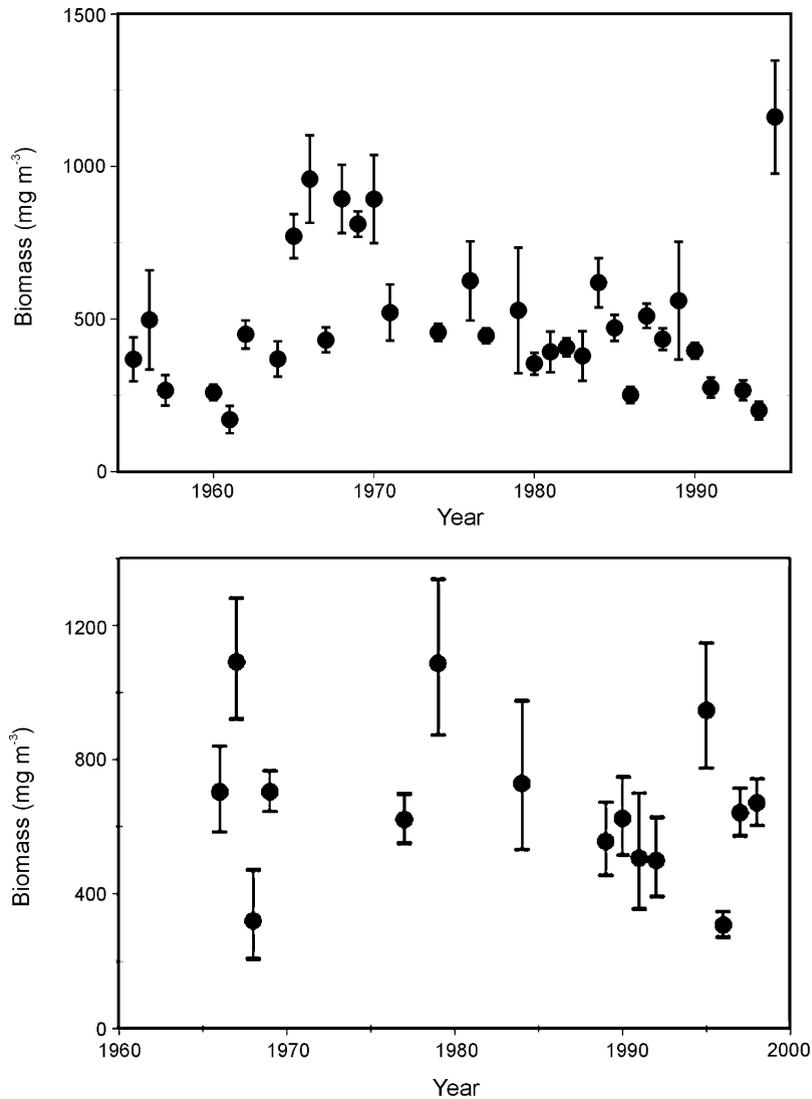


Fig. 3. T/S *Oshoro Maru* zooplankton biomass time series: (A) Annual means and standard errors of preserved wet weight from oceanic stations (> 150 m; adapted from Table 1 of Sugimoto and Tadokoro, 1997), (B) annual biomass means and standard errors at shelf stations from selected years—Group 1 = 1966–1969; Group 2 = 1977, 1979, 1984, 1989; Group 3 = 1990–1992; Group 4 = 1995–1998. Shelf means and standard errors calculated from 4th root transformed data.

3.2. Species concentrations

April 1995–1999 SEBSCC zooplankton concentration data for *Acartia*, *Calanus*, *Metridia*, and *Pseudocalanus*, from the middle shelf, and May *Acartia*, *Calanus*, *Metridia*, *Neocalanus*, and *Pseudocalanus* from the outer shelf were compared to PROBES 1980 and 1981 collections. It was

necessary to look at different months for the middle (April) and outer shelf (May) because there was only one April outer shelf station sampled in 1980 and 1981.

Over the middle shelf in April there were significant differences among years for all four taxa examined. Three of the four taxa (*Acartia*, *Calanus*, and *Pseudocalanus*) had significantly

Table 1
Results of a posteriori tests for differences among years in species concentration

Taxon	Bonferroni-corrected <i>P</i> -value for multiple comparisons	Significant differences between individual years
Middle shelf		
<i>Acartia</i> spp.	$P < 0.001$	1980, 1981 < 1996, 1997; 1980 < 1998, 1999
<i>Calanus marshallae</i>	$P < 0.001$	1980, 1981 < 1995, 1998
<i>Metridia pacifica</i> ^a	$P < 0.02$	1980 < 1998; 1981 > 1996, 1997
<i>Pseudocalanus</i> spp. ^a	$P < 0.03$	1980 < 1996, 1998, 1999
Outer domain		
<i>Acartia</i> spp.	$P < 0.002$	1980, 1981 < 1996, 1997, 1998
<i>Calanus marshallae</i>	$P < 0.001$	1980, 1981 < 1996, 1997, 1998; 1981 < 1999
<i>Metridia pacifica</i>	$P < 0.001$	1980 > 1999
<i>Neocalanus</i> spp.	$P < 0.002$	1980, 1981 < 1996; 1980 > 1999
<i>Pseudocalanus</i> spp.	$P < 0.002$	1980, 1981 < 1996, 1997

^a Failed Levene's test for homogeneity of variances.

Note that in each case ANOVA first documented significant differences among all years for each of the species-domain combinations in this table ($P < 0.05$). In the table, we report only those multiple comparisons where the concentration in recent years was significantly different than in either 1980, 1981 or both. Thus, the Bonferroni corrected probabilities are conservative because they correct for all year pairs.

lower concentrations in the early 1980s than in recent years (Table 1). *Metridia*, an outer shelf and basin species, had lower concentrations in 1980 than 1998, but was more concentrated in 1981 than either 1996 or 1997. Although the April transformed data for *Metridia* and *Pseudocalanus* failed to pass Levene's Test (see Methods), May middle shelf transformed data for the same species passed the test and the multiple comparison results for May were the same as those for April.

Acartia, *Calanus*, and *Pseudocalanus* had at least 1 year of high concentrations before 1997 and 1998 (Figs. 4A, 5A and 6A). Abundance of *Acartia* has decreased since 1996. *Calanus* and *Pseudocalanus* had opposing maxima and minima in 1995 and 1996, but their ranked order of years by concentration was exactly the same for 1997–1999.

Species collected over the outer shelf also had significant differences among years. *Acartia*, *Calanus*, and *Pseudocalanus* had the most differences between recent years and the early 1980s, with recent years having the highest concentrations (Table 1). *Metridia* had only one significant year-pair difference (1980 > 1999), and there was no clear trend for higher or lower concentrations in recent years for *Neocalanus*. As on the middle shelf, there was a least 1 year of high concentration before 1997 and 1998 (Figs. 4B, 5B, 6B and 7B),

and in all five cases there was a trend for decreasing abundance since 1996. Note that spring concentrations of *Calanus* over the outer shelf were very high in 1996 relative to other years and middle shelf concentrations. That same year (1996) had the highest concentrations of the other four taxa, as well.

3.3. Stage composition of species

We examined the percentage of individuals within selected copepodite stages among years for four of the species-domain combinations (Fig. 8). Over the outer shelf, *Neocalanus* was earlier in its ontogenetic development during 1980 and 1981 than during the period 1995–1998. During 1980 and 1981, CII and CIII copepodites constituted 50–70% of the population, while during the latter period (1995–1999) CIV and CV copepodites were 60–70% of the total by number.

The stage compositions for the remainder of the taxon-domain comparisons were highly variable from 1 year to the next. There were no consistent differences between the two time periods in the stage composition of *Pseudocalanus* over the outer shelf. Over the middle shelf, *Pseudocalanus* stage distributions were also variable among years, with the extremes being a population dominated by

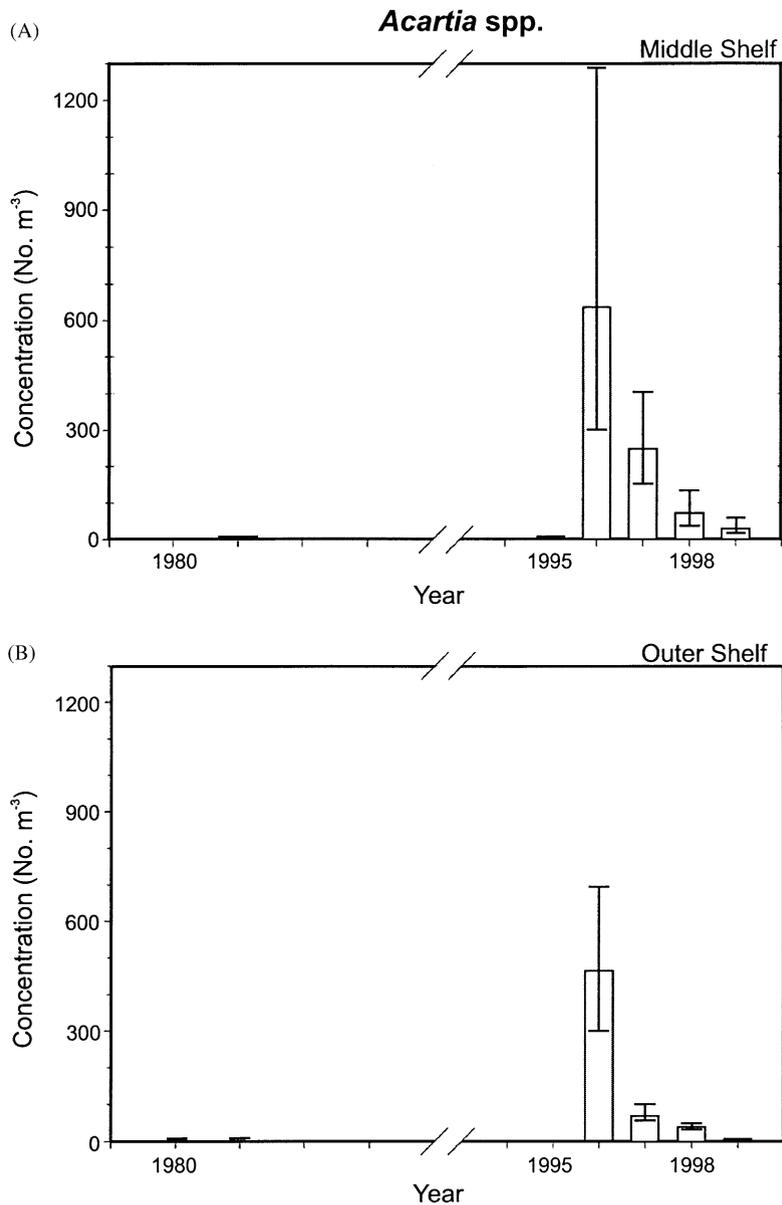


Fig. 4. Mean concentration and standard error of *Acartia* spp. in the southeastern Bering Sea. Mean and standard error were calculated using the variance stabilizing transform $Y = X^{0.11}$. (A) Middle shelf; (B) Outer shelf.

adults (1997) and a population dominated by CII + CIII copepodites (1981).

There were also no obvious patterns in the stage distribution of *Calanus* over the middle shelf between the two time periods. This was due, in part, to the very different patterns observed in

1980 and 1981 making it difficult to characterize the 1980s based on only 2 years. Adults dominated stage distributions in 3 out of 5 years in the late 1990s. The last 2 years in this data record are notable for the predominance of early copepodites.

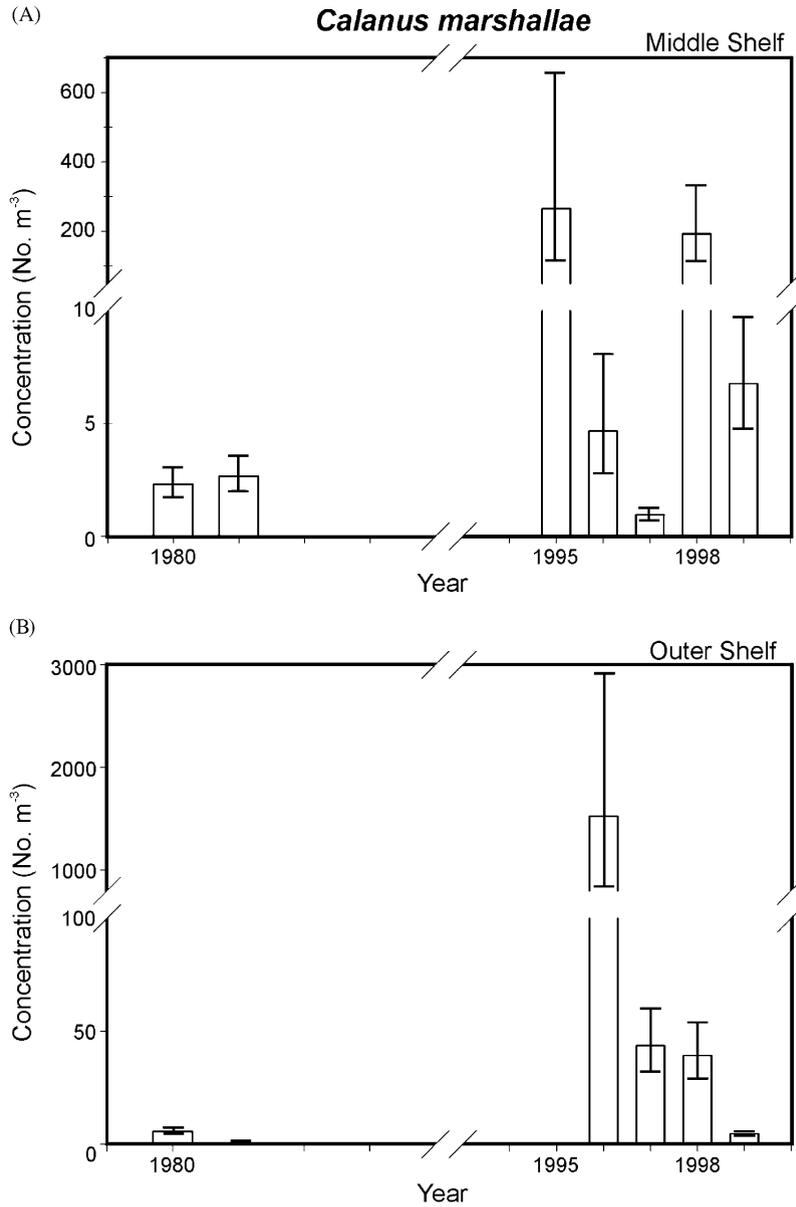


Fig. 5. Mean concentration and standard error of *Calanus marshallae* in the southeastern Bering Sea. Mean and standard error were calculated using the variance stabilizing transform $Y = X^{-(0.12)}$. (A) April, Middle shelf; (B) May, Outer shelf.

4. Discussion

Broad-scale patterns of zooplankton species distribution and abundance have been described

for the southeastern Bering Sea (e.g., Cooney and Coyle, 1982; Smith and Vidal, 1984; Vidal and Smith, 1986). Renewed attention to this marginal sea now focuses on deviations from the patterns

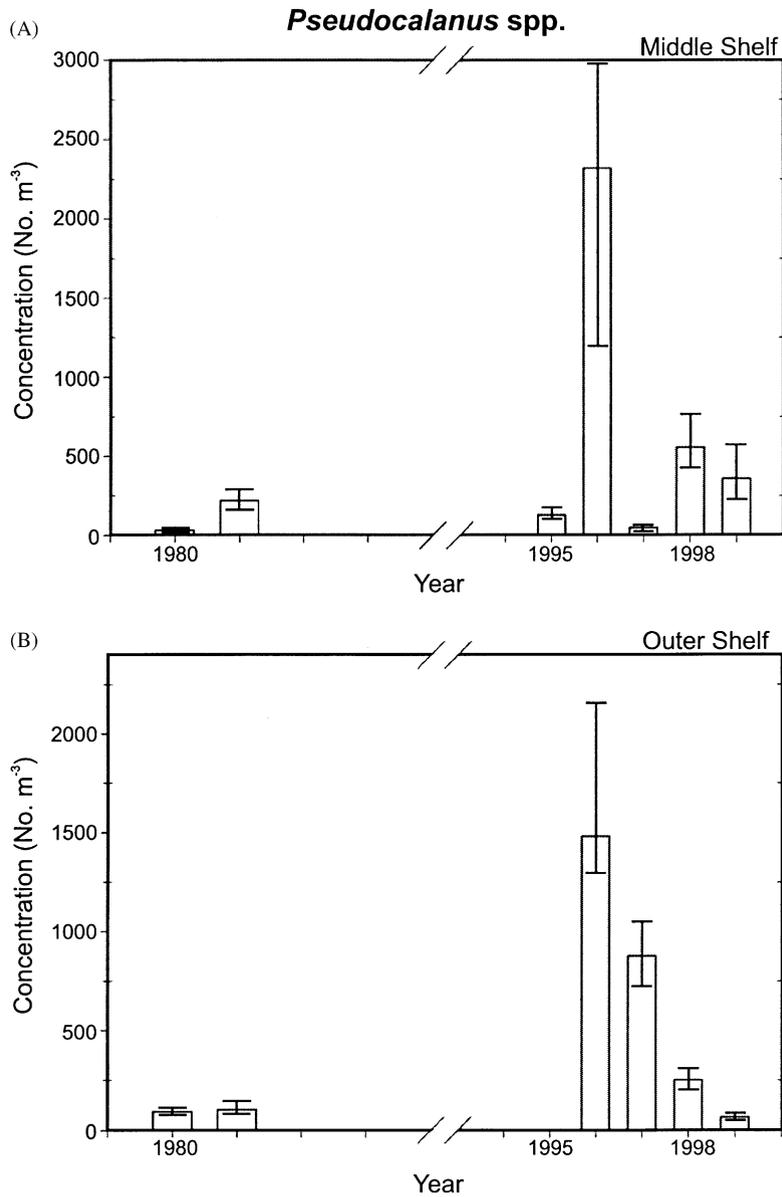


Fig. 6. Mean concentration and standard error of *Pseudocalanus* spp. from the outer shelf of the southeastern Bering Sea. Mean and standard error were calculated using the variance stabilizing transform $\ln(X + 1)$. (A) April, Middle shelf; (B) May, Outer shelf.

described in the early 1980s (e.g., Coyle and Pinchuk, 2002; Stockwell et al., 2001). The general patterns described by Cooney and Coyle (1982) and Smith and Vidal (1984) remain valid, but our

results demonstrate that for selected copepod taxa there were considerable differences among years and decades for abundance and community composition.

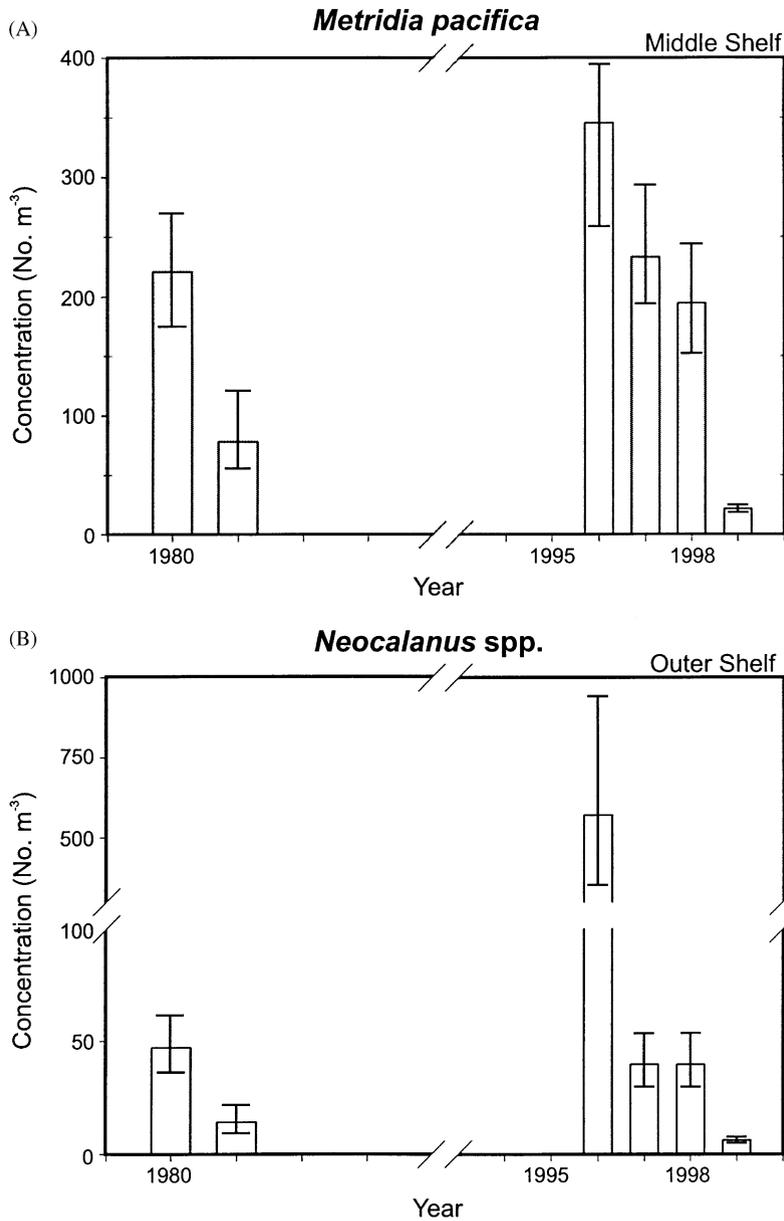


Fig. 7. Mean May concentration and standard error of outer shelf species. (A) *Metridia pacifica*. (B) *Neocalanus* spp. Mean and standard error for *M. pacifica* were calculated using the variance stabilizing transform $\ln(X + 1)$ whereas the best transform for *Neocalanus* spp. data was $Y = X^{-0.09}$.

4.1. Biomass

The biomass differences we found among shelf domains have been previously reported for the spring and summer, but for much shorter time periods (1–3 years; Smith and Vidal, 1984;

Springer et al., 1996). This report confirms the generality of that pattern and establishes it for a much longer time period (1950s to present).

The T/S *Oshoro Maru* data documented a decline in zooplankton biomass over the Bering Sea basin from the late 1960s to the early 1990s

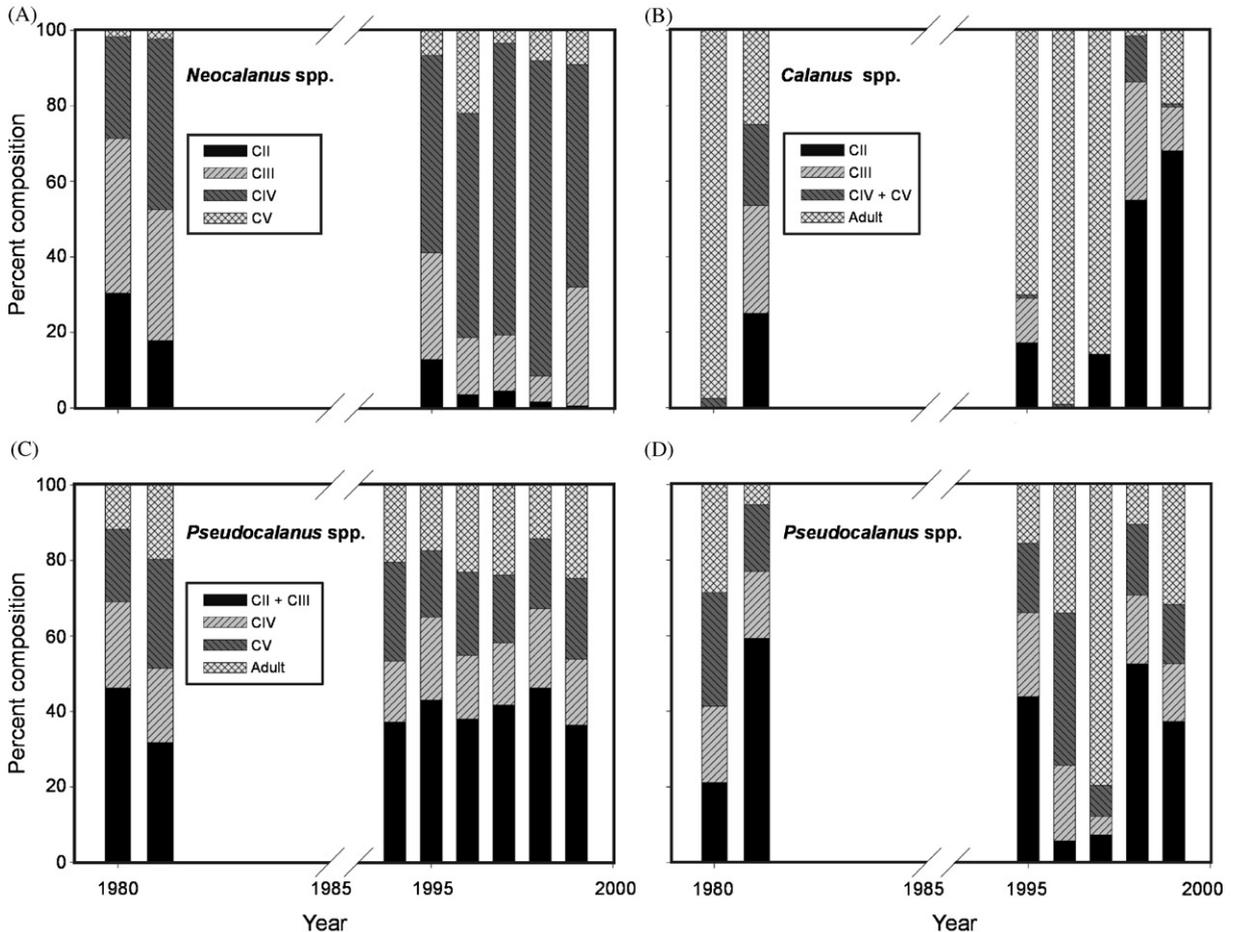


Fig. 8. April stage composition of selected copepod species by domain. Stages and stage combinations were selected to match those reported in Smith and Vidal (1986) and are different among the genera. (A) *Neocalanus* spp. sampled in April from the outer shelf; (B) *Calanus marshallae* sampled in April from the middle Shelf; (C) *Pseudocalanus* spp. sampled in April from the outer shelf; (D) *Pseudocalanus* spp. sampled in April from the middle shelf.

(Sugimoto and Tadokoro, 1997). We were unable to detect, however, any trend or differences in *shelf* zooplankton biomass among our selected time periods. Further, Hunt et al. (2002b) demonstrate that there were no detectable temporal trends in zooplankton biomass for any of the three southeastern Bering Sea shelf domains. Our inability to detect differences may be due to the inherent within-year variability in plankton biomass (Fig. 3B) combined with considerable interannual variability in the sampling effort and location of

samples (Fig. 1). In certain years there was little or no sampling on the shelf (Fig. 1B). Mackas (1995) determined that time-series analysis of zooplankton abundance anomalies for the British Columbia (Canada) coastal region required a substantial number of samples (> 16–25) to detect a 2–3 fold difference in interannual variations given the inherent variance of samples from that region. In most years, the number of T/S *Oshoro Maru* biomass samples (as well as the species abundance samples reported here) was well below that criterion.

4.2. Species concentrations

Our results document statistically significant increases in spring copepod concentrations between the early 1980s and the late 1990s. These taxa (*Acartia*, *Calanus*, *Pseudocalanus*) are important in the trophic ecology of the middle and outer shelf (Cooney and Coyle, 1982; Walsh and McRoy, 1986). Alternative explanations may exist for the results: (1) phytoplankton clogging of the fine mesh MOCNESS nets used in the early 1980s may have resulted in low catches; (2) differences in species concentrations among years reflects a difference in the timing of the spring zooplankton population increase, rather than an increase in absolute magnitude (e.g., Mackas et al., 1998); (3) the differences are due to a change in geographic distribution, rather than abundance of the dominant zooplankton taxa. We discuss the first alternative explanation below and the second in the section on stage composition. We do not discount the third alternative, but cannot address it due to the limited geographical extent of our sampling.

We do not believe that the lower species concentrations in the early 1980s relative to the late 1990s were due to net clogging. PROBES investigators were aware of the potential for net clogging. They quickly retrieved the two surface MOCNESS nets to reduce the filtered volume and prevent or minimize net clogging (Smith, Univ. Miami, pers. comm.). In addition, the April 1980 PROBES data used here were collected before the height of the spring phytoplankton bloom (May 16–17) when large diatoms dominated the phytoplankton community (Kocur, 1982). The data used for the outer shelf comparisons were close to the time of maximal cell concentration. In addition, *Phaeocystis pouchetti* concentrations were high at the outer shelf station (Station 8) in 1980 ($4.9 \times 10^6 \text{ ml}^{-1}$), but were inconsequential in 1981 (Kocur, 1982). Note that Stockwell et al. (2001) also concluded that recent species concentrations were higher in June 1997 than 1981 over the Middle Shelf and Coastal Domains for the month of June. It is unlikely that the June PROBES samples suffered from net clogging. Thus, we believe that the increased concentration of selected

zooplankton taxa (this work and Stockwell et al., 2001) were pervasive events.

4.3. Stage composition

An alternative interpretation for the observed increased concentrations of taxa between the two time periods (early 1980s vs. late 1990s) is that the population size did not increase only the timing of population growth. That is, the egg production and mortality rates for the taxa were relatively constant between the two time periods, but timing of egg production was later or rate of development was slower in the 1990s than the early 1980s. Similar stage compositions (or no consistent differences in some cases; Fig. 8) between the two time periods for many of the taxa suggest that the recent higher concentrations were in fact real and not due to a uniform shift in the timing of development of these populations.

Examination of the stage composition of selected species among years revealed a recent shift towards earlier predominance of CV *Neocalanus*. This also has been described for the central Gulf of Alaska where the shift was strongly correlated with large-scale interannual and decadal ocean climate fluctuations (Mackas et al., 1998). The change in development rate in the Gulf was too large to be exclusively the result of temperature-dependent physiological processes, so Mackas et al. (1998) hypothesized that it was the result of interannual differences in survival between early vs. late fractions of an annual cohort. It is remarkable that the southeastern Bering Sea shelf and Gulf of Alaska oceanic populations of *Neocalanus* show the same temporal shift in stage composition (i.e. later stages now more prevalent than before for the same calendar dates). Further investigation is warranted to examine if the coastal Gulf of Alaska and oceanic Bering Sea basin populations of *Neocalanus* are behaving similarly.

4.4. Zooplankton responses to temporal variability—interannual period

The Bering Sea ecosystem rapidly responds to climatic events (Napp and Hunt, 2001). We expected to see a response by the zooplankton

community to the anomalous climatic events of 1997 and 1998. We hypothesized that there would be elevated zooplankton biomass and concentrations relative to previous years due to the increased spring new production (Rho, 2000) and warmer seawater temperatures (Stabeno et al., 2001). We were unable to detect, however, differences in zooplankton biomass among recent years (Fig. 3B). The *Oshoro Maru* estimates of summer zooplankton biomass in the years in 1997 and 1998 were not different from adjacent years or selected years in previous decades (Fig 3B). Thus, we reject the hypothesis that the anomalous climatological, physical and biological (e.g., coccolithophore bloom) events of 1997 and 1998 had a discernable impact on zooplankton biomass. This result does not preclude the possibility of substantial affects on particular species in the zooplankton community. Variations in total biomass in response to oceanographic conditions can be much less (and harder to detect) than variations in responses by individual species or functional groups (Mackas et al., 2001).

With respect to differences in individual species, our observed concentrations of selected copepod taxa before the atmospheric and upper ocean anomalies (1994–1996) were as high or higher than the concentrations during and after the event which began in May 1997. Thus, there remains considerable question as to whether elevated concentrations of numerically dominant copepods observed in the summers of 1997 and 1998 (Stockwell et al., 2001) were due to the proximate anomalies (Overland et al., 2001; Stabeno et al., 2001) or to longer-period phenomena.

4.5. Zooplankton responses to temporal variability—decadal period

Long-term trends in plankton biomass and species composition are observed in the North Atlantic and the northeast Pacific Oceans. For example, in the northeastern Atlantic, the NAO is hypothesized to affect local weather conditions and the timing and magnitude of the spring phytoplankton bloom (Mann and Lazier, 1996). The NAO is also hypothesized to affect the biomass of *Calanus finmarchicus* in the north-

eastern and northwestern sectors (Heath et al., 1999; Greene and Pershing, 2000).

In the northeast Pacific Ocean, regime shifts are recognized as major low-frequency events determining biomass levels and species distributions (e.g., Brodeur and Ware, 1992; Hollowed and Wooster, 1995; Francis et al., 1998; Hare et al., 1999; Hare and Mantua, 2000). The eastern Bering Sea, however, appears to respond on decadal, rather than multi-decadal periods as in the North Pacific Ocean (Bond and Adams, 2002). With the exception of the T/S *Oshoro Maru* data, the Bering Sea shelf, unlike other parts of the northeast Pacific (McGowan et al., 1998), lacks long-term plankton data sets necessary to test hypotheses regarding the linkages between climate and biology. Sugimoto and Tadokoro (1997) concluded that the interannual variability of oceanic zooplankton in the Bering Sea basin was controlled by predation from pink salmon, while longer (decadal) trends were most heavily influenced by bottom-up processes.

Our result (no difference in shelf zooplankton biomass among time periods) is somewhat surprising. Regime shifts are reported to have occurred in 1977 and 1989 (Hare and Mantua, 2000). Recent observations of a shift in foraging grounds for baleen whales from the southeastern Bering Sea shelfbreak to the middle shelf (Tynan et al., 2001) also suggest a change in the carrying capacity of the shelf. We only examined copepods with our species concentration data, and not other important taxa (e.g., euphausiids, chaetognaths, pteropods, or gelatinous zooplankton), so one might argue that a higher proportion of the production may have shifted to copepods in the late 1990s at the expense of these other groups. Euphausiid densities were low in 1997 and 1998 (Coyle and Pinchuk, 2002; Stockwell et al., 2001), but they were not significantly different from early summer concentrations in 1981. Concentrations of large scyphomedusae increased dramatically in the early 1990s (Brodeur et al., 1999), but concentrations of planktivorous fishes have decreased (Hunt et al., 2002b).

The observed trends of recent increases of copepod species over the southeastern Bering Sea shelf occurred during the same time period when

northern boreal shelf copepod species off the coast of North America were being replaced by temperate species with southern affinities (Peterson, 1999; Mackas et al., 2001). Mackas et al. (2001) demonstrate that plankton communities were responding to changing current patterns along the west coast. The eastern Bering Sea is far removed from the transition between temperate and boreal biogeographic provinces, and it receives only a small fraction of its water from the Alaska Coastal Current (Stabeno et al., 2002). It is much more likely that if these events are linked, it is through the atmosphere, rather than through oceanic (advective) teleconnections (e.g., Overland et al., 2001).

4.6. Control of Bering Sea zooplankton populations

The Oscillating Control Hypothesis (Hunt et al., 2002b) proposes that long-term climate forcing determines the structure and function of the southeastern Bering Sea shelf ecosystem. In other ecosystems, control of zooplankton production may be predominantly bottom-up (Aebischer et al., 1990), top-down (Shiomoto et al., 1997; Reid et al., 2000) or some combination of both processes (Verity and Smetacek, 1996; Sugimoto and Tado-koro, 1997; Verheye and Richardson, 1998). In the southeastern Bering Sea it is hypothesized to oscillate between the two, sometimes showing evidence for both mechanisms as the system transitions from one climate regime to the next (Hunt et al., 2002b).

The Bering Sea has recently been in a “warm phase” where diminished influence of sea ice and cold winters make it more likely that pelagic primary production increases and remains in the water column rather than sinking to the benthos (Hunt and Stabeno, 2002; Hunt et al., 2002b; Tynan et al., 2001). Most, but not all, evidence supports the claim of increased primary production, enhanced water-column utilization of new production, and increased secondary production. Although isotopic analyses of whale baleen suggests a 30–40% decline in seasonal carbon fixation in the northern Bering Sea between 1966 and 1997 (Schell, 2000), estimates of new production (from nutrient draw-down) and stable isotope

analyses of biogenic sediment suggest increasing nutrient availability (1999 > 1998 > 1997; Smith et al., 2002) and new production in 1997 and 1998 that was 30% higher than during PROBES (Rho, 2000). In addition, demersal fish populations (fed, in part, by benthic infauna that require detrital rain of pelagic production) have been increasing (Hunt and Stabeno, 2002; Hunt et al., 2002b; Livingston et al., 1999). These observations suggest increasing rather than decreasing production.

In addition to food availability, temperature can be an important variable regulating zooplankton growth and production (Corkett and McLaren, 1978; Huntley and Lopez, 1992). Spring and summer atmospheric NP pattern modes contributed to anomalously high pressure over the Bering Sea and Alaska during the 1990s resulting in warmer air temperatures (Bond and Adams, 2002). These warmer air temperatures have led to warmer summer water temperatures. Micro- and meso-zooplankton with low maximum food rations can be expected to respond with faster developmental rates and shorter generation times. *C. marshallae*, which in the Bering Sea normally has only one generation per year, was observed to have two generations in a year characterized by a warm summer (Smith and Vidal, 1986). Conversely, low water column temperatures and low copepod biomass in the spring of 1999 led to estimates of secondary production that were only 3–4% of the estimated production in the previous two (warm) springs, 1997 and 1998 (Coyle and Pinchuk, 2002).

Predators also may have a large impact on zooplankton biomass, potentially masking changes in secondary production. Some predators of zooplankton also have increased in recent years (jellyfish, Brodeur et al., 1999; chaetognaths, Baier and Terazacki, unpublished), while others (forage fish) have decreased (Hunt and Stabeno, 2002; Hunt et al., 2002b). Age-0 pollock, which can deplete their zooplankton prey resource around the Pribilof Islands (L. Ciannelli, pers. comm.), can be as abundant along the 1000-km-long inner front of the southeastern Bering Sea shelf as they are around the Pribilof Islands (Coyle and Pinchuk, 2002). Predation pressure from recent increases in large marine mammals, and a shift in

their foraging habitat (Tynan et al., 2001), may also directly and indirectly (Atkinson et al., 1999) exert influence on the mesozooplankton biomass.

Our data do not allow us to distinguish among different alternatives for a single control mechanism for zooplankton production in the Bering Sea. In fact, there is evidence to suggest that the primary mechanism is not static, but oscillates between control from above and control from below as the climate state of the southeastern Bering Sea changes (Hunt et al., 2002b). Regardless of the causative mechanism, our results, as well as those of many other investigators, point to the critical need for long-term observations of the Bering Sea ecosystem. A firmly established program for long-term observations would ensure that: (1) we can test our hypotheses about the mechanisms of population and ecosystem control; (2) we can correctly identify when changes will occur; (3) we can predict their impact on this resource-rich ecosystem.

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