The Rise and Fall of Zooplankton Populations in Recent Decades on the SE Bering Sea Shelf - Bottom-Up and Top-Down Control of Two Copepod Genera

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Introduction

For 10 years we have participated in research on the eastern Bering Sea shelf ecosystem to learn about physical and biological mechanisms that affect the survival of the early life history stages of pollock (*Theragra chalcogramma*). The ultimate goal is to predict recruitment strength of future year classes with a known level of uncertainty. In the process, we studied the pelagic ecosystem of the shelf to determine how physics and biology interact to affect plankton production and pollock prey availability. We have also observed and will begin to calculate how biology affects top-down forcing on plankton populations. For this poster we compare zooplankton biomass and species abundance data collected from the southeast Bering Sea Middle Shelf Domain to examine temporal trends in relation to environmental variability. Summer zooplankton biomass (wet weight) data were collected by the Hokkaido University from the T/S Oshoro Maru between 1955 and 1999. Species concentration data for dominant copepod taxa (*Acartia* spp., *Calanus marshallae*, and *Pseudocalanus* spp.) were obtained from PROBES (1980 & 1981; Processes and Resources of the Bering Sea Shelf; Smith, and Vidal, 1986), BS FOCI (Bering Sea Fisheries Oceanography Coordinated Investigations), and SEBSCC (Southeast Bering Sea Carrying Capacity) for 1995-1999.

Conclusion

The Oscillating Control Hypothesis (Hunt *et al*., submitted; Hunt, S10-014) provides a framework for discussion of what controls the pelagic ecosystem of the southeastern Bering Sea. The hypothesis states that control from below dominates during cold regimes, control from above is prevalent during warm regimes, and there is a temporary decrease in predation pressure on zooplankton following a shift from a cold, to warm regimes. Recent programs (BS FOCI, SEBSCC, and Inner Fronts) have greatly increased our knowledge of climate control of bottom-up processes, but we are relatively ignorant of natural mortality rates. We need to know how top-down and bottom-up processes simultaneously act on zooplankton to limit their production and standing stock. Too often we focus on only one mode of control for pelagic populations. In reality, populations are simultaneously affected by processes influencing both their birth and death rates (e.g. Ohman and Hirche, 2001).

Point #1

A Contradiction In Our Zooplankton Data?

We were unable to find a statistically significant temporal trend in the T/S Oshoro Maru data (Fig. 1A; Hunt *et al*., submitted; Napp *et al*, accepted). There are, however, statistically significant differences in the concentrations of copepod taxa between the mid to late 1990s and the early 1980s (Fig.1b & c, and Table 1). We do not feel these two results contradict each other; it is possible for a bulk property (zooplankton biomass) to remain constant over time while individual components (concentration of particular taxa) change.

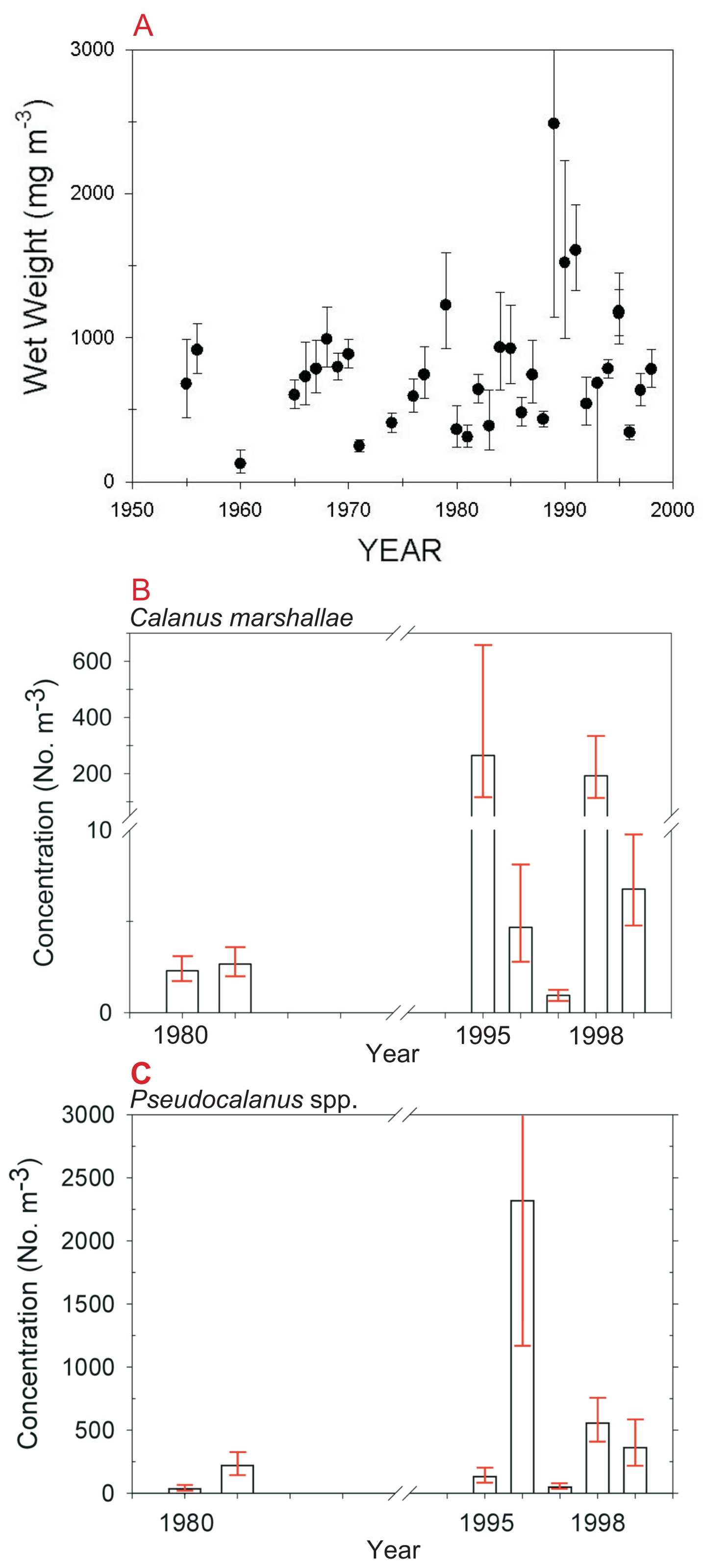

Figure 1. Mean (± SE) of zooplankton biomass and concentration from the southeast Bering Sea shelf. A) Summer zooplankton biomass; B) April *C. marshallae* concentrations; C) April *Pseudocalanus* spp. concentrations.

Table 1. Results of *a posteriori* tests for differences among years in species concentration during spring. ANOVA first documented significant differences among all years ($P < 0.05$). We report only those comparisons where concentration in recent years is significantly different than in either 1980, 1981 or both. Bonferroni corrected probabilities are conservative because they correct for all year pairs.

Taxon	Bonferroni-corrected P-value for multiple comparisons	Significant Differences Between Individual Years
Acartia spp.	$P < 0.001$	1980, 1981 < 1996, 1997; 1980 < 1998, 1999
Calanus marshallae	$P < 0.001$	1980, 1981 < 1995, 1998
Pseudocalanus spp.	$P < 0.03$	1980 < 1996, 1998, 1999

Point #2

Environmental Variability Affects Bottom-up Processes For Some Species More Than Others.

The Bering Sea shelf ecosystem rapidly responds to atmospheric forcing (Napp and Hunt, 2001). One important mechanism for such forcing is changes in the latitudinal extent and duration of sea ice (e.g. Napp *et al*., 2000; Wyllie-Echeverria and Wooster, 1998). There was a tendency for later arrival of ice and a shorter duration from 1975 to 1998 that appeared to reverse in 1998 (Fig. 2; Hunt *et al*., submitted). The arrival of sea-ice affects the timing, magnitude, and duration of the spring phytoplankton bloom (Hunt *et al*., submitted; Stabeno *et al*., 2001).

C. marshallae and *Pseudocalanus* spp. populations may respond differently to the environmental effects of sea ice. *C. marshallae* begins reproduction before the spring phytoplankton bloom and copepodites appear to be recruited over a relatively short duration, mainly during the bloom (Fig. 3; Baier and Napp, submitted). In contrast, *Pseudocalanus* spp. reproduces continuously through the spring and summer (e.g. Dagg *et al*., 1984). Also the development of *Calanus* is slower and more affected by cold temperatures than is *Pseudocalanus* (Fig. 4). Thus *Calanus* populations are likely more susceptible than *Pseudocalanus* to variability in bottom-up processes driven by sea-ice fluctuations.

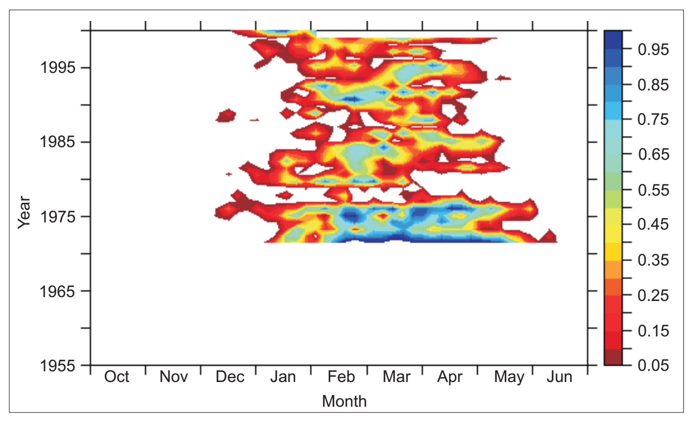

Figure 2. Percent concentration of sea-ice cover over the eastern Bering Sea shelf between 57 and 58°N

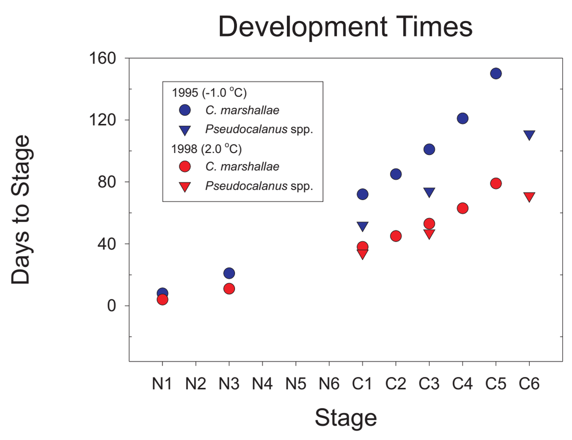

Figure 4. Estimated time of temperature-dependent development of *Calanus* and *Pseudocalanus* at two temperatures. Belehrádek's temperature-dependent growth function was used for both taxa (*C. finmarchicus*, R. Campbell and E. Durbin, unpublished; *Pseudocalanus* spp., Corkett and McLaren, 1978).

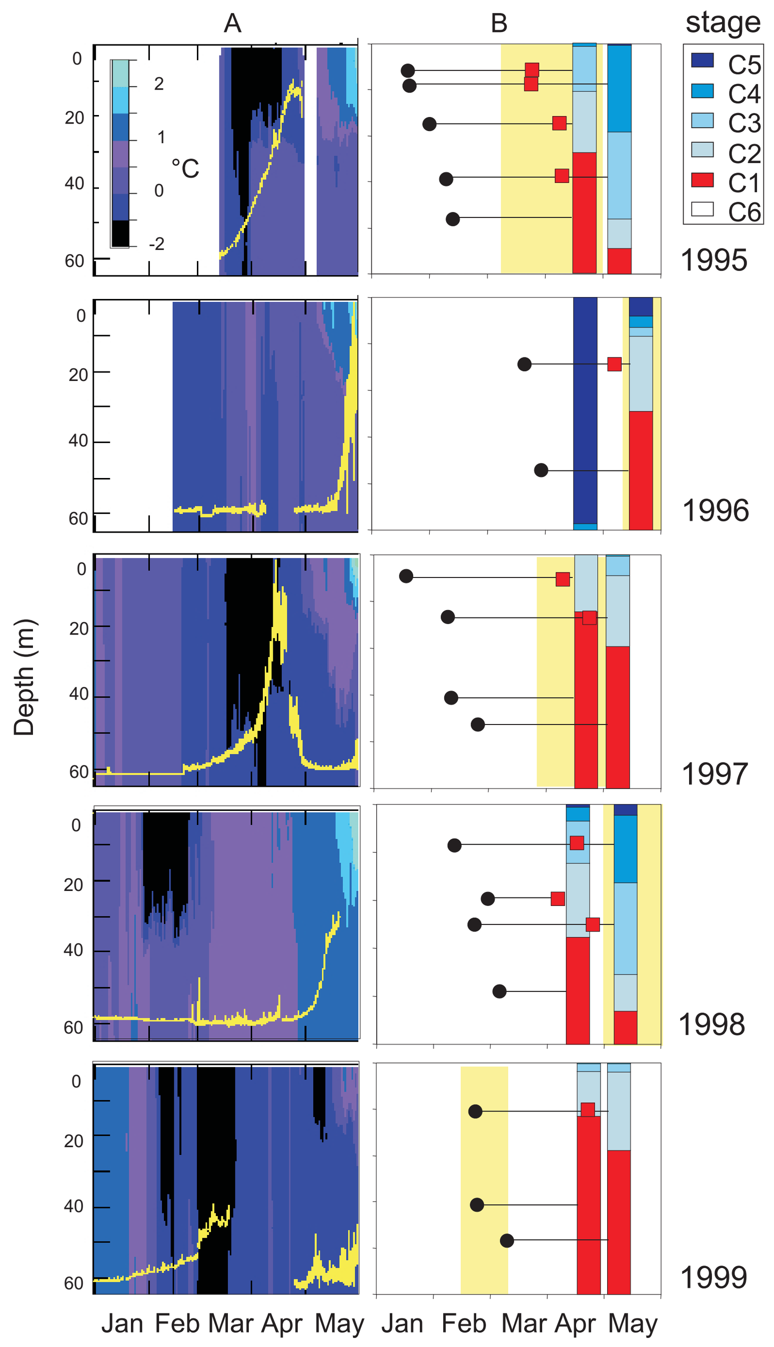

Figure 3. Development of SE Bering Sea Middle Shelf *C. marshallae* copepodite populations (Baier and Napp, submitted). (A) Time series of water column temperature and fluorescence measured at a Middle Shelf mooring (modified from Stabeno *et al*., 2001). Ice was present when the coldest temperatures were measured (black); white areas signify no data. Chlorophyll fluorescence (yellow line) was measured at approx. 10 m and was normalized to the maximum fluorescence measured for that year. (B) Percent composition and estimated development chronology for copepodites sampled in April and May. Time to C1 and egg stages were backcalculated using Belehrádek's temperature-dependent growth function, parameterized for *C. finmarchicus* (R. Campbell and E. Durbin, unpublished). Horizontal lines pointing to stages sampled in April and May identifies estimated time at egg stage (black dot) and C1 (red square) for that stage, respectively.. For example, we estimate that C2 sampled in late April 1995 were hatched in late January and molted to C1 early April.

Point #3

Pinpointing Bottlenecks In Top-down Control Is A Difficult, Multi-variate Problem As There Are Many Predators For Each Prey Type.

Several important predators of copepods have shown a trend of increasing abundance in recent years. Scyphomedusae (jellyfish) biomass dramatically increased in 1990 (Fig. 5; Brodeur *et al.,* 1999). Chaetognaths are more abundant than they were in the early 1980s (Fig. 6). Increased foraging activity of planktivorous marine mammals on the southeast Bering Sea shelf has been observed (Tynan, submitted). *Calanus* and *Pseudocalanus,* however, do not show the corresponding decline in concentration we would expect if secondary production remained constant (compare Figs 5 & 6 with Figs. 1b & c). Other vertebrate predators such as forage fish (e.g. age-0 Walleye pollock, *Theragra chalcogramma*) would also be expected to impact plankton populations. Bio-energetics models reveal that it is possible for age-0 pollock to locally deplete their copepod prey resources, particularly in areas of high juvenile fish abundance (Ciannelli *et al*. in prep.). Abundance of age-0 pollock in the southeastern Bering Sea shelf has been sampled in recent years, and there is some indication that years of high summer abundance of juveniles are followed by years of lower *Calanus* and *Pseudocalanus* concentrations (compare Fig. 7 with Fig. 1b & c).

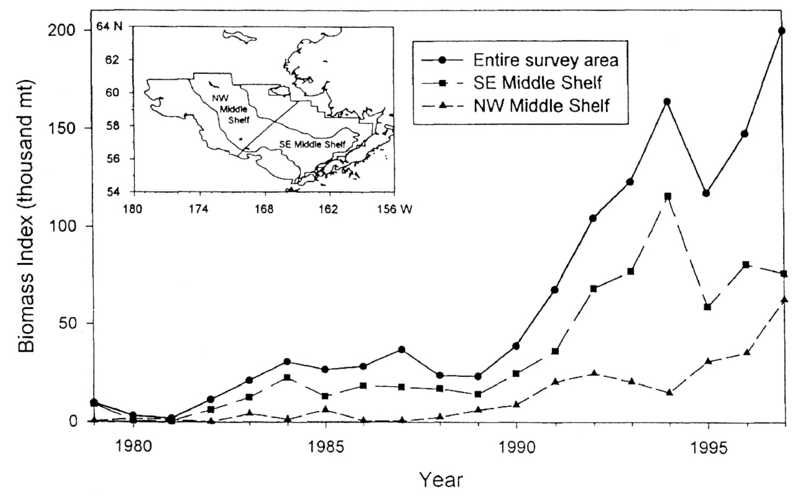

Figure 5. Time series of scyphomedusae biomass from the eastern Bering Sea (Brodeur *et al*., 1999).

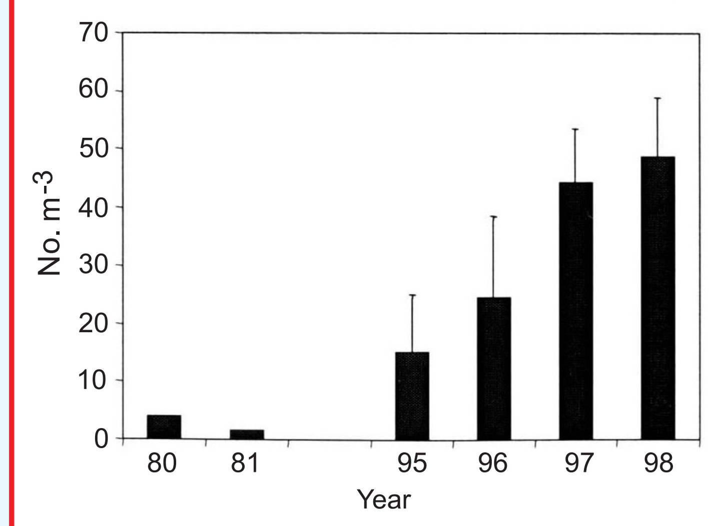

Figure 6. Mean (±SE) May concentrations of chaetognaths.

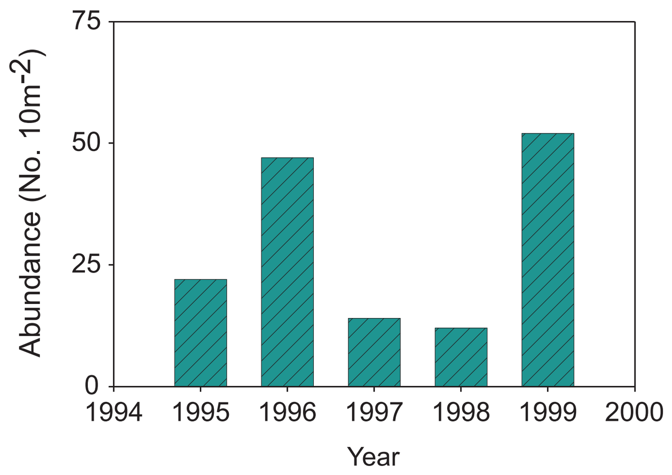

Figure 7. Summer rough counts of age-0 pollock captured during collaborative cruises on the T/S Oshoro Maru (Hokkaido University). Approximately 20 - 30 stations were sampled each year over the Outer and Middle Shelf Domains between Unimak Pass and the Pribilof Islands.

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