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Interannual variability in a predator–prey interaction: climate, chaetognaths and copepods in the southeastern Bering Sea

C. T. BAIER[1]* AND M. TERAZAKI[2]

[1]NOAA/NMFS/AFSC, 7600 SAND POINT WAY, NE. BIN C 15700, SEATTLE, WA 98115-0070, USA AND [2]OCEAN RESEARCH INSTITUTE, THE UNIVERSITY OF TOKYO, 1-15-1 MINAMIDAI, NAKANO-KU, TOKYO 164-8639, JAPAN

*CORRESPONDING AUTHOR: Christine.Baier@noaa.gov

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The interaction of the chaetognath Sagitta elegans with the copepod community of the southeast Bering Sea middle shelf was examined in relation to environmental conditions during 1995–1999. Predation impact was estimated for 2 years, 1995 and 1997, using gut content analysis, experimentally derived digestion time (DT) and abundances of chaetognaths and prey. Pseudocalanus concentrations correlated with water temperature and Calanus marshallae with sea ice extent. Sagitta elegans were less abundant but individuals were larger in 1995, when C. marshallae predominated, compared to 1997, when Pseudocalanus and Acartia were the primary prey. Predation by S. elegans removed <1% standing stock day^{-1} of Pseudocalanus or C. marshallae in 1995 and 1.7 to 2.3% of Pseudocalanus in 1997. The percent of the copepod community biomass required by chaetognaths was estimated to be <1% in 1995 compared with 8–12% in 1997. Calanus marshallae may be more vulnerable than Pseudocalanus to cumulative predation effects because of its reproductive strategy. The effect of chaetognath predation on the copepod community depends on which copepod species is predominant and its susceptibility to cumulative predation effects, as well as on daily predation impact, both of which varied between years with different climatic conditions.

INTRODUCTION

The southeast Bering Sea shelf is a highly productive region that supports an abundance of life, including marine mammals, seabirds and commercially important fish. The middle shelf in particular is an important habitat for larval and juvenile fish, which provide forage for higher trophic levels (Napp *et al.*, 2000). The Bering Sea is a high latitude sea and a marginal ice zone, subject to great seasonal and interannual fluctuations in environmental conditions. Sea ice dynamics dominate spring physical processes over the shelf. Sea ice is not formed *in situ* but is formed in the northeast and pushed onto the southeast shelf by winds (Stabeno *et al.*, 1998). Its presence, extent and persistence are highly variable. Sea ice dynamics directly affect the spring phytoplankton bloom: the bloom occurs early in association with sea ice in March or April but is delayed until the water column stratifies in May or June if ice retreats early or is absent (Stabeno *et al.*, 2001). Climatic variability during 1995–1999 was exceptional, spanning the range of ice extent and water temperature conditions observed over the southeast Bering Sea shelf during the past three decades (Wyllie-Echeverria and Wooster, 1998; Baier and Napp, 2003).

Understanding how copepod populations are affected by climatic variability is an important step towards understanding the mechanisms that link climate and higher trophic levels. Recent attention has focused on the importance of predation mortality on copepod populations (Eiane *et al.*, 2002; Hirst and Kiørboe, 2002). Chaetognaths are abundant carnivores that feed on a variety of zooplankton and fish larvae, but their main

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prey are copepods (Feigenbaum and Maris, 1984). Several studies have shown that chaetognath predation can significantly affect populations of copepods (Szyper, 1978; Kimmerer, 1984; Stuart and Verheye, 1991). For example, Sameoto (Sameoto, 1973) estimated that *Sagitta elegans* consumed 36% of annual secondary production in Bedford Basin, making them the most important copepod predators there. Chaetognaths dominate the zooplankton biomass over the southeast Bering Sea inner shelf in late spring (Coyle and Pinchuck, 2002) and around the Pribilof Islands in late summer (Schabetsberger *et al.*, 2000; Ciannelli *et al.*, 2004). Smith and Vidal (Smith and Vidal, 1986) found higher abundances of *S. elegans* in a cool year (1980) compared with a warm year (1981) and suggested that higher predation by chaetognaths as well as lower temperatures may have contributed to reduced numbers of small copepods over the middle shelf in 1980. Kotori (Kotori, 1976) estimated that the average abundance of *S. elegans* on the eastern Bering Sea shelf was 25 m^{-3}, accounting for 0.4–60.5% of the total zooplankton biomass in summer, and the carbon requirement of the chaetognath community was 10% of secondary productivity. However, to our knowledge there have been no quantitative studies of chaetognath predation over the southeast Bering Sea shelf.

The present article builds upon a study of climate-induced variability in populations of the copepod *Calanus marshallae* in the southeast Bering Sea (Baier and Napp, 2003). Here we examine the interaction of a predator, *S. elegans*, with the copepod community during years (1995–1999) with different climate conditions. Abundances of chaetognaths and the dominant copepod species on the middle shelf were estimated during April and May of these years. Seasonal dynamics of chaetognaths and their copepod prey were examined during February–September 1998 and 1999. Diel feeding patterns were examined using data collected in May 2000. We quantified the effects of predation by the chaetognath *S. elegans* on copepods during April and May of 1995 and 1997.

METHOD

Environmental sampling

Environmental variables including mean water temperature at 20 m, timing of the phytoplankton bloom, mean summer shelf bottom temperature and sea ice extent were compared with patterns of zooplankton abundance. Average water column temperature from CTD profiles at each station where chaetognaths were collected for feeding rate (FR) estimation were used in digestion and FR calculations. The mean temperature at 20 m depth was measured from March 14–April 30, during which period temperature changed little and the water column was well mixed; this measurement was intended to approximate that which zooplankton were exposed to during their development prior to our May sampling. These data and the timing of the bloom onset were obtained from a subsurface biophysical mooring that was deployed in February of each year at Site 2 (Stabeno *et al.*, 2001) (Fig. 1). Water temperature was measured with either Seacat SBE 16-03 sensors or Miniature Temperature Recorders (MTR). WetLabs fluorometers at depths of 5–11 m generated a time series of fluorescence used to determine the timing of the spring phytoplankton bloom (Hunt and Stabeno, 2002). Mean summer shelf-bottom temperature, which reflects conditions during the previous winter, was measured using temperature recording devices mounted on the head rope of bottom trawl gear, deployed during annual Alaska Fisheries Science Center bottom trawl surveys of about 350 stations over the southeast Bering Sea shelf. The bottom trawl station grid extended from 54.6° N to 61° N latitude and covered the outer and middle shelf domains; only middle shelf temperatures were used in our study (G. Walters, Seattle, personal communication). Ice cover along longitude 169° W was digitized from weekly National Oceanic and Atmospheric Administration (NOAA) ice charts (S. Salo, Seattle, personal communication).

Zooplankton collections

Zooplankton collections were made on the southeastern Bering Sea middle shelf (Table I; Fig. 1). Samples were collected and experiments were conducted aboard the RV *Miller Freeman*. Zooplankton samples for interannual comparisons were collected in April and May 1995–1999 using bongo or Tucker trawl (1996 only) tows. Additional samples collected in February, July and September 1998 and February and September 1999 were examined for seasonal patterns of abundance and copepod stage composition. At each station, temperature was sampled using a SeaBird 911+ CTD; these data were averaged over the depth of the water column. Bongo samplers were 60- and 20-cm diameter frames fitted with 333- and 153-μm mesh nets, respectively. The 20-cm bongo was attached to the towing wire 1 m above the 60-cm frame (Incze *et al.*, 1997). A SeaCat CTD was located 1 m above the 20-cm frame to supply real-time measurements of net depth. Double oblique tows were made ~5–10 m above the bottom, at a speed of 2 knots with tow durations ranging from 6 to 9 min. Calibrated flowmeters were used to estimate the volumes filtered by each net. Clarke-Bumpus nets (153-μm mesh) were nested inside each 1-m^2 Tucker trawl net (333-μm mesh). The trawl was towed from 5 m off the bottom to the bottom of the thermocline (net 1) and from

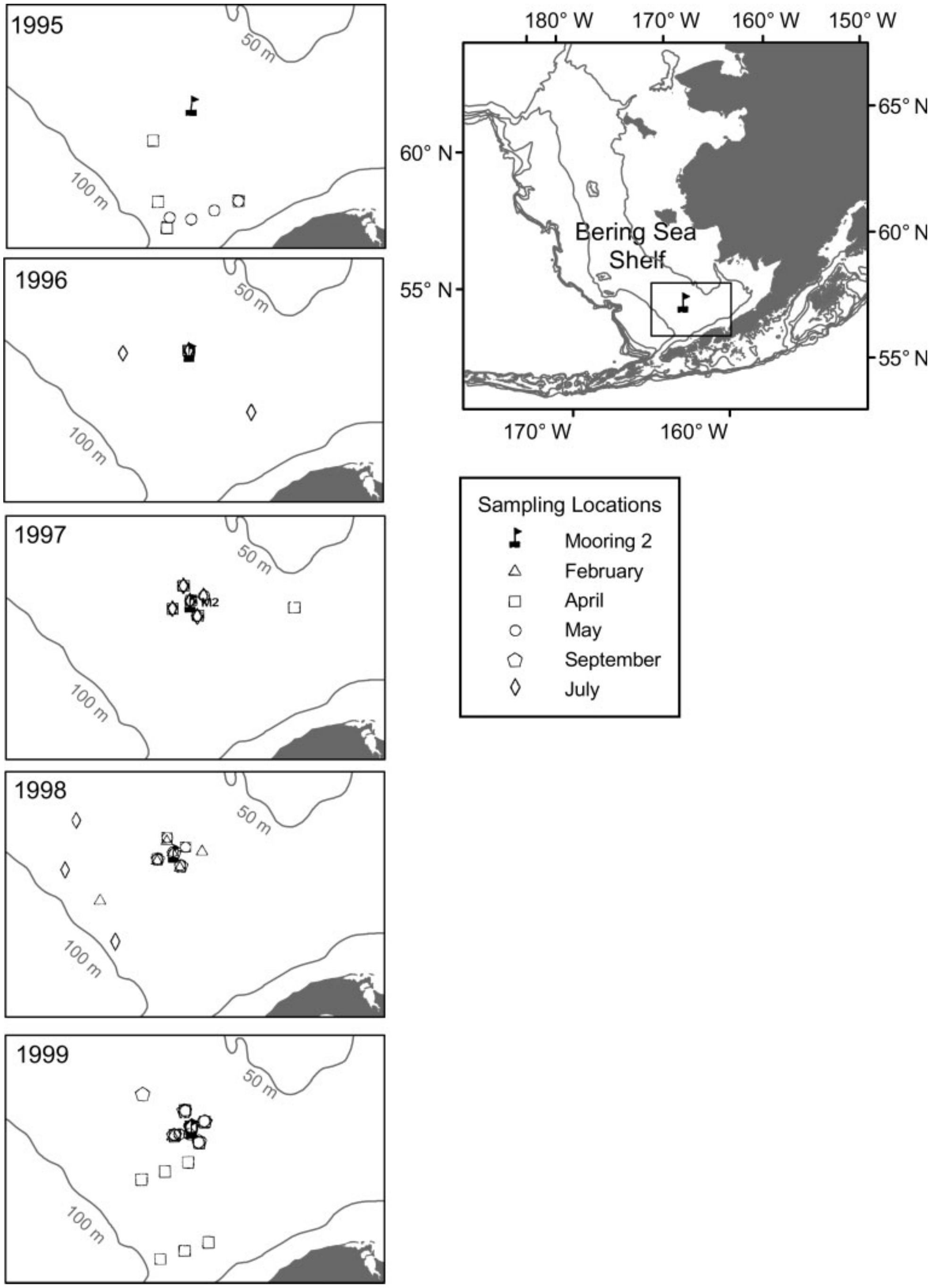

Fig. 1. Locations of moored sensors (mooring 2) and zooplankton/CTD sampling stations for 1995–1999.

the bottom of the thermocline to the surface (net 2) using wire angle and length of wire out to calculate gear depth. Data from the depth-discrete Tucker trawl samples were averaged over depth for comparison with bongo tows. All samples were preserved in 5% formalin : seawater. Samples were enumerated, copepods identified and staged, and chaetognaths separated out at the Polish Plankton Sorting and Identification Center, Szczecin, Poland. Chaetognaths were identified to species only for 1995 and 1997, and *S. elegans* was the only species found. Subadult *Acartia* spp. and nauplii of all copepod species were excluded from the counts, because these small stages were not quantitatively retained by the net mesh sizes used. Sorted subsamples were returned to Seattle.

Table I: Number of samples collected on southeast Bering Sea middle shelf by year and month

	February	April	May	July	September
1995		4	4		
1996		2	2	4	
1997		5	5	5	
1998	6	4	5	3	3
1999	1	13	7		7
2000			18		

Copepod and chaetognath abundances were compared between April and May 1995–1999 and February and September 1998–1999.

Chaetognath and copepod concentrations were represented as both numerical concentrations and biomass. Carbon weight of *S. elegans* was estimated from chaetognath lengths using the regression (Conway and Robins, 1991):

$$C = 0.0473L^{3.14}$$

Copepod carbon weights were estimated for each copepod species and stage using carbon weights compiled by Incze *et al.* (Incze *et al.*, 1997).

Chaetognath diel feeding patterns were examined to determine whether our gut content samples for 1995 and 1997, collected mainly in daylight, were representative of feeding over a 24-h period. Bongo nets (333-μm mesh) were deployed near mooring 2 at 4-h intervals over two 24-h time series during May 2000. Samples were sorted at the Alaska Fisheries Science Center in Seattle. A Folsom Plankton Splitter was used to obtain ~200 *S. elegans* from each sample for gut content analysis.

Gut content analysis

Gut content analysis was performed on *S. elegans* collected at three stations each in April and May 1995 and 1997 and from two diel feeding series in May 2000. All gut content samples were taken during daylight, except one in April 1995. Only 333-μm mesh samples were examined to avoid the higher potential for net feeding in the 153-μm mesh nets. Specimens of *S. elegans* were staged using a dissecting microscope. Total length was measured to the nearest millimetre using a 1-mm grid. Stage was determined according to Thomson (Thomson, 1947): Juvenile, gonads not developed; I, gonads form; II, small ova present and III, some large ova appear (and ovaries are long, up to first fin). Prey position in the gut was determined by dividing the gut lengthwise into three equal parts: 1, anterior gut; 2, midgut and 3, posterior gut. Prey in the mouth and foregut were excluded from the analysis. The degree of digestion was noted. Prey were excised from chaetognath guts on a slide in glycerin which was diluted with distilled water and tinted with methylene blue. Gut contents were identified to the lowest taxonomic level possible. Copepods in early stages of digestion were identified and their prosome length (*PL*) was measured at 25×, to the nearest 0.02 mm, using an ocular micrometer on a dissecting microscope. Copepods in an advanced state of digestion were identified from the shape and size of their mandibles in comparison to a collection of mandibles made from concurrently collected ambient zooplankton samples. *Calanus marshallae*, *Pseudocalanus* spp., *Acartia* spp., *Oithona* spp. and *Metridia* spp. were identifiable from their distinct mandible shapes. Relationships between mandible blade width (*MW*) and *PL* were developed for *C. marshallae* and *Pseudocalanus* spp. (Fig. 2). These equations were used to estimate *PL* of digested copepods.

Digestion time

Digestion times (DTs) were determined experimentally at sea during May 2000. *Sagitta elegans* were captured in vertical tows of a 333-μm mesh, 1-m ring net with a solid codend, or a 333-μm mesh, 60-cm bongo net. Five experiments were performed using a total of 68 chaetognaths collected from water with surface temperatures of 1.4, 2.0, 2.5, 3.9 and 4.4°C. The codend was placed in a bucket of surface seawater immediately upon retrieval. All samples were quickly and gently emptied from unrinsed nets into buckets half full of surface seawater.

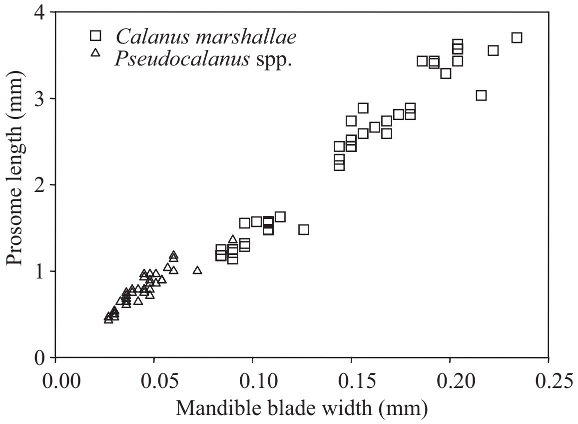

Fig. 2. Relationship of mandible blade width (*MW*) to prosome length (*PL*) for *Calanus marshallae* and *Pseudocalanus* spp. For *C. marshallae*, $PL = (18.95 \times MW) - 0.442$ ($n = 49$, adjusted $R^2 = 0.954$, $P < 0.000$). For *Pseudocalanus* spp., $PL = (15.173 \times MW) + 0.108$ ($n = 40$, $R^2 = 0.850$, $P < 0.000$).

In the laboratory the bucket was placed in a basin of ice and water while the sample was sorted.

Small aliquots of the dilute samples were poured into a glass quadrant dish for examination. Chaetognaths with prey were transferred using a wide bore pipette into individual 475 mL jars filled with 35-um filtered surface seawater from the same station as the chaetognaths. The time of isolation and position of prey were noted. Jars were placed in an incubator set to the ambient temperature at a depth of 3–5 m.

Approximately every hour, incubator and water temperature were recorded, and chaetognaths were examined until prey were egested or could no longer be seen in the gut. Then each chaetognath was examined with a dissecting microscope to measure total length and ensure that there were no prey remnants. Chaetognaths ranged in length (mm) from 12.8 to 32.0 (mean = 20 ± 3.8). The time to egestion was multiplied by two to account for digestion that occurred before observations began, as recommended by Feigenbaum (Feigenbaum, 1979). A mean DT and temperature was calculated from these data. Data from this cruise were plotted with data from the literature and a nonlinear regression was run for mean DT on temperature using the Gauss–Newton estimation method (Engelman, 2000).

Feeding effects

Effects of chaetognath predation on copepods (percentage of standing stock removed daily) were estimated from chaetognath feeding rates (FRs) (number of prey consumed per chaetognath per day) and ambient concentrations (number m^{-3}) of chaetognaths and prey. Predation effects on *Acartia* spp. and *Oithona* spp. were not estimated since ambient concentrations of the early stages of these species were not available.

FRs were estimated from the following equation, modified from Bajkov (Bajkov, 1935):

$$FR = \left[\frac{\text{mean } NPC}{DT(\text{h})}\right] \times 24$$

where *NPC* is the number of prey per chaetognath, and *DT* is estimated from mean water column temperature (from CTD data for each station) using the equation developed from our digestion experiments and literature values. The number of prey was not adjusted for prey loss by regurgitation or defecation during sampling (Baier and Purcell, 1997), because data on sampling effects are not available for cold-water chaetognaths.

Feeding effects were calculated as

$$\frac{FR_i \times \text{number of } S.\,elegans}{\text{number of copepods}_i} \times 100$$

where i is the copepod species.

Estimated feeding effects were compared with dry weight-based chaetognath food requirements approximated using our data combined with literature values. Dry weight of *S. elegans* was estimated from chaetognath lengths using the regression (Conway and Robins, 1991):

$$DW = 0.1951L^{2.99}$$

Copepod dry weight was estimated using a carbon : dry weight ratio of 0.47 (Kotori, 1976). *Sagitta elegans* daily ration was estimated using a weight-specific daily ration of 0.02, based on ranges for stage II and stage III *S. elegans* of 0.017–0.023 at 0°C (Feigenbaum, 1982) and 0.018–0.22 at −1.7 to 1.2°C (Falkenhaug, 1991).

Statistics

All statistical analyses were performed using Systat software. Comparisons of zooplankton concentrations among years within months, and among months within years, were made using analysis of variance (ANOVA) with a Fisher's LSD on fourth root-transformed data. Spearman's rank correlation test was used to analyse relationships between copepod and chaetognath concentrations and environmental variables. Comparisons of chaetognath length and prey length in April and May 1995 and 1997 were made using GLM with Bonferroni adjustment on untransformed data.

RESULTS

DT

DTs (minutes) for all temperatures ranged from 110 to 1588 with a mean of 699 ± 387 SD (Fig. 3). There were no significant relationships between DT and temperature or DT and chaetognath length within this temperature range, probably because of the size variability of the prey. However, a nonlinear regression of the mean DT from these experiments combined with literature values over a temperature range of 0–15°C produced a curve similar to that derived for *S. elegans* by Pearre (Pearre, 1981) from the relationship of DT to temperature in fish, plus two estimations of *S. elegans* DT (Kuhlmann, 1977; Feigenbaum, 1979) (Fig. 3). The regression, $DT = 11.58e^{-0.0787T}$ was used to determine DT at each station, based on average

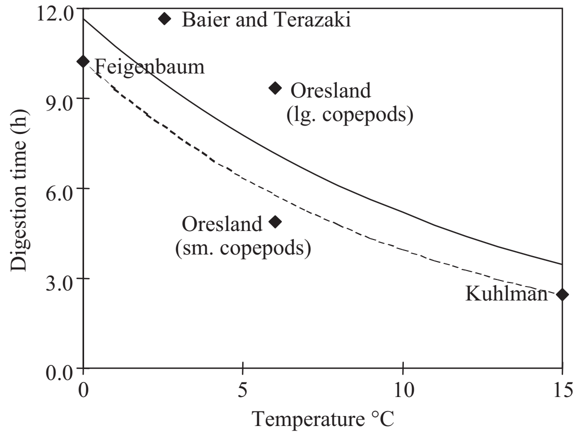

Fig. 3. Nonlinear regression of digestion time (DT) on temperature. Solid line: $DT = 11.58e^{-0.078T}$ with a corrected R^2 of 0.785, for experimentally determined DTs from this study and the literature (Kuhlmann, 1977; Feigenbaum, 1979; Øresland, 1987). Broken line: $DT = 10.24e^{-0.095T}$, derived by Pearre (Pearre, 1981).

water column temperature from CTD profiles, for FR calculations.

Interannual variability in climate and zooplankton populations

Environmental conditions and zooplankton assemblages were highly variable among the years we examined (Table II; Fig. 4). *Calanus marshallae* abundances were high in 1995 and 1998 ($P < 0.001$); sea ice extended far south in both years though the water temperature was cold in 1995 and warm in 1998. *Pseudocalanus* spp. concentrations were high in 1996 and 1998, the warmest years ($P < 0.001$). Abundances of *S. elegans* increased between 1995 and 1997–1998, then decreased markedly in 1999 ($P < 0.01$). There were no significant changes in zooplankton concentrations between April and May of any year.

Table II: Summary of environmental variables for 1995–1999

Year	Bloom onset	March–April temperature (°C)	Ice extent (°N)	Bottom temperature (°C)
1995	Late March	–1.0	56.88	1.7
1996	Mid May	0.0	57.63	3.4
1997	Late March	–0.8	57.13	2.8
1998	Early May	1.7	56.38	3.3
1999	Late January	–0.3	57.38	0.8

Timing of phytoplankton bloom onset at mooring site 2, mean surface temperature during March 14–April 30 at 20 m at mooring site 2, southernmost latitude of sea ice extent and mean middle shelf bottom temperature.

There were a number of correlations among climatic indices and zooplankton abundances (Table III). Bottom temperature and the timing of the phytoplankton bloom were correlated ($P < 0.01$). *Calanus marshallae* was most abundant in years with southernmost sea ice extent, and *Pseudocalanus* spp. abundance was positively correlated with early spring water column temperature. Abundances of chaetognaths, *Pseudocalanus* and *Acartia* were positively correlated as were *C. marshallae* and *Oithona*.

Spring zooplankton communities contrasted sharply between 1995 and 1997, the two years for which we estimated chaetognath predation effects (Fig. 4). In 1995, the copepod community was dominated by the large copepod, *C. marshallae*, and *S. elegans* abundances were low. In 1997, the small copepods *Acartia* and *Pseudocalanus* were numerically predominant, and chaetognath abundances were high.

Total copepod community carbon was much greater in both April and May 1995 than in 1997 ($P < 0.05$), but chaetognath biomass did not differ significantly between years (Table IV). Although numerical concentrations of copepods were similar in 1995 and 1997 (Table V), biomass was higher in 1995 because of the much greater size of *C. marshallae* individuals compared to *Pseudocalanus* and *Acartia*. Copepods other than *C. marshallae* and *Pseudocalanus* spp. contributed very little to total copepod carbon (Table IV). Chaetognath carbon biomass m^{-3} was not significantly different between years, because the smaller size of individual chaetognaths in 1997 compensated for their greater abundance in that year.

Sagitta elegans were significantly larger in both April and May 1995 than in 1997 ($P < 0.001$) but reached sexual maturity earlier and at smaller sizes in 1997 (Fig. 5). Chaetognath lengths increased from 18.6 ± 0.2 SE to 20.1 ± 0.2 mm ($P < 0.02$), between April and May 1995. In 1997, the April and May lengths were not significantly different. The percentage of reproductively mature (stage 3 ovaries) *S. elegans* was lower in both April and May 1995 than in 1997.

Seasonal patterns

Stage distributions over the course of the spring and summer seasons showed distinct differences between *C. marshallae* and *Pseudocalanus* spp. (Fig. 6). *Calanus marshallae* appeared to produce only one main cohort in each year; 1–2 stages predominated in each month of sampling, with progressively later stages in each sampling period from February to September. In contrast, all stages of *Pseudocalanus* spp. were represented during each sampling. No trend in monthly copepod abundances was consistent between the 2 years, but chaetognath populations were highest in September of both 1998 and 1999 ($P < 0.02$).

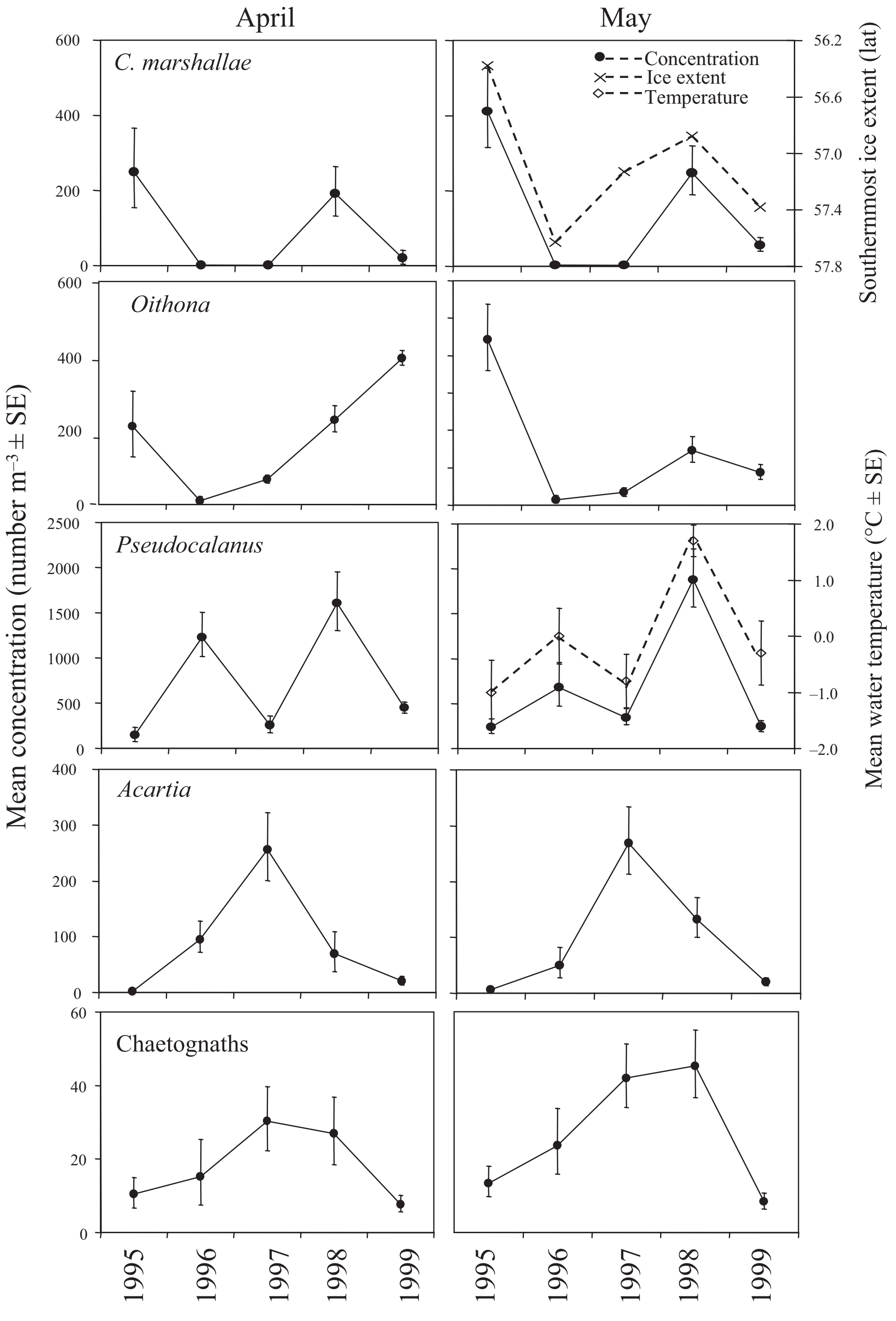

Fig. 4. Abundances of chaetognaths and copepods during April and May 1995–1999. Latitude of maximum southern sea ice extent is shown on the panel with *Calanus marshallae*; mean water temperature for March 14–April 30 is shown with *Pseudocalanus* spp. Number of stations are shown in Table I.

Diet

Sagitta elegans diets qualitatively reflected the copepod community composition in each year (Fig. 7). The dominant prey type consumed in 1995 was *C. marshallae*, and in 1997, *Pseudocalanus* spp. and *Acartia* spp. In 1997, *C. marshallae* was present in very low ambient concentrations and was virtually absent from chaetognath guts. 'Other' prey in the guts were primarily copepod nauplii, while 'other' in the

Table III: Correlation matrix of mean May concentrations of copepods and chaetognaths with environmental variables for the southeast Bering Sea middle shelf for 1995–1999

	Chaetognaths	*Pseudocalanus*	*Acartia*	*Calanus*	*Oithona*	Bloom	Temperature	Ice
Pseudocalanus	Positive*							
Acartia	Positive*	NS						
Calanus	NS	NS	NS					
Oithona	NS	NS	NS	Positive**				
Bloom time	NS	NS	NS	NS	NS			
Water temperature	NS	Positive**	NS	NS	NS	NS		
Ice extent	NS	NS	NS	Positive**	Positive**	NS	NS	
Bottom temperature	NS	Positive*	NS	NS	NS	Positive**	NS	NS

Zooplankton concentrations (number m^{-3}); timing of the onset of the spring phytoplankton bloom; water temperature from a moored sensor on the middle shelf at 20 m depth averaged over March 14–April 30; southernmost latitude of sea ice extent and mean middle shelf summer bottom temperature. Statistically significant Spearman correlations are listed as positive or negative relationships. NS, not statistically significant.
*$P < 0.10$, **$P < 0.05$.

Table IV: Estimated carbon biomass of the copepod community and Sagitta elegans over the southeast Bering Sea middle shelf

	Zooplankton carbon weight (mg m^{-3} ± SE)			
	April 1995	May 1995	April 1997	May 1997
S. elegans	6.9 ± 1.5	7.3 ± 2.7	9.6 ± 2.7	13.0 ± 4.4
Pseudocalanus spp.	1.1 ± 0.3	0.9 ± 0.4	1.8 ± 0.3	2.6 ± 0.5
Calanus marshallae	58.1 ± 14.5	25.2 ± 3.1	0.3 ± 0.1	0.4 ± 0.1
All copepods	59.4 ± 13.3	28.3 ± 3.4	3.0 ± 0.5	4.0 ± 3.4

ambient samples were mainly *Oithona* (nauplii were not counted from ambient samples). *Oithona* was not an important prey item for the chaetognaths that we examined at any time; only 10 were found in a total of 4657 chaetognath guts examined.

The range of prey sizes consumed by chaetognaths was greater in 1995 than in 1997, and mean prey size was larger in May 1995 than 1997 (Fig. 8). There was no significant difference in mean prey size between the two years in April, or between April and May in 1997. In 1995, however, mean prey size (mm ± SD) increased from 1.13 ± 0.18 in April to 1.85 ± 0.16 in May ($P < 0.004$), significantly larger than that of May 1997 (0.989 ± 0.22, $P < 0.04$).

Predation effects

Predation effects on copepod standing stocks were higher in 1997 than in 1995 (Table V). In 1997, *S. elegans* were more abundant than in 1995 ($P < 0.001$). Total abundances of copepods were not markedly different between years, but *C. marshallae* was much more abundant in 1995 ($P < 0.001$). The NPC was lowest in May 1995, when *C. marshallae* copepodites made up 64% of the diet. The NPC was higher in April 1995 when nauplii and *Pseudocalanus* spp. were a substantial portion of the diet, and in 1997 when *Pseudocalanus* spp. and *Acartia* spp. were most prevalent (Table V; Fig. 7). There was no evidence of diel feeding patterns. DTs were slightly longer due to cooler temperatures (°C ± SD) in 1997 (–1.3 ± 0.0, April; –0.9 ± 0.0, May) compared to 1995 (1.0 ± 0.9, April; 1.7 ± 0.3, May) (Table V). FRs were highest in April 1995 and May 1997 because of the relatively large NPC. However, because of the high predator : prey ratios in both April and May 1997, predation impacts were higher then. Thus daily predation impact was greater on the small copepods that predominated in 1997 than on *C. marshallae* in 1995.

The difference between years was more pronounced when examined in terms of copepod community biomass required by chaetognaths (Table V). *Sagitta elegans*

Table V: Feeding rates and effects of Sagitta elegans on copepod standing stocks, and estimated biomass requirements of S. elegans, for the Bering Sea middle shelf during April and May 1995 and 1997

	1995		1997	
	April	May	April	May
Zooplankton standing stock (individuals m^{-3} ± SE)				
S. elegans	14 ± 3	12 ± 5	45 ± 17	50 ± 15
Pseudocalanus	233 ± 80	202 ± 42	313 ± 10	473 ± 126
Calanus marshallae	489 ± 148	346 ± 134	2 ± 1	14 ± 6
Copepods	1089 ± 229	971 ± 214	747 ± 53	876 ± 97
S. elegans feeding				
Digestion time (h)	10.7	10.1	12.8	11.5
Number of prey individuals^{-1}				
Pseudocalanus	0.03	0.01	0.06	0.08
C. marshallae	0.06	0.09	0.00	0.00
All copepods	0.18	0.11	0.15	0.20
All prey	0.35	0.14	0.23	0.35
Number of prey individuals^{-1} day^{-1} (all prey)	0.78	0.33	0.42	0.74
Percentage of standing stock consumed day^{-1}				
Pseudocalanus	0.4	0.1	1.7	1.7
C. marshallae	0.4	0.7	0.0	1.8
All copepods	0.5	0.3	1.7	2.3
Zooplankton dry weight (mg m^{-3})				
S. elegans	18.6	19.4	27.2	33.6
Copepods	126.4	60.2	6.4	8.5
S. elegans ration required day^{-1} (mg dry weight m^{-3})	0.37	0.39	0.54	0.67
Percentage of copepod dry weight required day^{-1}	0.3	0.6	8.4	7.9

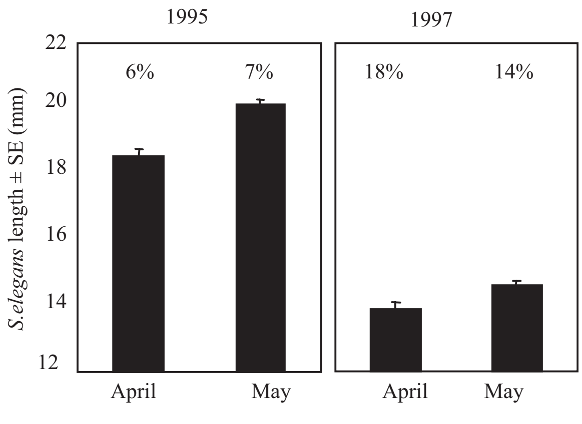

Fig. 5. Mean length of *Sagitta elegans* in April ($n = 274$) and May ($n = 324$) 1995 and April ($n = 337$) and May ($n = 334$) 1997 over the southeast Bering Sea middle shelf. Percent reproductively mature shown above each bar.

biomass was not significantly higher in 1997 than in 1995. However, copepod community biomass was much lower in 1997 ($P < 0.05$). The estimated percentage of total copepod community biomass required by *S. elegans* was 8–12% in 1997 compared to <1% in 1995 (Table V).

DISCUSSION

Interannual variability in climate and zooplankton populations

The years 1995–1999 spanned the range of sea ice and temperature conditions that occurred in the southeast Bering Sea during the past 34 years (Wyllie-Echeverria and Wooster, 1998; Baier and Napp, 2003). 1995 and 1999 were the coldest, iciest years in decades, comparable to conditions before a 1977 'regime shift' (Niebauer, 1998). In 1996 and 1998, water temperatures were unusually warm, but there was very little ice over the southeast Bering Sea shelf in 1996, while ice penetrated further south in 1998 than in the past 30 years. Depth-averaged temperatures in 1997 were near average.

Zooplankton concentration, biomass and species dominance changed dramatically from year to year during

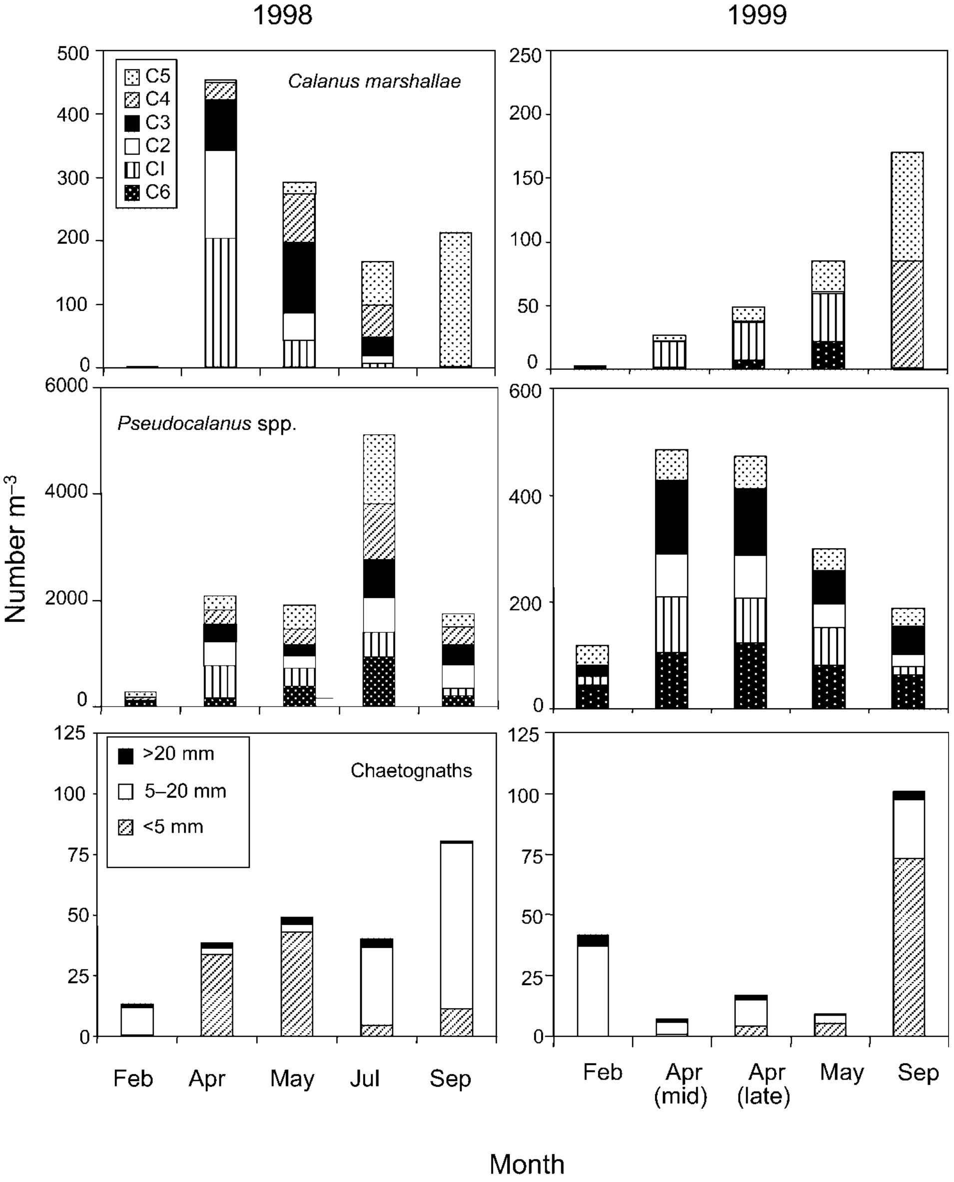

Fig. 6. Stage compositions of *Calanus marshallae* and *Pseudocalanus* and size composition of chaetognaths during February–September 1998 and 1999. Note different sampling periods and different scale.

1995–1999. Copepods were abundant with *C. marshallae* dominant in 1995 and abundant with *Pseudocalanus* numerically dominant in 1998. Total copepod abundance was relatively low in 1996, 1997 and 1999. In a study using different data sources, summer middle shelf zooplankton biomass was particularly high in 1995 and lower in 1996 than most years (Napp *et al.*, 2002).

Some of the patterns that we observed in copepod populations were explained by climatic variability. Spring abundance of *Pseudocalanus* spp. was greatest when spring water temperatures were warm, while *C. marshallae* was most abundant following extensive ice cover. Data from the Bering Sea middle shelf show that springtime sea temperatures are important in limiting the growth of small copepods such as *Pseudocalanus* (Dagg *et al.*, 1984). The positive relationship between *C. marshallae* copepodite abundance and ice extent has previously been examined (Baier and Napp, 2003). The timing of *C. marshallae* copepodite recruitment correlated with the onset of the phytoplankton bloom, which can occur early, in association with sea ice, in years when ice cover reaches the southeast middle shelf. The magnitude of copepodite abundance in May was related to sea ice extent, regardless of the timing of the bloom, but the mechanism behind this relationship is unclear.

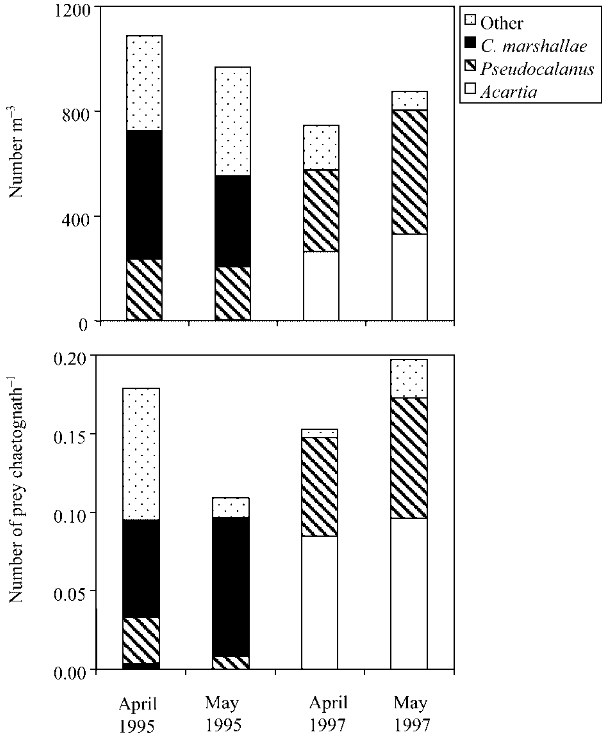

Fig. 7. Copepod prey composition in chaetognath guts compared with concentration of available copepod prey in April and May 1995 and 1997. Non-copepod prey, including nauplii, not shown. Only adult stage of *Acartia* spp. are shown for ambient samples.

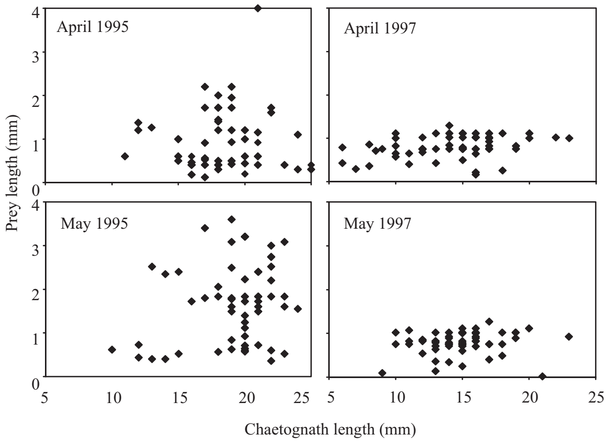

Fig. 8. Chaetognath length versus prey length during April and May 1995 and 1997. Not shown: one 14-mm prey *Sagitta elegans* in May 1997.

Correlations between copepod species may be related to their respective responses to interannual versus seasonal modes of variance. In our study, concentrations of *C. marshallae* and *Oithona* spp. were correlated, and populations of *Pseudocalanus* spp. and *Acartia* spp. were correlated. Similar species were grouped in a long-term (1961–1991) study of the Gulf of Maine, in which copepod taxa were categorized, using eigen vector filtering, according to their main type of variability. *Calanus finmarchicus* (a sibling species of *C. marshallae*) and *Oithona* spp. were classified as interannually dominated (only year-to-year variation is important) while *Pseudocalanus* spp. and *Acartia* spp. were found to be intermediate between interannually and seasonally dominated (an interannual trend is present but seasonal variation is not negligible) (Licandro *et al.*, 2001). The species whose major variance mode is interannual are supposed to be particularly sensitive to climatic changes.

Predator–prey interactions

The size structure of the chaetognath populations in 1995 and 1997 mirrored that of the copepod community on both a yearly and monthly basis. *Sagitta elegans* were larger in 1995, when large *C. marshallae* were the dominant copepod species, and smaller in 1997 when the small copepods, *Pseudocalanus* spp. and *Acartia* spp., were predominant. Chaetognaths increased in size between April and May 1995, while the stage/size of *C. marshallae* increased from primarily C1-3 to C3-4 between April and May 1995 (Baier and Napp, 2003). Chaetognath size did not increase significantly between April and May 1997, when *Pseudocalanus* and *Acartia* were predominant.

The size of prey consumed by chaetognaths increased between April and May 1995 but not between months in 1997. Mean prey size was larger in May 1995 than in either April or May 1997. Saito and Kiørboe (Saito and Kiørboe, 2001) showed maximum clearance rates on prey sizes 6–10% of *S. elegans* length. Our results varied within a similar range: mean prey lengths were 5% (April 1995), 10% (May 1995), 6% (April 1997) and 7% (May 1997) of mean chaetognath length.

In our study, the percent of reproductively mature chaetognaths was higher in both April and May 1997 than in 1995, and chaetognaths were smaller in 1997, suggesting that they matured earlier and to a smaller size in 1997. Somatic growth is generally thought to stop with onset of maturity (Pearre, 1991). Chaetognaths develop and grow faster in warmer temperatures, but mature at a larger size in lower temperatures (Pearre, 1991). The concentration and composition of food also affects size at maturity. Pearre (Pearre, 1982) suggested that because of energetic considerations, a scarcity of large prey could limit chaetognath final size even in a food-rich environment. The water column temperature integrated over March and April was similar in 1995 and 1997, but the instantaneous water column temperatures measured using CTDs at the stations where chaetognaths were collected in April and May were warmer in 1995. Large prey in the form of *C. marshallae* were plentiful in the environment and in chaetognath guts in 1995 and virtually absent in 1997.

Our FR estimates were within the range of literature values for *S. elegans* at low temperatures. *Sagitta elegans* consumed 0.3–0.8 prey individual^{-1} day^{-1} at temperatures of –1.3 to 1.7°C in 1995 and 1997. Literature values ranged from 0.2 to 1.3 prey individual^{-1} day^{-1} at temperatures of <0–6°C (Feigenbaum, 1982; Øresland, 1987; Falkenhaug, 1991; Brodeur and Terazaki, 1999).

Effects of chaetognath predation on copepod populations were relatively high compared with results of the few other studies that quantified chaetognath feeding in cold-water habitats. We estimate that *S. elegans* consumed 0.3–2.3% of copepod standing stock each day. By comparison, *S. elegans* consumed 0.08–0.22% of copepod standing stock in the Barents Sea (Falkenhaug, 1991), and *Eukrohnia hamata* consumed 0.03–0.06% of large copepods, and 0.10–0.58% of small copepods, in Antarctica (Øresland, 1990). Our feeding estimates were subject to unquantified biases that could lead to underestimated (prey loss during sampling, undersampled small chaetognaths) or overestimated (undersampled small copepods) effects on the copepod community. The lack of preadult copepodites in ambient counts especially affects the estimate for 1997 when *Acartia* spp. adults were prevalent in the copepod community. However, literature estimates have similar limitations: zooplankton were counted from 153- to 333-μm nets in this study and from 375 (Falkenhaug, 1991) and 300-μm mesh (Øresland, 1990) in literature studies. Neither our study nor those we compare with address prey loss during sampling, which has been estimated to be as much as 50% of gut contents in tows of durations <2 min (Baier and Purcell, 1997); in this study, tows ranged in duration from 6 to 9 min.

Daily predation effects were greater in 1997 than in 1995, and the difference between years was driven by the difference in chaetognath numbers and copepod biomass. Chaetognath biomass was similar between years, but copepod community carbon biomass was much lower in 1997. This difference between years is less likely than numerical concentration to be much affected by the undersampling of small *Acartia* spp. copepodites; the adults contributed little to the total, and the even smaller early copepodites would have to be present in very high numbers to increase it appreciably.

Daily predation estimates do not take into account cumulative predation effects or how they might depend on the prey species' reproductive strategy. Øresland (Øresland, 1990) points out that even very low but continuous feeding could be important during winter when little copepod production takes place. Effects of low daily rates of sustained predation similarly may accrue over the summer season for prey species that have long generation times. In our study, *Pseudocalanus* appeared to reproduce throughout the season while *C. marshallae* produced only one cohort in both 1998 and 1999. Thus daily predation pressure on copepods was higher in 1997, when *Pseudocalanus* was predominant, but the *C. marshallae*-dominated copepod community of 1995 was more vulnerable to cumulative effects.

SUMMARY

Chaetognaths and different copepod species responded differently to climate conditions, resulting in a unique zooplankton assemblage in each year during 1995–1999. *Calanus marshallae* were most abundant in years of greatest ice extent, and *Pseudocalanus* spp. populations were greatest in warm years. Chaetognath populations showed no relationship with the indices of interannual climate variability that we considered. Both population and individual size of the chaetognaths reflected those of their prey during the two years we examined: chaetognaths were large and relatively few in 1995, when large *C. marshallae* with long life cycles were dominant, and chaetognaths were small and abundant in 1997, when *Pseudocalanus* spp. and *Acartia* spp., small copepods with short generation times, were dominant. Daily predation pressure by chaetognaths was greater in 1997 than in 1995, but the copepod population in 1995 was more vulnerable to cumulative predation effects.

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