Climate-induced variability in *Calanus marshallae* populations

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Calanus marshallae is the dominant mesozooplankton copepod species over the south-eastern Bering Sea middle shelf. Climate-induced changes in the magnitude and timing of production by C. marshallae may affect the living marine resources of the Bering Sea shelf ecosystem. We examined spring-time abundance, gonadal maturity and stage distributions of C. marshallae copepodites during five consecutive years (1995–1999) that spanned the range of variability observed over the past 34 years in terms of water temperature and ice cover. We compared our results with previous work conducted during cool (1980) and warm (1981) years [Smith, S. L. and Vidal, J. (1986) Cont. Shelf Res., 5, 215–239]. The spring phytoplankton bloom began relatively early in association with ice (1995, 1997, 1999), but began late when ice was absent or retreated early (1996, 1998). Egg production began well before the bloom and continued over a long duration. Copepodites, however, were recruited during a relatively short period, coincident with the spring phytoplankton bloom. The relationship between brood stock and spring-generation copepodite abundances was weak. Copepodite concentrations during May were greatest in years of most southerly ice extent. Copepodite populations were highly variable among years, reflecting interannual variability in the atmosphere–ice–ocean system.

INTRODUCTION

Calanus marshallae (Frost, 1974) is an important component of the zooplankton community over the south-eastern Bering Sea middle shelf, and is the only large copepod that reproduces there (Vidal and Smith, 1986). The Bering Sea ecosystem supports important commercial fisheries and a high biomass of marine mammals and seabirds (National Research Council, 1996). Nauplii and copepodites are important prey of larval and juvenile fish; for example, *C. marshallae* copepodites constituted 63% of the prey items consumed by age-1 walleye pollock (*Theragra chalcogramma*) during the summer in the eastern Bering Sea (Grover, 1991). Variability in copepod production therefore potentially affects the Bering Sea ecosystem and its commercial fisheries (e.g. Walsh and McRoy, 1986; Napp *et al.*, 2000).

The life history of *C. marshallae* populations in the south-eastern Bering Sea has been described previously (Smith and Vidal, 1986). Stage 5 copepodites (C5) are believed to overwinter on the shelf, moult to the adult stage in late winter–early spring and produce one or two cohorts each year. Egg production has been reported to begin before (Naumenko, 1979; Smith and Vidal, 1986), during (Vidal and Smith, 1986), and after (Flint *et al.*, 1994) the spring phytoplankton bloom. Spring concentrations of *C. marshallae* were higher during a cool year than during a warm year (Smith and Vidal, 1986). These years (1980 and 1981), however, do not represent the full range of environmental conditions that occur in the region.

The south-eastern Bering Sea is directly influenced by atmospheric forcing, which shows large interannual fluctuations correlated with the North Pacific circulation, El Niño–Southern Oscillation, and Pacific Decadal Oscillation (Niebauer *et al.*, 1999; Overland *et al.*, 2001; Stabeno *et al.*, 2001). This forcing is manifested regionally through the Aleutian Low Pressure System, which affects local winds and surface heat flux, and therefore the formation and movement of sea ice (Ohtani and Azumaya, 1995; Niebauer, 1998). The south-eastern shelf is a marginal ice zone, subject to great variability in the timing and extent of seasonal sea-ice cover (Wyllie-Echeverria and Wooster, 1998). Ice is not formed *in situ* on the south-east shelf but is advected over it by north-east winds, sometime between November and June; the presence, extent and persistence of ice cover fluctuate with interannual variations in these winds and with local water temperature.

Sea-ice dynamics dominate spring physical processes over the shelf, directly affect the development of the phytoplankton bloom and are thought to influence the population dynamics of higher trophic levels (Napp *et al.*, 2000; Hunt *et al.*, 2002). An early phytoplankton bloom occurs when the ice is advected over the shelf during March or April, while in the absence of ice the bloom is delayed until May or June (Stabeno *et al.*, 2001). The biomass of scyphomedusae over the south-eastern Bering Sea shelf increased dramatically during the 1990s, concurrent with increased extent and persistence of ice cover; the authors hypothesized that this was because early life stages of jellyfish depend on ice-associated phytoplankton blooms and the consequent high secondary production (Brodeur *et al.*, 2000). Poor recruitment of walleye pollock, *Theragra chalcogramma*, in cold years has been attributed to cannibalism resulting from overlapping distributions of larvae/juveniles and adults, which avoid the coldest water (Wyllie-Echeverria and Wooster, 1998; Wespestad *et al.*, 2000).

We examined springtime populations of *C. marshallae* on the middle shelf (between 50 and 100 m isobaths) during 5 consecutive years that spanned the full range of temperature and ice extent observed during the past 34 years (Stabeno *et al.*, 1998; Wyllie-Echeverria and Wooster, 1998). Data on *C. marshallae* reproduction and abundance were synthesized with environmental data to investigate how *C. marshallae* populations respond to short-term climate variability. Understanding the linkages between environmental forcing and *C. marshallae* population dynamics is a first step towards understanding how this ecosystem may respond to longer-term changes in climate.

METHOD

Collections were made between February and September 1995–1999 over the middle shelf of the south-eastern Bering Sea (Figure 1; Table I). Shipboard observations were made from the NOAA ship 'Miller Freeman', and time-series of physical and fluorescence data were obtained from moored instruments.

Zooplankton collections

We assumed that within each year the population sampled in May was the same as that sampled in April. This assumption, based on sluggish circulation over the shelf, is probably valid for the middle shelf, where mean current speed is <1 cm s^{-1} (Coachman, 1986). Patterns of copepodite abundance and stage composition in 1998 and 1999, when our temporal coverage was most complete, do not contradict this assumption.

Mesozooplankton was sampled using bongo nets (1995, 1997–1999), and a Tucker trawl equipped with Clarke–Bumpus net frames (1996). Copepod nauplii were sampled only in April 1996, using a CalVET net. Bongo samplers comprised 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. A SeaCat CTD was located 1 m above the 20 cm frame to telemeter net depth. Double oblique tows were made to ~5–10 m from the bottom. Clarke–Bumpus nets (153 μm mesh, 25 cm diameter) 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 base of the thermocline (net 1) and from the base of the thermocline to the surface (net 2), using wire angle and length of wire to calculate gear depth. Data from the depth-discrete Tucker trawl samples were integrated over the water column for comparison with those from the bongo tows. Vertical tows with CalVET nets (53 μm mesh) for copepod nauplii were made to 60 m depth. Calibrated flowmeters were used to estimate the volumes filtered by each net. All samples were preserved in 5% formalin:sea water.

Copepodites were enumerated at the Polish Plankton Sorting and Identification Center, Szczecin, Poland. Copepodite stages 3–6 (C3–C6) were assumed to be quantitatively retained by the 333 μm mesh, while C1 and

Table I: *Number of stations sampled by year and month*

	Conditions	February	April	May	July	September
1995	Heavy ice, off-shelf winds		5	5		
1996	Little ice, on-shelf winds		2	2	4	
1997	Near-normal forcing and ice		3	5	5	
1998	Cool early but an early thaw	6	6	5	4	3
1999	Warm early, heavy ice late	1	15	7		7

Qualitative synopsis of conditions (air temperature, wind forcing and ice cover) on the south-eastern Bering Sea shelf [modified from (Bond and Adams, 2002)].
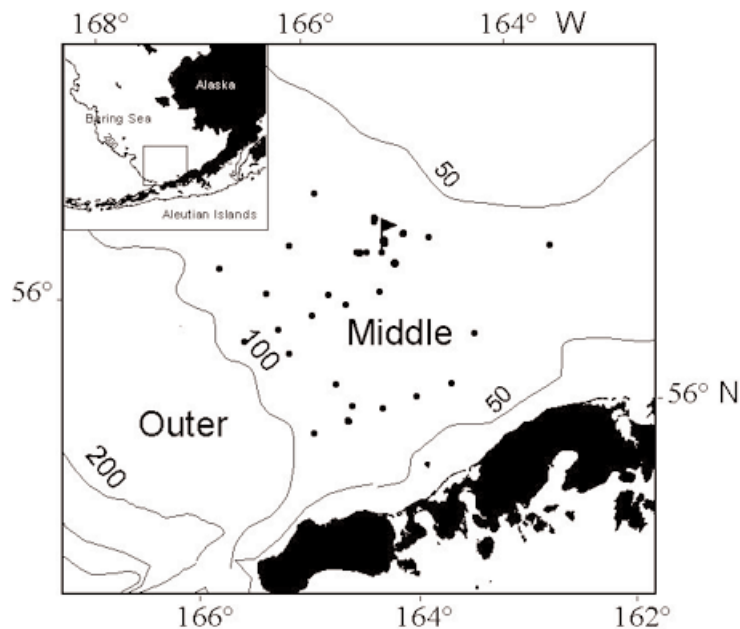
Fig. 1. South-eastern Bering Sea middle shelf, showing site of mooring (flag) and zooplankton sampling stations. Years and months sampled are listed in Table I. 1995 samples were collected from southern cross-shelf transect, 1996–1998 from the northern area, and 1999 from both northern and southern cross-shelf transects.

C2 were counted from the 153 μm mesh samples (Incze *et al.*, 1997). Sorted subsamples were returned to the Alaska Fisheries Science Center in Seattle. April 1996 CalVET samples for *Calanus* nauplii were processed in Seattle.

In Seattle, female *C. marshallae* were measured and gonadal maturity was assessed. Approximately 50 females from each station were randomly selected to determine length and gonadal maturity. The specimens were cleared using a 1:1 mixture of ethanol (70% solution) and glycerine. The state of oogenesis was determined using the following criteria, which are slightly modified from Tourangeau and Runge (Tourangeau and Runge, 1991): stage 1—no oocytes formed, small ovary visible; stage 2—anterior oviducts with single rows of small, clear oocytes (~50 μm); stage 3—anterior oviducts filled with clear, amorphous oocytes (~70 μm); stage 4—ventral loop of anterior oviducts filled with translucent oocytes (~100 μm); stage 5—ventral loop of anterior oviducts filled with opaque, round, oocytes (~150 μm); stage 6—posterior oviducts with rows of opaque, round oocytes (~150 μm). Females in stages 4–6 were considered to be reproductively mature.

Birth dates and dates of previous moults were estimated for copepodite stages collected in April and May using Campbell's temperature-dependent growth function for *Calanus finmarchicus* under satiating food concentrations at temperatures of 4–12°C (Campbell *et*

al., 2001b). Bering Sea *in situ* temperatures were averaged over depth and then time (February–April) from mooring data. The water column was well mixed and its temperature changed little during that period. Campbell's function assumes that food does not limit growth, so development times in nature may be longer than our estimates.

Calculated development times for *C. marshallae* using Campbell's equation were comparable with laboratory and field observations (Table II). The calculated duration of C1–3 combined was 20 days at 3°C. Vidal and Smith's field-derived estimate was 21 days at similar temperatures (Vidal and Smith, 1986). Development time to naupliar stage 3 at 3°C in our laboratory was 9.6 ± 1.3 days (unpublished data), compared with 9.4 days predicted by Campbell's equation.

Environmental sampling

A subsurface biophysical mooring was deployed in February of each year at Site 2 [Figure 1; (Stabeno *et al.*, 2001)]. It was replaced in May by a surface mooring. Water temperature was measured every 5–10 m from near surface to bottom 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. Ice cover along longitude 169°W was digitized from weekly NOAA ice charts

(S. Salo, Pacific Marine Environmental Laboratory, personal communication). South-eastern Bering Sea shelf summer bottom temperature data were collected from temperature recording devices mounted on the head rope of the bottom trawl gear, deployed during annual bottom trawl surveys sampling ~350 stations over the south-eastern 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 (G. Walters, NOAA/National Marine Fisheries Service, personal communication).

Statistical analyses

Copepod abundances were compared among years and among months within years using analysis of variance (ANOVA) on natural log-transformed data, and multiple comparisons were made using a Bonferroni adjustment. Spearman's rank correlation test was used to analyse relationships among the mean abundance of *C. marshallae*, date of first appearance of C1, and environmental variables. Results from the present study were compared with data from spring 1980–1981 (Smith and Vidal, 1986).

RESULTS

Climate, sea ice and the spring phytoplankton bloom

Diverse climate, sea ice and phytoplankton bloom conditions were observed during 1995–1999 in the south-eastern Bering Sea (Table I). Mean summer bottom temperatures ranged from 3.4 to 0.8°C during 1996, 1998, 1997, 1995 and 1999 (ordered from warmest to coldest). Ice was advected over the middle shelf mooring as early as February (1996, 1998, 1999) and as late as mid-March (1995, 1997) (Figure 2). Ice cover remained at the mooring for as little as 1 week in 1996, and as long as 1 month in 1995 (Figure 2). In years with ice cover after February (1995, 1997 and 1999), fluorescence increased relatively early, just after the ice arrived (Figures 2 and 3A). In 1996 and 1998, when ice retreated early, fluorescence remained low until May, when the water column began to warm and stratify (Figures 2 and 3A). Smith and Vidal made their observations during 1980, a cool year with ice present several times at the mooring site, and in 1981, which was warm and ice-free all year [Figure 2; (Smith and Vidal, 1986)].

Brood stock and egg production

Abundances of adult female *C. marshallae* differed markedly among years (Table III). In both April and May, concentrations of females were very high in 1995 compared with all other years ($P < 0.01$). In May, concentrations in 1999 were lower than in all other years ($P < 0.01$). Concentrations of females were similar between April and May in all other years except 1999, when the number of females dropped significantly in May ($P < 0.01$).

During the two years for which February samples were available, the terminal moult from overwintering C5 to adult occurred before February, long before the spring bloom. In February of 1998 and 1999, 98 and 93%, respectively, of copepodites sampled were C6 females. The remainder were C5.

Table II: Estimated development times for C. marshallae on the middle shelf

	Year	T (°C)	NI	NIII	C1	C2	C3	C4	C5
Days to stage									
Campbell's equation	1995	−1.0	8	21	72	85	101	121	150
	1996	0.0	6	17	57	67	80	95	118
	1997	−0.8	8	20	68	80	95	113	141
	1998	1.7	5	12	40	47	56	67	84
	1999	−0.3	7	18	61	72	85	101	126
Stage duration (days)					C1	C2	C3		
Campbell's equation		3.0			6	6	9		
(Vidal and Smith, 1986)		3.0			6	7	8		

Days to stage were calculated using Campbell's temperature-dependent growth function for *Calanus finmarchicus*. T = *in situ* water column temperature (March 14–April 30 at 20 m depth). Calculated stage durations (C1–C3) of *C. marshallae* at 3°C compared with field-derived estimates from Vidal and Smith (Vidal and Smith, 1986).
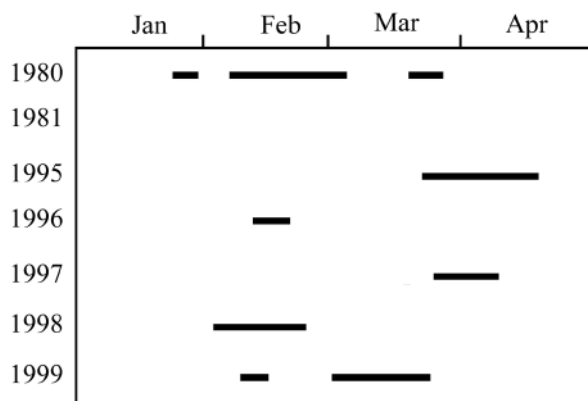
Fig. 2. Dates of ice cover (interpreted from satellite data) at mooring site.

Eggs were produced over a long period, beginning well before the spring phytoplankton bloom (except in 1999, when fluorescence began to increase in late January) and continuing at least into May. Reproductively mature females were present in February (90% in 1998 and 39% in 1999), April (>90% in all years except 1996 when 72% were mature), and virtually all females were mature in May of all years (Table III). Birthdates calculated using Campbell's equation for the dominant copepodite stages sampled in April and May ranged from as early as mid-January (1995) to the end of March (1996) (Figure 3B). Samples for nauplii were collected only during April 1996, when *Calanus* nauplii were present in concentrations of $18 \pm 3 \text{ m}^{-3}$ well before the onset of the phytoplankton bloom in mid-May.

Copepodite recruitment

Although egg production was protracted, copepodites were recruited during a relatively short time (Figure 3B and C). Typically, two dominant copepodite stages were present during a given sampling period. The exception, 1997, showed relatively even proportions among C2–C5 in July, but total numbers were very low. The progression of apparent copepodite cohorts through developmental stages over spring and summer was discernible in 1998, when temporal sampling coverage was most complete.

The timing of copepodite recruitment coincided approximately with the spring phytoplankton bloom (Figure 3A and B; Table IV). An exception was 1998, when C1–C3 were abundant in April, before water column fluorescence increased in May. The first appearance of C1 occurred as early as March (1995) and as late as the end of May (1996). Spring copepodite stage development was relatively advanced following cold conditions early in the year (1995, 1998) compared with warm or average years. The predominant G1 (spring generation) stages in May 1995 and 1998 were C3 and C4. In May of 1996, 1997 and 1999, C1 was the predominant stage.

Copepodite abundances, and the timing of peak abundances, varied greatly between years (Figure 3C). In 1995 and 1998, when ice extended south of 57°N, abundances were high in April–May. Very few copepodites were present during April–May in 1996, but extremely high concentrations of late-stage copepodites were sampled in July 1996, suggesting recruitment began after our May samples were collected. In both 1997 and 1999, abundances remained low throughout the season.

High abundances of G1 copepodites (C1–C5) did not require high broodstock abundance (Figure 3C). Mean April [$158 \pm 158 \, (n \, \text{m}^{-3} \pm \text{SD})$] and May ($62 \pm 25$) concentrations of females in 1995 were significantly higher than in the other years ($<5 \text{ m}^{-3}$). However, May concentrations of G1 copepodites in 1995 (517 ± 99) were not significantly higher than in 1998 (289 ± 99), when there were

Table III: Mean concentration (no. m^{-3}) and gonadal maturity of C. marshallae C6 females over the Bering Sea middle shelf

Year	Concentration ± SD			% Mature		
	February	April	May	February	April	May
1995		158 ± 158	62 ± 25		91	94
1996		5 ± 1	6 ± 4		72	99
1997		1 ± 1	1 ± 0		99	99
1998	3 ± 2	4 ± 2	2 ± 2	90	94	100
1999	2 ± 0	2 ± 2	0 ± 0	39	99	100

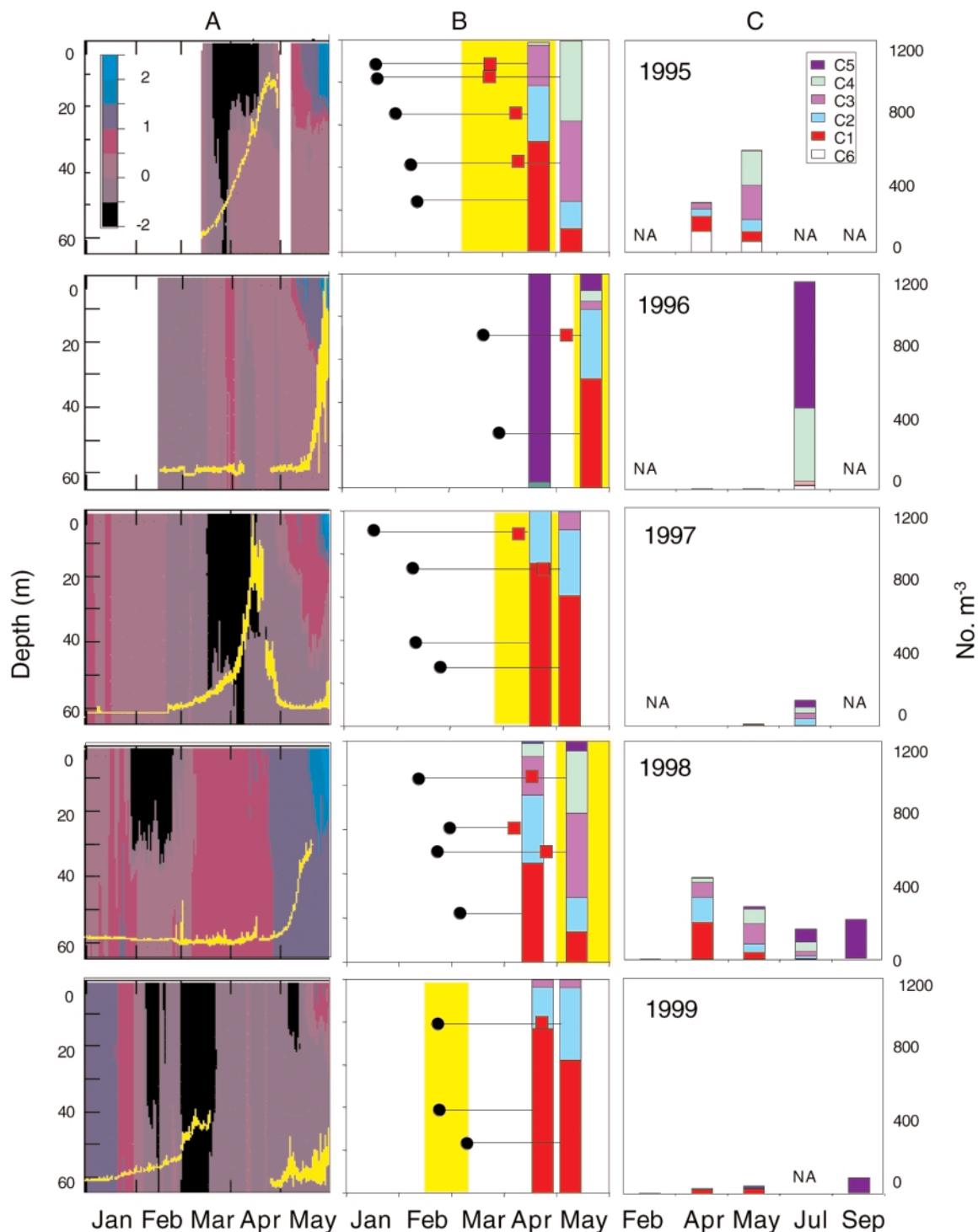Number of samples shown in Table I.

Fig. 3. Development of *C. marshallae* copepodite populations in relation to the spring phytoplankton bloom and water column structure during 1995–1999. (**A**) Colour scale shows temperature data from mooring. Ice was present during periods of coldest temperature (black). White area = no data. Yellow line = fluorescence at 10 m depth, normalized to maximum value for each year [modified from (Hunt *et al.*, 2002)]. (**B**) Per cent composition and estimated development time of copepodites (excluding C6) sampled in April and May. Time to C1 and egg stages was back-calculated using Campbell's temperature-dependent growth function. Horizontal lines pointing to stages sampled in April and May identify estimated time at egg stage (black dot) and C1 (red square) for that stage. For example, C2 sampled in April 1995 were hatched in late January and moulted to C1 in early April. Duration of the spring phytoplankton bloom is indicated by yellow background shading. (**C**) Mean abundance and stage composition of copepodites C1–C6 between February and September, 1995–1999. NA indicates no data available.

Table IV: Top: relation of C. marshallae population timing (C1 appear) and abundance of May G1 copepodites (May C1–C5) to environmental factors; bottom: Spearman correlation matrix

Year[a]	Bottom temp. (°C)	PDO index	Ice extent[b] °N	Bloom onset	C1 appear	May C1–C5 m^{-3}
1981	3.6	0.662	57.38	Early May	Early May	10
1996	3.4	0.244	57.63	Mid-May	After mid-May	1
1998	3.3	1.238	56.38	Early May	Mid-April	290
1980	2.8	0.472	57.63	Late April	Late April	32
1997	2.8	0.244	57.13	Late March	Early April	9
1995	1.7	−0.606	56.88	Late March	Late March	516
1999	0.8	−0.454	57.38	Late January	Mid-April	45

	Bottom temp	PDO index	Ice extent	Bloom onset	C1 appear
PDO index	*				
Ice extent	ns	ns			
Bloom onset	**	ns	ns		
C1 appear	*	ns	*	*	
May C1–C5	ns	ns	*	ns	*

[a] Years ordered by mean south-eastern Bering Sea shelf summer bottom temperatures; [b]ice extent is southernmost latitude of sea ice extent; bloom and copepodite data for 1980–1981 from Smith and Vidal (Smith and Vidal, 1986). **$P < 0.01$; *$P < 0.05$; ns = not significant.

few females. Thus high numbers of G1 copepodites were associated with high abundances of females in 1995, but relatively few females produced a large cohort in 1998.

Climate effects

Our results (1995–1999) combined with data from 1980–1981 (Smith and Vidal, 1986), showed statistically significant correlations as follows: mean shelf bottom temperature was linked to the Pacific Decadal Oscillation; the onset of the spring phytoplankton bloom began earlier in years of cold bottom temperature; the timing of copepodite recruitment (C1 appear) was earlier in years of cold bottom temperature, more southerly ice extent and early bloom onset; the magnitude of copepodite abundance (May C1–C5 m^{-3}) was greatest in years of most southerly sea ice extent (Table IV).

DISCUSSION

Climate and *C. marshallae* dynamics

Our sampling period (1995–1999) spanned the full range of sea ice and temperature conditions that occurred in the south-eastern Bering Sea over the past 34 years (Wyllie-Echeverria and Wooster, 1998). Around 1977 or 1978, Bering Sea ice extent decreased abruptly, by about 5%,

and has since remained lower, while spring air temperatures over the Bering Sea increased by 0.2°C decade^{-1} between 1960 and 1990 (Weller *et al.*, 1997). The period from 1978 to 1999 is considered a 'warm' phase of the Pacific Decadal Oscillation. Within this particular stanza of warm years, however, 1995 and 1999 were the coldest, iciest years in recent decades, comparable with conditions before the 1977 'regime shift' (Niebauer, 1998), while 1996 and 1998 were unusually warm. Conditions in 1998 were strongly influenced by climate forcing of a different temporal period, the El Niño–Southern Oscillation (Overland *et al.*, 2001).

The timing and magnitude of *C. marshallae* production on the south-eastern Bering Sea shelf was extremely variable among the years of our study period, reflecting environmental conditions. The first copepodites were recruited as early as March (1995) and as late as the end of May (1996), and there was a 500-fold range in spring copepodite abundances among years. Our data set was relatively limited in its spatial and temporal coverage and total number of samples. It does not offer conclusive results for all aspects of the relationship between climate and *C. marshallae* population dynamics, and some relationships may exist that were not detectable from only 5 years of data, given the inherent variability of the system. However, these clear patterns emerged: (i) egg production

occurred over a long period, beginning well before the spring bloom; (ii) spring copepodite recruitment occurred over a shorter time, approximately coinciding with the spring bloom; (iii) the relationship between standing stock of females and G1 copepodites was weak; (iv) the timing of the spring bloom and copepodite recruitment was earlier in cold years; and (v) the highest spring abundances of *C. marshallae* occurred in years of greatest southern sea extent.

Broodstock and egg production

The terminal moult to adult female occurred before February, and well before the spring bloom, in the 2 years for which we had February data. In the coastal Oregon upwelling system, dormant *C. marshallae* C5 'awaken' and moult to maturity around the same time as in the Bering Sea (Peterson, 1998). For the Oregon population, the terminal moult occurs months before upwelling begins, during a downwelling period when surface water is transported shoreward, carrying the adults onto the narrow shelf (Peterson, 1998). In the Bering Sea, *C. marshallae* is thought to overwinter on the wide shelf, requiring no transport mechanism. Possible cues for the cessation of diapause and the terminal moult, such as day length and temperature, are very different in these two areas and do not explain the observation that in both populations copepodites 'wake up' at about the same time.

Although the timing of the terminal moult is notably similar, *C. marshallae* apparently has a different reproductive strategy in the Bering Sea shelf and Oregon upwelling regions. In Oregon, egg production is tightly coupled with high phytoplankton concentrations associated with upwelling events, and there are several generations each season (Peterson, 1998). In the Bering Sea, the main spring cohort was born before the bloom in most years. In general, only one generation is produced by the Bering Sea population, although two discrete generations were noted in 1981, a 'warm' year (Smith and Vidal, 1986). Generation number is difficult to define from the data available for both the Oregon and Bering Sea ecosystems. In the former, samples were collected relatively frequently in a highly advective system, while in the latter, sample collection was infrequent in a system where advection is considered to be very low and spatial homogeneity is high.

Different intraspecific spawning patterns have been observed for *C. finmarchicus*, which typically reproduces during the spring phytoplankton bloom [reviewed in (Hirche, 1996)], but spawns before the bloom in some areas (Runge and de LaFontaine, 1996; Durbin *et al.*, 1997; Miller *et al.*, 1998; Niehoff *et al.*, 1999). Based on our results, we speculate that Bering Sea *C. marshallae* may share fewer life history traits with populations of the same species in the Oregon upwelling zone than it does with, for example, arctic *C. glacialis*, a true shelf population that spawns independently of the bloom and over a long duration (Hirche and Kwasniewski, 1997; Ohman *et al.*, 1998). This hypothesis deserves scrutiny; we believe future intensive study of the life-history traits and strategies of *C. marshallae* relative to the rest of the *C. finmarchicus* lineage is warranted.

During our study, egg production began well before the spring bloom and continued over a long period, at least into May. Nearly all females contained mature oocytes in February 1998, and 39% did in February 1999. In pre-bloom egg production experiments in February 2000, 98% of females in the experiments were reproductively mature and they produced an average of 46 eggs clutch^{-1} (unpublished data). *Calanus marshallae* nauplii (stages 1–3) were present in April 1996, a month before the bloom began. The copepodite stages that were most abundant in April and May were born well before the spring phytoplankton bloom in most years, according to our back-calculations. From these data we conclude that reproduction began early and copepodites born before the spring bloom represented the main cohort at least in 1998, and probably in 1995, both years of high copepodite concentrations. However, conclusive proof that pre-bloom spawning constitutes the bulk of annual recruitment would require more frequent sampling of the same population, particularly in late May and June when bloom and post-bloom nauplii would recruit to the copepodite stages.

Knowledge of the occurrence and relative importance of early, pre-bloom, egg production is beginning to emerge. For example, Niehoff *et al.* concluded that pre-bloom egg production by Norwegian Sea *C. finmarchicus* was equal to production during and after the bloom (Niehoff *et al.*, 1999); the low fecundity of pre-bloom females was compensated by the large numbers of ovigerous females. Our findings agree with Naumenko's observations of ovigerous female *C. marshallae* (formerly identified as *C. glacialis*) and *Calanus* nauplii in the southeastern Bering Sea in January (Naumenko, 1979). We calculated that egg production began as early as January, and we found that a large percentage of females were ovigerous and producing clutches in February. Our results suggest that female *C. marshallae* in the south-eastern Bering Sea can be both abundant and fecund before the bloom. Back-calculated birthdates of copepodites surviving until the spring demonstrate that pre-bloom egg production can be very important for Bering Sea *C. marshallae* populations.

If pre-bloom egg production is important to Bering Sea *C. marshallae*, then what sources of energy support egg production? In other systems, egg production before the

bloom has been shown to be fuelled by energy sources such as depot lipids, omnivory and ice algae [e.g. (Smith, 1990; Tourangeau and Runge, 1991; Hirche and Kattner, 1993; Ohman and Runge, 1994; Runge and de Lafontaine, 1996; Miller *et al.*, 1998; Niehoff *et al.*, 1999)]. Peterson determined that, at 10°C in the laboratory, *C. marshallae* achieved maximum egg production rates at phytoplankton concentrations above 450 µg C l^{-1}, but clutches were still produced at concentrations below 60 µg C l^{-1} (Peterson, 1988). We know very little about the pre-bloom food availability in the Bering Sea, particularly under the ice. A rough estimate of prey carbon available before the bloom is ~12 µg C l^{-1} [heterotrophic micro-plankton 1–10 µg C l^{-1} (Howell-Kübler *et al.*, 1996); nauplii 0.6–1.0 µg C l^{-1} (Napp *et al.*, 2000); *Oithona* spp. ~0.07 µg C l^{-1}; unpublished results]. If these numbers are representative, then predation could at best supplement female lipid stores. Naupliar growth may be supported by pre-bloom phytoplankton stocks that are insufficient for copepodid survival, or by omnivory (e.g. Merrell and Stoecker, 1998).

There are a number of potential advantages to spawning early and over a long period. Peterson suggested that Oregon coast *C. marshallae* compensated for low daily production (24 eggs female^{-1} day^{-1}) by reproducing over a long duration (Peterson, 1988). Eggs produced before the spring bloom also may be spared the deleterious effects of a poor maternal diet; some diatom species have been shown to decrease egg viability in the laboratory [e.g. (Poulet *et al.*, 1994; Uye, 1996; Ban *et al.*, 1997; Miralto *et al.*, 1999)], though *in situ* estimates show no negative relationships between diatom dominance and copepod egg viability (Irigoien *et al.*, 2002). A recent review suggested that only certain diatom species affect copepod egg viability, and that the negative effects of diatoms might also be mitigated by ingestion of other food species (Paffenhöfer, 2002). It is not known what prey items *C. marshallae* ingest during the spring bloom over the Bering Sea shelf. *Chaetoceros* and *Thalassiosira*, two diatom genera that inhibited copepod egg viability in laboratory experiments, dominate the early-middle stages of the bloom over the Bering Sea shelf, but heterotrophic dino-flagellates can also be very abundant during a diatom bloom in the nearby coastal Gulf of Alaska (Goering and Iverson, 1981; Howell Kubler *et al.*, 1996). Predation pressure may favour early spawning; Kaartvedt suggested that *C. finmarchicus* in the Norwegian sea spawn early to reduce parental exposure to predation by migrating fish. In the south-eastern Bering Sea, protracted reproduction may be 'bet hedging' to ensure that some pre-recruits coincide with favourable conditions in an environment subject to great interannual variability (Kaartvedt, 2000). We hypothesize that at least one of the favourable

conditions is that recruitment to C1 coincides with the onset of the spring phytoplankton bloom.

Copepodite recruitment

A recruitment bottleneck may occur at the egg, naupliar or early copepodid stages, through one of a number of possible mechanisms. For example, *C. finmarchicus* in the Norwegian Sea produces eggs well before the bloom, but net population growth does not occur until much later because of high egg mortality rates, attributed to canni-balism by adults and C5 copepodites before phyto-plankton prey were abundant (Ohman and Hirche, 2001). *Calanus hyperboreus* in the Barents Sea spawns in January or February, but nauplii do not develop beyond N3, the first feeding stage, until food concentrations increase during the much later spring bloom (Melle and Skjoldal, 1998). Effects of food limitation on *C. finmarchicus* on Georges Bank were most severe during late naupliar (N4–N5) and early copepodite (C2–C4) stages (Campbell *et al.*, 2001a). Hirche *et al.* found that *C. finmarchicus* in the Norwegian Sea produces eggs continually from March to June, but copepodites do not develop beyond the C1–C2 stages before the spring bloom, and then form a clear cohort (Hirche *et al.*, 2001). They suggested that this may be the result of different feeding mechanisms or food require-ments of young copepodite stages compared with nauplii and late stage copepodites.

For Bering Sea *C. marshallae*, the recruitment bottleneck appears to be around the first copepodite stage. Eggs were produced over a long duration—from February until at least May—but copepodites were apparently recruited during a relatively short period; there were typically two dominant copepodite stages at any given spring sampling time. Copepodite recruitment was approximately coinci-dent with the spring phytoplankton bloom, supporting Smith and Vidal's (Smith and Vidal, 1986) speculation that the life cycle of *C. marshallae* is timed so that most copepodid growth occurs during the bloom. An exception was 1998, a very cold spring with a February ice event when early copepodites were already abundant in April, before fluorescence increased in May. Fluorescence is a proxy for phytoplankton biomass and an imperfect index of zooplankton food, and 1998 might be an example of a situation in which fluorescence was an inadequate measure. To achieve a better understanding of the recruitment bottleneck, we need to assess the quantity and quality of the entire assemblage of potential prey, includ-ing both auto- and heterotrophs, during this critical period. In 4 of the 5 years that we observed, however, the increase in fluorescence appeared to coincide with conditions favourable to C1 recruitment.

A recruitment bottleneck at the C1 stage, coupled with the weak relationship between brood stock and G1

copepodite concentrations, suggests that differential survival, rather than birth rate, may be most important in determining the timing and magnitude of *C. marshallae* copepodite populations. If differential survival explains the coincidence of copepodite recruitment with the spring bloom, there must be differences in the food requirements of, or predation pressure on, nauplii and copepodids to cause a bottleneck between these stages. However, the differential survival hypothesis has yet to be tested for Bering Sea *C. marshallae* populations [cf. (Ohman and Hirche, 2001)].

The influence of climate

The existence of a strong link between climate and copepod population dynamics has previously been established for other regions. For example, higher abundances of *C. finmarchicus* are correlated with low sea surface temperatures in the Gulf of Maine (Licandro *et al.*, 2001) and a 40-year decline in California Current zooplankton biomass is associated with increased temperature (McGowan *et al.*, 1998). Long-term fluctuations in the north-east Atlantic correlate well with the NAO index (Planque and Reid, 1998). However, the mechanisms for these relationships are poorly understood (Planque and Fromentin, 1996; Planque and Reid, 1998). Similar linkages between climate and plankton are beginning to be seen in the Bering Sea and the Gulf of Alaska, but hypotheses regarding the exact mechanisms remain to be tested (Brodeur and Ware, 1992; Sugimoto and Tadokoro, 1997; Brodeur *et al.*, 2000; Napp *et al.*, 2002).

Sea ice extent was the strongest determinant of spring copepodite abundance in our study. Our data set does not provide an explanation for this relationship, but ice cover might affect copepod recruitment through its effect on food resources, predation, or both. Ice cover might affect the bloom *magnitude*, which we were not able to assess. Ice algae also may be an important source of food for copepodites. Runge *et al.* found that phaeopigments in *C. glacialis* guts increased 10-fold at the commencement of a bloom of interfacial ice algae, and concluded that sedimenting ice algae, and diatoms seeded from the interfacial layer and actively growing in the water column, were a major source of nutrition for spring copepod production in Hudson Bay (Runge *et al.*, 1991). The presence of sea ice may also result in lower predation pressure on copepods. For example, planktivorous fish, such as walleye pollock (*Theragra chalcogramma*), tend to avoid the Middle Shelf Domain, where *C. marshallae* resides, when sea ice is present (Wyllie-Echeverria and Wooster, 1998).

Conclusions

Our results suggest a scenario linking annual variability in the atmosphere–ice–ocean system with copepod population dynamics: *C. marshallae* produces eggs over a long duration, beginning well before the spring phytoplankton bloom. Spring copepodites are recruited over a relatively short period, coincident with the bloom. Both timing and magnitude of copepodite recruitment are highly variable among years. The abundance of recruits is not related to parental abundances, but is highest in years with the most extensive ice cover. This study provides insight into how longer-term climatic changes, through their effect on sea ice and temperature, may alter the dynamics of the Bering Sea Shelf zooplankton community.

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