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## Effects on zooplankton of a warmer ocean: Recent evidence from the Northeast Pacific

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### Abstract

The consequences for pelagic communities of warming trends in mid and high latitude ocean regions could be substantial, but their magnitude and trajectory are not yet known. Environmental changes predicted by climate models (and beginning to be confirmed by observations) include warming and freshening of the upper ocean and reduction in the extent and duration of ice cover. One way to evaluate response scenarios is by comparing how “similar” zooplankton communities have differed among years and/or locations with differing temperature. The subarctic Pacific is a strong candidate for such comparisons, because the same mix of zooplankton species dominates over a wide range of temperature climatologies, and observations have spanned substantial temperature variability at interannual-to-decadal time scales. In this paper, we review and extend copepod abundance and phenology time series from net tow and Continuous Plankton Recorder surveys in the subarctic Northeast Pacific. The two strongest responses we have observed are latitudinal shifts in centers of abundance of many species (poleward under warm conditions), and changes in the life cycle timing of *Neocalanus plum-chrus* in both oceanic and coastal regions (earlier by several weeks in warm years and at warmer locations). These zooplankton data, plus indices of higher trophic level responses such as reproduction, growth and survival of pelagic fish and seabirds, are all moderately-to-strongly intercorrelated ( $|r| = 0.25\text{--}0.8$ ) with indices of local and basin-scale temperature anomalies. A principal components analysis of the normalized anomaly time series from 1979 to 2004 shows that a single “warm-and-low-productivity” vs. “cool-and-high-productivity” component axis accounts for over half of the variance/covariance. Prior to 1990, the scores for this component were negative (“cool” and “productive”) or near zero except positive in the El Niño years 1983 and 1987. The scores were strongly and increasingly positive (“warm” and “low productivity”) from 1992 to 1998; negative from 1999 to 2002; and again increasingly positive from 2003-present. We suggest that, in strongly seasonal environments, anomalously high temperature may provide misleading environmental cues that contribute to timing mismatch between life history events and the more-nearly-fixed seasonality of insolation, stratification, and food supply.

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## 1. Introduction

Although model-based and observational evidence of global warming are becoming increasingly strong (IPCC, 2001), the future effects of a sustained warming trend on the pelagic plankton and fish communities of mid and high latitude ocean regions remain uncertain. Interpretation and prediction of ecological consequences of global warming impacts are difficult for several reasons: temperature and ecosystem variability occurs naturally at a wide range of temporal and spatial scales, ecological and climatic interactions are complex and nonlinear, and future temperatures at any given location may fall above the range of historical observations for that region. Nevertheless, comparisons between ocean regions and between years that differ in mean temperature but are similar in species composition are likely to provide useful clues.

The subarctic Northeast Pacific provides one useful comparison site. Its physical and biological oceanography have been studied intensively for more than 50 years. One consequence is that the taxonomic status, diet, life histories, and spatial distribution patterns of the dominant copepod species are relatively well known. Total mesozooplankton biomass and productivity are strongly dominated by large-bodied calanoid copepods. Seaward of the continental shelf, these include “interzonal migrant” species in the genus *Neocalanus* with one year life cycles (extending to two years in the coldest parts of the NW Pacific) in which spring and early-mid summer feeding and growth in the upper ocean alternates with a prolonged dormant period much deeper in the water column. Along the margins, these species are joined/replaced by *Calanus marshallae* and *Pseudocalanus* spp. The subarctic Pacific shares with the Bering Sea this same set of dominant mesozooplankton species, plus many additional zooplankton taxa and environmental characteristics (cf. Smith and Vidal, 1986; Coyle et al., 1996; Mackas and Tsuda, 1999; Coyle and Pinchuk, 2003). Life history strategies such as annual or biennial life cycle, lipid accumulation, and seasonal dormancy (Conover, 1988) are also shared with the *Calanus* species (*Calanus hyperboreus*, *Calanus glacialis*, and *Calanus finmarchicus*) that dominate the copepod community in the Arctic Ocean and high latitude regions of the Atlantic.

The remainder of this paper is structured as follows:

- Section 2 describes our data sources and sampling and analysis methodologies.
- Section 3 summarizes the environmental conditions that zooplankton are likely to encounter if and when high latitude oceans become warmer, and how the changing and unchanging factors may interact to produce ecological challenges.
- Section 4 contains results from new and/or updated Northeast Pacific time series describing trends and multi-year fluctuations of upper ocean temperature (Section 4.1), zooplankton biomass and community composition (Section 4.2), copepod life cycle phenology (Section 4.3), and survival and growth of ‘predator’ species that depend on the zooplankton for food either directly or at one-trophic-step separation (Section 4.4).
- Section 5 attempts to relate these time series using multivariate correlation and ordination, and returns to a discussion of how further warming of high latitude oceans might produce mismatch of environmental and biological seasonality.

## 2. Data sources and methodologies

Sources for the time series of data and statistical indices used in this paper are summarized in Table 1, and zooplankton sampling locations are shown in Figs. 1 and 2.

### 2.1. Zooplankton net tows from NE Pacific research cruises and monitoring surveys

Vertical net tows have been collected in the NE Pacific for several decades to monitor upper-ocean zooplankton abundance, biomass, and species and age structure composition. The main repeat sampling areas are indicated in Fig. 1, and include the immediate vicinity of Ocean Weather Station P (OSP hereafter, 50°N, 145°W), Line P (from the mouth of Juan de Fuca Strait to OSP), and the British Columbia continental margin from 48 to 51°N.

Table 1  
Description and sources of data and indices describing NE Pacific zooplankton, environmental, and predator variability at seasonal and/or interannual time scales

Data set	What was measured	Duration	Location	Primary references for original data
OSP/Line P time series	Mesozooplankton biomass (+some species ID)	1956–1980, intermittent since 1980	Ocean Station P (50°N 145°W)	Fulton (1983), Waddell and McKinnell (1995)
	Temperature and salinity profiles and anomalies	1956–present		Crawford et al. (2007), Tabata and Weichselbaumer (1992), Freeland and Cummins (2005)
Continental margin time series	Mesozooplankton abundance/biomass by species/stage,	1979–present	Vancouver Island continental margin (48–51.5°N)	Mackas et al. (2001), Mackas et al. (2004)
	Coastal sea-surface temperature anomalies	1934–present	Amphitrite Point (48° 33'N, 125° 19'W)	Institute of Ocean Sciences, Sidney, BC, Canada
North Pacific Continuous Plankton Recorder surveys	Mesozooplankton abundance/biomass by species/stage, surface temperature/salinity	1997 + 2000–present	Subarctic NE Pacific	Batten et al. (2003b), Batten and Welch (2004), this paper
'PDO' and 'Victoria' indices of large scale SST	Empirical orthogonal functions of N. Pacific SST variability	1900–present	Extratropical N. Pacific Ocean	Mantua et al. (1997); Bond et al. (2003)
Copepod life cycle timing vs. year and location	Biomass and stage composition of <i>N. plumchrus</i> from net tows and CPR	1957–present, but several data gaps	Alaska Gyre and BC continental slope	Mackas et al. (1998); Batten et al. (2003b), this paper
Marine survival of coho salmon	Return/smolt ratios of coho from selected index stocks	1970s–present	40–47°N for Oregon Production Index (OPI), ~49°N for Canadian	P. Lawson, pers. com. for updated OPI DFO Canada for Canadian stocks, this paper
Growth rate of coho salmon	Anomalies of size-at-date of fish that entered the ocean in the current year	1998–present	Vancouver Island continental margin	This paper
Sablefish recruitment	Estimated # of age 1 fish	1974–present	US west coast	Schirripa and Colbert (2006)
	Year class strength from age structure	1960–1997	British Columbia	King et al. (2000)
Auklet reproductive success	Number and size of fledglings per egg laid	1994–present	Triangle Island colony (~51°N 129°W)	Bertram et al. (2001) + M. Hipfner pers. com.

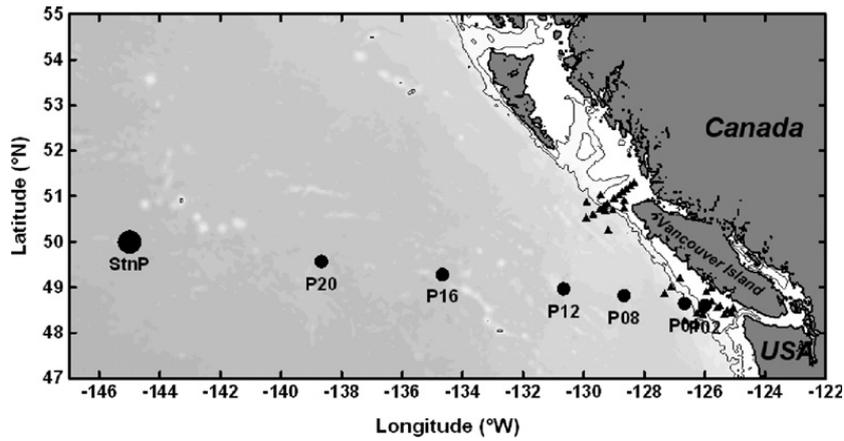


Fig. 1. Standard locations for Canadian zooplankton monitoring in the subarctic NE Pacific using upper-ocean vertical net hauls. Circles are Line P and OSP, and are sampled 2–3 times per year. Triangles are continental margin monitoring locations, sampled 3–6 times per year. Depth contour lines are 200 m and 1000 m isobaths. Deeper bathymetry indicated by grey-scale shading.

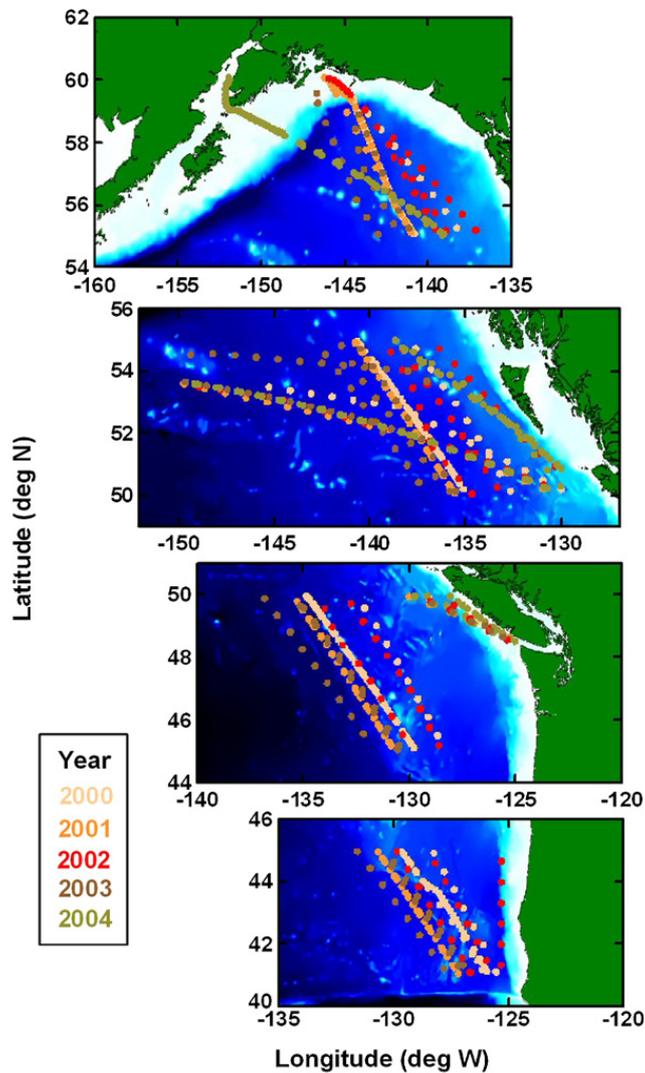


Fig. 2. Locations of fully-processed Continuous Plankton Recorder samples (dots) from the subarctic NE Pacific, color coded by year of sampling. Panels correspond to the latitudinal bands used to group samples for analysis of *Neocalanus* life cycle timing. Bottom depth indicated by background shading.

### 2.1.1. Oceanic subarctic Pacific

From 1956 to 1981, weather-observing ships occupied OSP on a rotating basis, providing platforms from which very frequent 0–150 m net tows were collected throughout the year. Samples were analyzed routinely for wet weight biomass and in some instances for species composition (Fulton, 1983; Waddell and McKinnell, 1995; Mackas and Tsuda, 1999). Biomass in the upper 150 m changes seasonally by factors of 8–20. However, there has also been large interannual variations of mean and maximum biomass which appear to coincide with changes in climatic and fishery regimes (e.g. Brodeur et al., 1996), and are not artifacts of changes in sampling gear during the weathership program (McKinnell and Mackas, 2003). Much of our present understanding of the life cycles, interzonal migration, and seasonal dormancy of *Neocalanus* spp. in the NE Pacific also comes from sets of deep tows (to 2000 m) and detailed species/stage identifications (Miller et al., 1984; Miller and Clemons, 1988) sampled during the OSP weathership time series.

The semi-continuous occupation of OSP by the weatherships ended in 1981, and the zooplankton sampling at OSP has subsequently been much less frequent and regular. However, three very large multi-investigator research programs (SUPER (Miller, 1993a), Canadian JGOFS (Boyd and Harrison, 1999a), and SOLAS/SERIES (Harrison et al., 2006)) provided intensive 2–3 week bursts of sampling in individual seasons and years. Vertical bongo net tows (0–150 m) collected along Line P since the mid 1990s have provided 1–3 day snapshots of late winter, spring, and late summer zooplankton populations in most years.

### 2.1.2. British Columbia continental margin

Zooplankton time series data from the Vancouver Island continental margin are available for most of the previous 25 years. Sampling and analysis protocols are detailed elsewhere (Mackas et al., 2001, 2004). Briefly, vertical bongo net hauls (near bottom to surface on the continental shelf, 250 m to surface over the continental slope) are collected at 10–30 standard locations per survey, and about 4–5 surveys per year. Within-season and within-region averages were used to estimate average seasonal cycles, and deviations from these climatologies are used to calculate annual log scale biomass anomalies for dominant copepod species, and are then further averaged within groups of species sharing similar distributions and environmental preferences.

## 2.2. North Pacific Continuous Plankton Recorder surveys

Continuous Plankton Recorder (CPR) surveys of the Subarctic Pacific zooplankton began in 1997 and are presently maintained along two routes (Fig. 2). The ‘north–south’ route runs between Alaska (Prince William Sound or Cook Inlet) and the west coast of the US (Long Beach, California from 1997 to 2003; Seattle, Washington in 2004). A longer but less frequent ‘east–west’ route runs between Japan and the Canada–US border. The two routes intersect in the eastern Gulf of Alaska and give total coverage within the subarctic Northeast Pacific of about 7–8 crossings year<sup>-1</sup>, with about half of these occurring spring through early summer.

The CPR sampler and its deployment and sample processing methodologies (Batten et al., 2003a) are the same as have been used in the Atlantic for seven decades. Briefly, a mechanical towed body (the CPR) is towed behind commercial ships at a depth of about 10 m. Water and plankton enter a small hole at the front of the sampler, and are progressively caught, rolled up, and formalin-preserved between two ribbons of silk gauze (mesh aperture 0.27 mm). The movement of the gauze is mechanically driven by a propeller at the tail of the CPR and is proportional to distance traveled: each 10.16 cm panel of gauze filters a total of about 3.1 m<sup>3</sup> of water and represents an average of about 18.5 km (10 nautical miles) along track. At the end of each trip, the netting cartridges are offloaded and shipped to a laboratory for sectioning and labeling of the gauze, followed by identification and enumeration of retained zooplankton by species and stage.

To compare latitudinal and interannual variability in timing, we grouped the samples from the NE Pacific CPR “north–south” and “east–west” transects into four approximately equal bands of latitude (Fig. 2): 55–60°N, 50–55°N, 45–50°N and 42–45°N. There was some between-year variability in the longitude of the CPR transects, owing to variations in the ship’s routes and (more significantly) to a 2004 eastward relocation and shortening of the north–south transect (Cook Inlet – Puget Sound since 2004 vs. Prince William Sound – California in earlier years). The vast majority of samples are oceanic, but some in the northern-most box are on the Alaskan shelf, and some in the 45–50°N box are over the continental shelf and slope off the west coast of

Vancouver Island. The consequences for observed life history timing of these variations in sampling location are discussed later.

The number of transect lines and samples collected in offshore areas during spring and early summer varies with latitude from 2 or 3 lines per year in the northern- and southern-most regions (crossed only by the “north–south” transect) to 6 lines per year in the 50–55°N band. Temporal resolution of seasonal changes in biomass and copepod developmental stage is therefore best in this band. For the portion of each transect line within a given latitude band, we calculated the mean numbers of *Neocalanus plumchrus/flemingeri* copepodites in stages C2–C5 (morphologies of these two species are sufficiently similar that they cannot be reliably discriminated in the flattened CPR specimens), and plotted these against the median sampling day for that portion of the transect (crossing of each latitude band usually took only 2–3 days). The approximate date of their annual peak biomass was estimated from changes over time in stage composition and body size ratios (see next section for details and assumptions) and, for the region between 48 and 55°N, also by plotting time sequences of total *N. plumchrus/flemingeri* biomass estimated from summed products of stage-dependent abundance and average body size.

### 2.3. Estimation of copepod life cycle timing vs. temperature and location

The zooplankton community in subarctic and Arctic ocean areas is relatively simple, and the seasonal cycle of total mesozooplankton biomass closely tracks the annual cycles of dormancy, reproduction, and somatic growth of a few large-bodied copepod species. In oceanic areas of the NE Pacific and Bering Sea, the annual peak in upper ocean biomass occurs in spring or early summer, and coincides with late stages of the growth season of *N. plumchrus*. Specifically, the biomass peak occurs after most copepodites have reached large individual size (C4 and C5), but before the majority of the C5 have left the upper layer and migrated downward to 400–1000 m where they enter a prolonged dormancy. Timing of their upper ocean biomass maximum can therefore be estimated by either of two indexing methods (Fig. 3): directly by measurements of their total biomass, or indirectly by examining their age/stage composition (Mackas et al., 1998). Because age structure varies more smoothly than local biomass, the stage ratio index gives more stable estimates when the number of samples is small or sampling interval is long. The exact timing correspondence between biomass and developmental stage depends on the spread of ages within the annual cohort – for example, if all individuals developed and migrated exactly in synchrony, the biomass peak would occur when all were C5 copepodites about to leave the surface layer. However, in the southeastern Alaska Gyre we have empirically observed that the biomass peak occurs when the *N. plumchrus* population is made up of about ~50–60% pre-dormant C5 copepodites (Fig. 3c and d). We will use both indexing methods in this paper.

As noted above, *N. plumchrus* and *N. flemingeri* are not separated in the CPR data. Batten et al. (2003b) successfully used the total percentage of C5 *N. plumchrus/flemingeri* in CPR samples from a single year (2000) to examine changes in developmental timing as a function of latitude. However, *N. flemingeri* appears and develops somewhat earlier than *N. plumchrus* in much of our study area (about 15–20 days at OSP, Miller, 1993b; Mackas et al., 1998). Lumping the two species therefore causes developmental timing estimates based on summed stage ratios to be earlier than estimates based on total biomass, or on the stage ratios of *N. plumchrus* alone. To produce CPR developmental timing indices that are intercomparable with the net tow results, we make use of the fact that *N. plumchrus* C5 are larger than *N. flemingeri* in the central and southern parts of the Alaska Gyre (Miller et al., 1992). “Large” (>4.2 mm total body length) and “small” (<4.2 mm) C5 *N. plumchrus/flemingeri* have been enumerated separately in the CPR samples collected since 2001, and for those years we use the date at which 50% of the total are “large C5” as our timing index. We will show (Section 4.3.2) that this assumption and correction appeared to be effective in the southern half of our study area, but may be less reliable in the northern half, where the between-species contrast in size is smaller and is confounded by within-species size differences between nearshore and oceanic-origin populations (Miller et al., 1992). For the 2000 CPR data, we have assumed a timing correction of 5 days (used by Mackas et al., 1998 for pre-1983 data from OSP).

We previously showed (Mackas et al., 1998) a strong correlation between *N. plumchrus* life cycle timing at OSP and local mixed layer temperature during March–May. We concluded that variability of cohort timing develops primarily during their surface-layer growing season, rather than through altered timing of

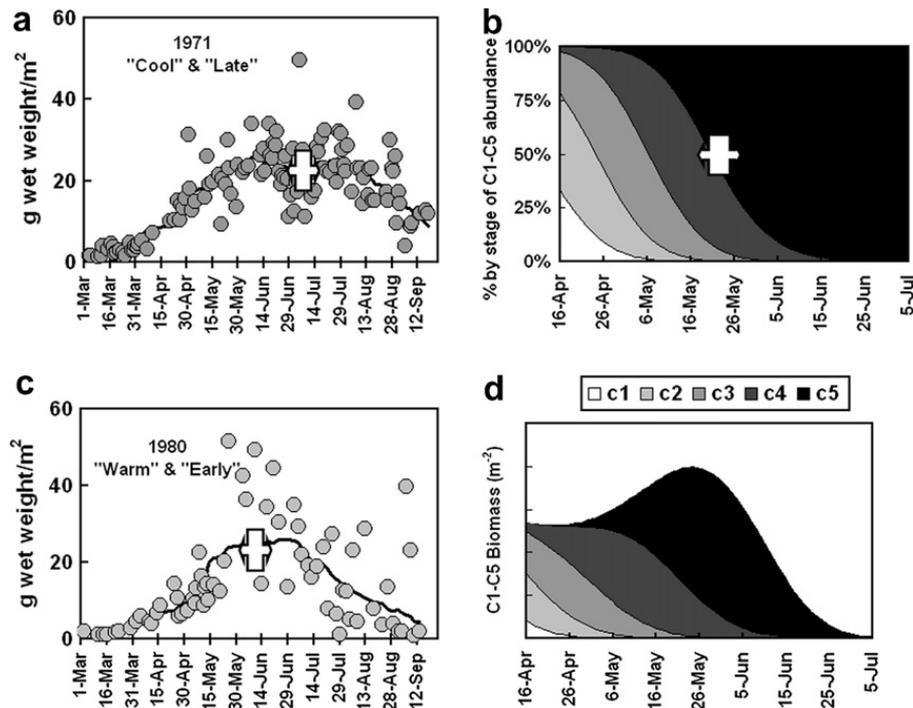


Fig. 3. Two alternative methods used for estimating timing of the annual upper ocean biomass maximum of the dominant subarctic Pacific copepod *Neocalanus plumchrus*. Left panels (a and c) show ~daily interval biomass time series from the OSP waterships sampling program. Circles are raw data points, line is a 20 point, 80% running trim-mean. White block arrows show the timing estimates and their approximate uncertainty. Right panels (b and d) illustrate timing estimation based on stage composition: (b) shows the change in % total abundance by stage as the annual cohort develops (simulated using literature estimates of stage duration and mortality), (d) shows the same developmental sequence weighted by individual body size. The biomass peak occurs when about 50–60% of the population is made up of pre-dormant C5 copepodites. White block arrow again shows the timing estimate and its approximate uncertainty.

maturation and spawning by their parent generation, and is caused by a combination of differential survival and altered developmental stage duration. In this paper, we add additional years to the Alaska Gyre time series, plus timing estimates for more nearshore populations of the same species along the Vancouver Island continental margin. For each year and location (Alaska Gyre vs. BC continental margin) for which we have net tow estimates of *N. plumchrus* life cycle timing, we have quantified the interannual cumulative variability of local spring season temperature as March–May degree days relative to a 6 °C baseline (see Mackas et al., 1998 for examples and additional detail). For this calculation, we have variously used temperature time series from nearby CTD casts, Argo float profiles, and/or monthly averages of sea-surface temperature available on the web. One caveat is that the zooplankton data come from fixed stations or linear sections. To compare phenology with temperature, we have assumed that the Eulerian (observed) and Lagrangian (inferred) time series of zooplankton and temperature are similar. This assumption can break down if and where there is very rapid advection across steep surface temperature gradients. The difference between Eulerian and Lagrangian temperature histories is relatively small in offshore areas because mean advection is slow ( $\sim 0.05\text{--}0.1\text{ m s}^{-1}$ ) and is also mostly along rather than across surface isotherms (Bograd et al., 1999; Freeland and Cummins, 2005; Batten and Freeland, 2007). However, cross-gradient flow is more rapid along the continental margins. Along the northeast margin of the subarctic Pacific, Lagrangian histories will tend to be warmer than Eulerian because the Alaska Current and Alaskan Stream bring water and animals from warmer upstream to cooler downstream locations. The sign of the difference is opposite in the northwest subarctic Pacific, where transport by the East Kamchatka and Oyashio Currents brings water and animals from cold upstream locations.

#### 2.4. Additional indices of upper ocean temperature

Global sea-surface temperature anomalies are taken from the NOAA National Climatic Data Center (<http://lwf.ncdc.noaa.gov/oa/climate/research/anomalies/anomalies.html#anomalies>) and are relative to

1901–2000 norms. For description of interannual variability of large scale North Pacific temperature patterns we have used monthly mean temperature and seasonal climatology maps from the NOAA Pacific Fisheries Environmental Laboratory (<http://las.pfeg.noaa.gov>) and the Principal Component (PC) time series of detrended North Pacific winter sea-surface temperature anomalies as published by Bond et al. (2003) and subsequently updated through 2005 (PICES, 2005; Bond pers. comm.). The spatial pattern and time series for the first EOF/PC in the Bond et al. (2003) analysis are nearly identical to those of the winter PDO index of Mantua et al. (1997). We will therefore use “PDO” as a shorthand identifier for this time series. Positive scores correspond to positive temperature anomalies in our study region (the subarctic NE Pacific). Bond et al. (2003) reported that their second EOF/PC (termed the “Victoria” pattern or index by McKinnell, 2004; a practice we repeat here) has accounted for most of the post 1990 SST variance. Positive scores for this component correspond to negative temperature anomalies in most of the Alaska Gyre, but weakly positive anomalies along the North American continental margin.

To describe interannual variability and trends of temperature in more localized regions, we use yearly average SST anomalies from the Amphitrite Point lighthouse (located on the SW coast of Vancouver Island at 48°33'N, 125°19'W; source data available at <http://www-sci.pac.dfo-mpo.gc.ca/osap/data/lighthouse/amphitrt.txt>), and averages along Line P of upper ocean (10–50 m) temperature anomalies (derived from more detailed data in Crawford et al., 2007).

### 2.5. Indices of success of higher trophic level species

We compared the zooplankton and temperature time series with time series for four fish and colonial seabird species that either consume zooplankton directly or feed on small forage fishes that consume zooplankton: coho salmon (*Oncorhynchus kisutch*), larval/juvenile sablefish (*Anoplopoma fimbria*), and Cassin's Auklet (*Ptychoramphus aleuticus*) and Rhinoceros Auklet (*Cerorhinca monocerata*). This focus on vertebrate predators is because of their perceived importance to people; it should be recognized that much of the total predation mortality on copepods is in fact imposed by other mesozooplankton such as chaetognaths, medusae, and euphausiids.

Although most Pacific salmon species and stocks commence a long range migration shortly after entering the ocean (initially alongshore and poleward on the continental shelf, later offshore into the deep ocean), many coho from the outer coasts of Vancouver Island, Washington and Oregon remain on the continental margin within 200–400 km of their natal streams until at least the fall of their first year at sea (Morris et al., 2007). Diet consists primarily of planktivorous forage fishes plus some large zooplankton. Variability of their annual growth trajectories (estimated from field measurements of length-at-date) and overall marine survival (estimated from return:smolt ratios of fish tagged prior to ocean entry) can therefore reasonably be compared to local oceanographic conditions. For the southwest outer coast of British Columbia, estimates of coho marine survival (referenced to year of ocean entry) are derived from two index sites on the outer coast of southern Vancouver Island: the Robertson Creek hatchery and Carnation Creek. For Oregon/Washington, we use the Oregon Production Index ratio of returns to released smolts (data provided by Peter Lawson, NOAA NMFS Newport Oregon).

We also include a shorter time series (1998–present; Trudel et al., 2007) of early marine growth rate anomalies of coho sampled off Vancouver Island by the Canadian High Seas Salmon Program (Welch et al., 2003). Summer growth rates (SG, mm/d) of juvenile coho salmon off Vancouver Island were estimated from the size of coho juveniles caught during the fall (October–November) using the equation:

$$SG = \frac{FL_C - FL_{OE}}{DY_C - DY_{OE}} \quad (1)$$

where  $FL_C$  is the size at capture,  $FL_{OE}$  the assumed size at ocean entry ( $\sim 120$  mm, Sandercock, 1991), and  $DY_C$  and  $DY_{OE}$  are, respectively, the day of the year at capture and assumed day of ocean entry ( $\sim 15$  May for WCVI, Spence, 1995). Attribution of these fish as outer coast residents is less certain than for the outer coast index stocks used for the survival rate estimates: many may have originated from and attained part of their prior growth in the Strait of Georgia, Puget Sound, and the Strait of Juan de Fuca.

Sablefish year-class strength time series are reported for the US west coast by Schirripa and Colbert (2006) and for the BC coast by King et al. (2000). Sablefish spawn at depths of several hundred meters. Newly-hatched larvae migrate upward to the sea-surface where they are epipelagic for much of their first year. First-feeding sablefish larvae (still at depth) feed almost entirely on *Neocalanus* nauplii (McFarlane and Beamish, 1992), while the diet of later stage larvae (10–30 mm body length) is dominated by copepods (Grover and Olla, 1987, 1990; McFarlane and Beamish, 1992), and juvenile diet is dominated by euphausiids and other large zooplankton.

Variability of reproductive success of planktivorous and piscivorous alcids at the large Triangle Island seabird colony (51°N, 129°W) was documented by Bertram et al. (2001) and has subsequently been monitored and reported by M. Hipfner (pers. comm., and in North Pacific Ocean Status Reports produced annually by Fisheries and Oceans Canada [web address = [http://www.pac.dfo-mpo.gc.ca/sci/psarc/OSRs/Ocean\\_SSR\\_e.htm](http://www.pac.dfo-mpo.gc.ca/sci/psarc/OSRs/Ocean_SSR_e.htm)]). For the comparison time series used in this paper, we have normalized Hipfner's and Bertram's 1995–2004 annual estimates of “fledgling production” for Cassin's and Rhinoceros Auklets. “Fledgling production” is defined as the mean mass (in grams) of fledgling produced per egg laid, and is calculated for each species as the product of hatching success (proportion of eggs laid that hatch) \* fledging success (proportion of hatched chicks that fledge) \* mean mass at fledging. Cassin's Auklets are preferentially planktivorous, and adults at the Triangle Island colony feed themselves and their chicks primarily on late-stage *Neocalanus* copepodites (Hedd et al., 2002). Rhinoceros Auklets are piscivorous, and at Triangle Island feed primarily on small planktivorous fishes such as sandlance (*Ammodytes hexapterus*), juvenile herring (*Clupea harengus pallasi*) and juvenile rockfish (*Sebastes* spp.).

## 2.6. Statistical comparison between time series

We use a combination of product-moment correlations and principal component ordinations to examine the strength and consistency of statistical associations among ocean warming, zooplankton population and life history responses, and success of finfish and seabird predator populations.

A constraint on (and the only non-standard feature of) our analysis is that the biological time series vary in their duration, completeness, and degree of overlap (Table 1, Figs. 5, 8, 9 and 14). The elements of the pairwise correlation matrix therefore differ in the sets of years from which they are calculated. We have assumed stationarity, and have also excluded pair-wise correlations for which the data series have fewer than 5 years of overlap (out of a maximum of 25 years). To make the temporal coverage less gappy and reduce the uncertainty of individual pairwise correlation estimates (and also because the estimated correlations were often larger as well as more stable for more aggregated data) we averaged the British Columbia and Oregon coho survival time series, and also the two sablefish recruitment time series, and used the correlations with these averages as input to the principal components (PC) ordination. Similarly, because the data series contain gaps, the PCs cannot be calculated in the usual way (by singular value decomposition of a complete variables vs. years data matrix). Instead, we have used an eigen decomposition of the correlation matrix as estimated above.

We show the PC results in two ways. Plots of the eigenvector coefficients for each of the variables on the first three PC axes show how strongly the different variables project onto these components, and also which variables respond most similarly. To summarize the temporal pattern of shared variability, we also report time series for the three leading principal components. For years in which all variables were measured, the PC scores are calculated conventionally as sums of the data time series weighted by their corresponding eigenvector components:

$$PC(i, t) = \sum_{j=1}^M (E(i, j) \bullet X_N(j, t)) \quad (2)$$

$PC(i, t)$  is the score for the  $i$ th PC in year  $t$ ,  $M$  is the number of data time series (14 for this analysis),  $E(i, j)$  is the component of the eigenvector for  $PC(i)$  corresponding to the  $j$ th data variable, and  $X_N(j, t)$  is the normalized time series (zero mean, unit standard deviation) for the  $j$ th variable in year  $t$ .

For years in which there are missing data, the absolute magnitude of the PC scores is biased toward zero because the ‘blank’ data do not contribute to the summation. We have compensated for this bias by multiplying the PC scores for those years by scaling vectors with elements:

$$S(i, t) = 1 / \left( \sum_{j=1}^M (E(i, j) \bullet D(j, t))^2 \right) \quad (3)$$

where  $S(i, t)$  is an estimated multiplicative correction factor ( $\geq 1$  by definition, average for this data set = 1.3, max = 2.9) for PC( $i$ ) in year  $t$ ,  $E$  is the array of Eigenvectors and  $D$  is a “data present” matrix with value = 0 if  $X$  was unmeasured in year  $t$ , and value = 1 otherwise. This is equivalent to renormalizing the eigenvectors so that the sums-of-squares of their active elements remains = 1.0 in all years. Because most data gaps are early in the time series, the larger correction factors (and greater uncertainty of the corrected PC scores) are for the years prior to 1985.

### 3. Characteristics of a warming ocean: mix of change and persistence

The upper-ocean environmental conditions predicted by various global warming scenarios and models will expose high latitude mesozooplankton communities to a challenging combination of change and persistence. Projected changes (IPCC, 2001) over the course of the next century include:

- Warmer mean temperatures (by 2–4 °C in the subarctic Pacific, 3–7 °C in the Bering Sea and Arctic Ocean).
- Reduced ice cover (both spatial extent and seasonal duration) where sea ice is now present.
- More winter precipitation (about 100 mm year<sup>-1</sup> in the subarctic Pacific) and more freshwater runoff from the British Columbia and Alaska coasts.
- Altered atmospheric pressure patterns, affecting both ocean current trajectories and the distribution and intensity of storms.

These changes are likely to have important consequences for the productivity and seasonal timing of phytoplankton and zooplankton. Some of these effects are negative, others positive. There is already evidence from the Alaska Gyre, western subarctic Pacific, and/or Bering Sea for several of them.

- Stronger and more persistent upper ocean density stratification due to surface layer warming and freshening. For example, Freeland and Cummins (2005) analyzed 1958–2004 data and found a shoaling trend of 56 m per century for the winter pycnocline depth at OSP.
- Reduced annual re-supply of macronutrients due to weakened erosion of and mixing across the winter pycnocline. For example, the warmer and more stratified 1992–1997 period showed about a 25% depletion in the start-of-growing-season concentrations of nitrate and silicate, relative to the cooler and less stratified 1974–1981 period (Whitney and Freeland, 1999).
- Conversely, reduced ice cover and reduced downward vertical mixing below the euphotic zone may reduce spring-season light limitation, and
- Warmer temperatures will contribute to higher light- and nutrient-saturated specific growth rates of phytoplankton (Behrenfeld and Falkowski, 1997) and faster development rates of zooplankton (McLaren, 1978), leading to
- An earlier and perhaps longer growing season.

Perhaps equally important, other environmental characteristics and constraints on biological productivity in high latitude ocean regions will change very little or not at all:

- Seasonality of daylength, solar elevation, and solar warming of the sea surface are determined by latitude and the tilt of the earth’s axis. The annual cycle of both instantaneous and total daily incident irradiance will therefore remain large (Fig. 4a).
- The amplitude of the seasonal cycle of upper ocean temperature will also remain large (Fig. 4b). In the eastern subarctic Pacific, the within-year seasonal range of temperature in the upper ocean is larger by a factor of about 2–4 than the trend per century of mean  $T$  °C predicted by the IPCC global warming scenarios. This seasonal range is even larger in the western subarctic Pacific and the Bering Sea.

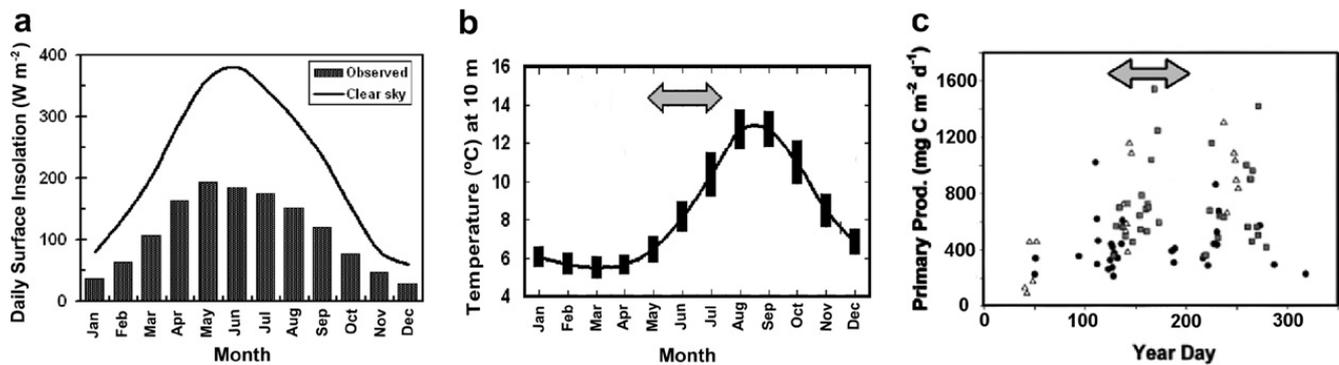


Fig. 4. Average seasonal cycles of sunlight, upper ocean temperature, and primary productivity at OSP (50°N 145°W). Note the large amplitudes, and the between-variable time lags. (a) Daily insolation. Columns are 1959–1975 averages for all measurements, plotted from data tabulated in Dobson and Smith, 1988. Line is the upper envelope for cloudless days. Note the sixfold range between winter minimum and early summer maximum, and the relatively large percentage reduction in all months due to cloud cover. (b) Mixed layer ( $z = 10$  m) temperature vs. month, from 1956 to 1990 averages tabulated by Tabata and Weichselbaumer, 1992. Line shows mean, boxes  $\pm$  one standard deviation. The annual range is about 7 °C, and the timing of the cycle lags incident sunlight by about 1/4 cycle. (c) Primary productivity, adapted from Boyd and Harrison (1999b). The annual range is about sevenfold. Timing of the peak is intermediate between the insolation and temperature maxima. Grey arrows indicate the observed range of seasonal timing for the *Neocalanus plumchrus* biomass maximum.

- Phytoplankton productivity (Fig. 4c) will continue to vary seasonally due to light limitation during a large part of each year.
- Large scale wind and upper-ocean current patterns are determined by the latitudinal and zonal gradients of insolation, ice cover, and temperature, and by the position of bathymetric obstructions and boundaries. Their seasonality is determined in large measure by the seasonal cycles of insolation and temperature. Both will persist in the Pacific under plausible warming scenarios, although there may be some shifting of spatial and seasonal gradients. The situation is less clear in the high latitude Atlantic and Arctic because of possible disruption of deep convection by surface layer freshening.

How and why would the unchanged seasonal cycles of the ocean environment influence the ability of marine biota to respond and adapt to lower frequency cycles or trends? One answer is that in high latitude regions, the periodic daily (light) and seasonal (light, temperature, stratification, transport) components of environmental variability will continue to impose the largest amplitude changes that marine zooplankton populations encounter. Each season is a large fraction of a zooplankton life span, and the life history strategies of many species show very heavy investment in adaptations (such as seasonal reproduction, migration, and dormancy) that exploit the predictably “good” parts, and minimize exposure during the difficult parts of the annual cycle. These evolved adaptations are effective if environmental variability falls within previously-encountered bounds *and* if the organism is able to synchronize its adaptive responses to environmental challenges, either because the environmental variability is strongly periodic (e.g. the diurnal and annual cycles) or because the environmental change has clear leading indicators that can cue behavioral or physiological response. Conversely, evolved adaptations (either life history and behavioral) are likely to be neutral or negative if the environmental variability is aperiodic, has weak precursor signals, or the precursor signals are misleading. We suggest that misleading thermal signals are likely under long term warming, and will discuss the implications in the final section.

#### 4. Time series observations

##### 4.1. Upper ocean temperatures

Fig. 5 shows 1958–2004 time series of global and NE Pacific upper-ocean temperature anomalies. Over this time span, the global SST anomalies (Fig. 5a, values relative to a 1901–2000 baseline climatology) are dominated by a cool episode extending from the mid-1960s to the mid-1970s, followed by a prolonged upward

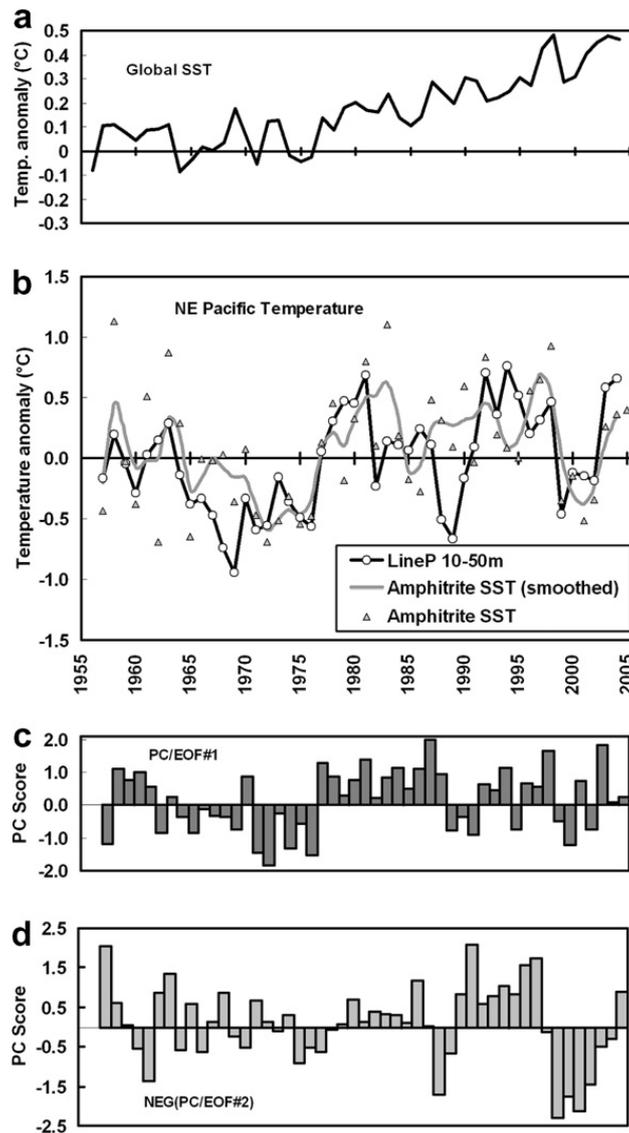


Fig. 5. Time series of upper ocean temperature anomaly indices: (a) global sea surface temperature, (b) within the Northeast Pacific: offshore (10–50 m depth stratum vertically and horizontally averaged along Line P, open circles and black line), and coastal (sea-surface temperature at Amphitrite Point lighthouse on southern Vancouver Island, annual and 3-year smoothing, grey triangles and line), (c, d) first and second principal components of de-trended North Pacific winter SST (the sign of the 2nd PC has been reversed to maintain a positive = warm graphical convention). Note the overall warming trend (a and b) overlaid by alternation of warm and cool ~decadal “regimes” and by shorter El Niño/La Niña events (b–d). The NE Pacific was generally cool in the intervals 1963–1976 and 1999–2002, moderately warm in the late 1970s–mid 1980s, and very warm from 1991 to 1998 and 2003 to 2005.

trend of about 1° per century. More locally, anomalies along Line P (Fig. 5b; values relative to 1958–2005; for additional along-line spatial resolution see Fig. 5 in Crawford et al., 2007) and at the Vancouver Island coast (Fig. 5b) show similar amplitude upward trends, but span a larger total temperature range, and retain much more variability at interannual to decadal time scales. Most of our zooplankton data come from years since the mid 1970s. During this interval, the decadal variation of temperature was strong. It included rapid warming in the mid 1970s, flattening or cooling in the mid-late 1980s, warming from the early 1990s through 1998, rapid cooling in 1999 and continuing negative temperature anomalies until 2002, and renewed warming since 2003. Intervals with especially strong changes in temperature occurred around 1976–1977, 1989–1990, and 1998–1999 (Fig. 5b). All of these have been identified as “regime shifts” by various authors. The shifts are even more apparent in the time series of SST PC scores (Fig. 5c and d), which also show that the spatial distribution of the positive temperature anomalies differed between the 1980s (dominated by positive “PDO”)

and 1990s (dominated by negative “Victoria” pattern). However it is also important to remember that the PCs omit any long-term warming trend if the temperature data are de-trended prior to their calculation.

Spatial gradients of seasonal average temperature across our study area are shown in Fig. 6. Note that the north-to-south latitudinal gradient is overlaid by a strong west-to-east and gyre-center-to-margin gradient resulting from gyre-scale advective patterns. This means that zooplankton resident near the center of the Alaska Gyre experience normally cooler temperatures in spring and summer than members of the same species located closer to the equator or to the North American continental margin.

#### 4.2. Zooplankton population size and spatial distributions

One mode of zooplankton response we have observed repeatedly during episodically ‘warm’ conditions consists of poleward shifts of spatial distribution boundaries and of zones of maximum abundance (Mackas et al., 2001; Batchelder et al., 2002; Peterson and Keister, 2003; Batten and Welch, 2004). Recent updates of

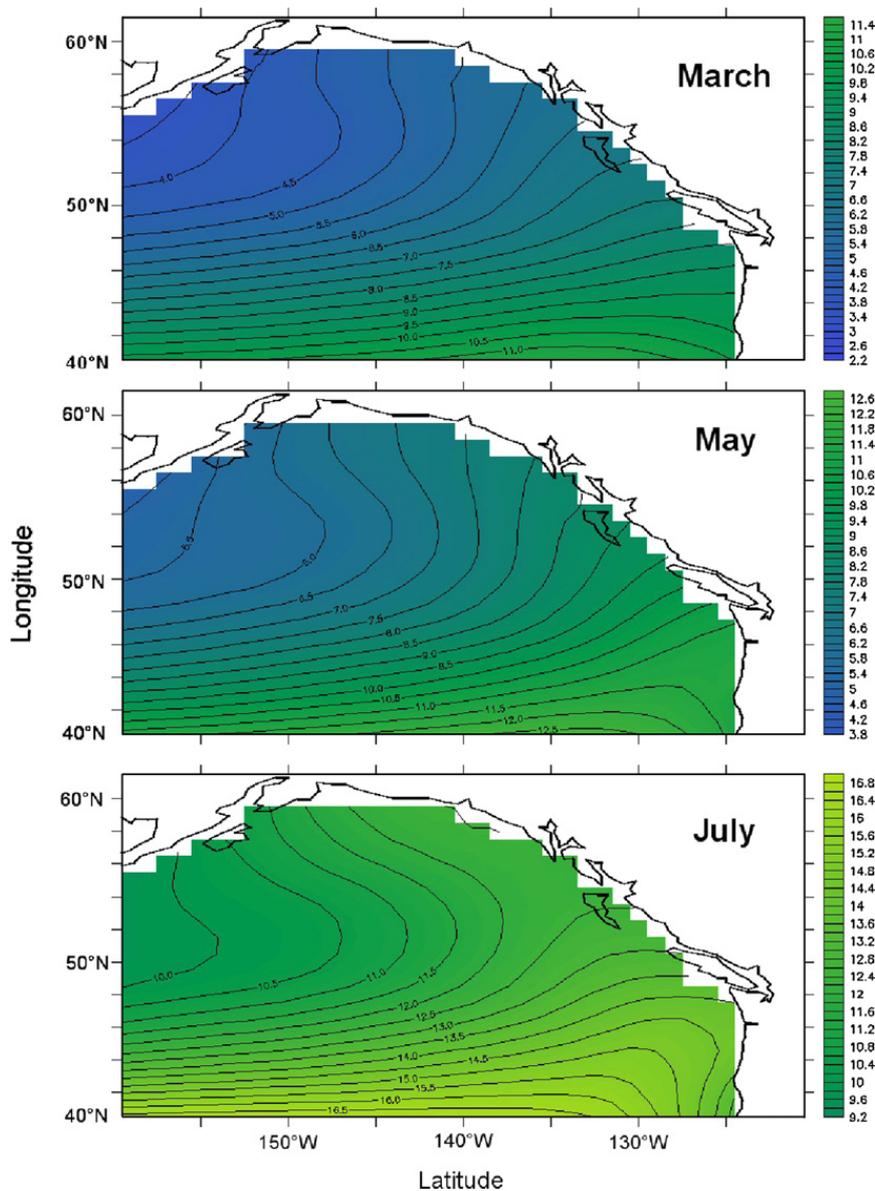


Fig. 6. 1997–2005 Monthly average patterns of sea-surface temperature in the Alaska Gyre during the spring-early summer *Neocalanus* growing season, from the Pacific Fisheries Environmental Laboratory GTS-SST archive. Spatial gradients to higher temperature are primarily north–south in the southern Alaska Gyre, but increasingly west-east in the northern Gyre.

this topic have been or are being published (Mackas et al., 2004; Keister et al., 2005; Batten and Freeland, 2007) so we will only summarize them here, plus discuss their potential importance to fish ecology in Section 4.4.

Fig. 7 shows summaries of the 1979–2005 annual biomass anomalies off the southern Vancouver Island continental margin averaged within three species groups with internally-similar zoogeographic distributions and time series (within-group correlations among species 0.7–0.9):

- “Boreal shelf” copepods (top panel, indexed by the average of the anomalies for *C. marshallae*, *Pseudocalanus mimus*, and *Acartia longiremis*; normally most abundant on the continental shelf from central Oregon to the Bering Sea).
- “Southern” copepods (middle panel, indexed by *Paracalanus parvus*, *Mesocalanus tenuicornis*, *Clausocalanus* spp., and *Ctenocalanus vanus*; normally most abundant south of our study area off the California coast).
- “Subarctic oceanic” copepods (bottom panel, indexed by *N. plumchrus*, *Neocalanus cristatus*, *Eucalanus bungii*, and *Metridia pacifica*; abundant seaward of the shelf throughout the subarctic Pacific).

Note the relative smoothness of the zooplankton anomaly time series (stronger year-to-year serial autocorrelation) compared to the temperature time series shown in Fig. 5.

The anomalies in Fig. 7 have been updated and normalized (to zero mean and unit standard deviation) from shorter, but taxonomically and spatially more detailed, time series reported in Mackas et al. (2001). Very similar patterns of interannual variability and statistical associations extend for at least 800 km alongshore, from central Oregon to the north end of Vancouver Island (Mackas et al., 2004). We review the earlier results, but will focus our description on results from the six years since 1999.

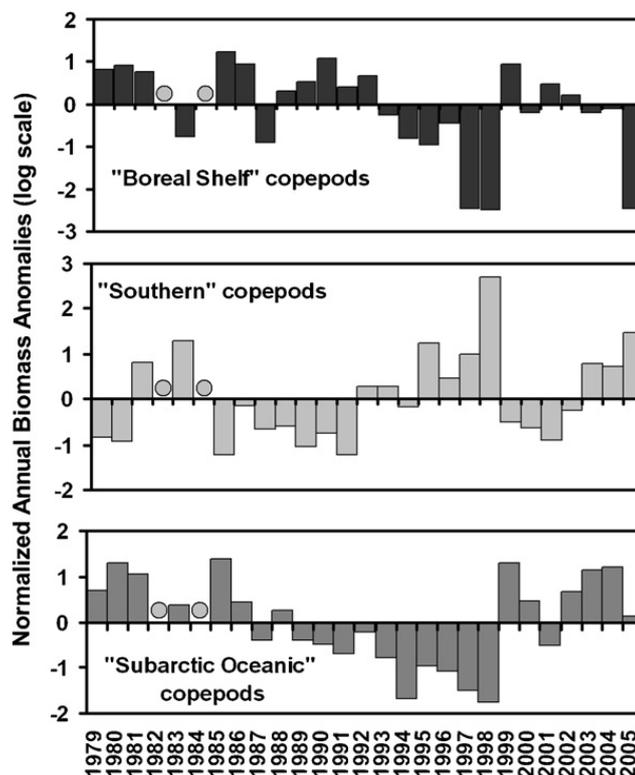


Fig. 7. 1979–2004 Time series of normalized biomass anomalies along the southern Vancouver Island continental margin for three copepod species groups. “Boreal shelf” and “Southern” copepods had near-mirror-image anomaly patterns. Circles indicate years with no or insufficient data. During the warm 1992–1998 interval, the “boreal shelf” species had much lower-than-average biomass and abundance, while the “southern” species had strong positive anomalies. The signs reversed briefly 1999–2002, but have subsequently returned to the mid 1990s patterns.

Throughout the time series, a dominant characteristic has been mirror-image variability of the “boreal shelf” and “southern” species groups. Mackas et al. (2001) previously showed that positive anomalies of the endemic “boreal shelf” copepods were associated with cool temperature and equatorward transport anomalies, while positive anomalies of the “southern” copepods were associated with warm temperatures and poleward transport. Warm temperatures along the Vancouver Island continental margin during most of the 1990s (Fig. 5b) were accompanied by prolonged and intensifying negative anomalies of the “boreal shelf” species, and positive anomalies of the “southern” species. During the 1999 La Niña event, upper ocean temperatures declined steeply and the zooplankton community off southern Vancouver Island reverted to a species mix similar to the late 1970s and early 1980s: weakly positive anomalies of the “boreal shelf” species group, and negative anomalies of the “southern” species group. This pattern persisted after the La Niña event ended, but only for four years (1999–2002). Since 2003, there has been a return to positive temperature anomalies, increasingly positive anomalies of the “southern” copepods, and increasingly negative anomalies of the “boreal shelf” group.

The anomaly time series for the “subarctic oceanic” group is determined by their spring and early summer abundance along the Vancouver Island continental shelf break and slope (not further offshore in the Alaska Gyre). In this relatively nearshore region, the sequence of rising and falling abundance has been broadly similar to the “boreal shelf” group. There are some important differences: the decline toward negative anomalies of the “subarctic oceanic” group started a few years earlier (~1988 vs. ~1991 for the “boreal shelf” group), and their post-1999 positive anomalies were larger and more persistent. Mackas et al. (2001) found an additional statistical dependence of the “subarctic oceanic” species on cross-shore transport (summer upwelling intensity) and supply of nutrients seaward of the shelf break. However, we will show in Section 4.3 that there is a second (and very large spatial scale) mode of temperature-associated interannual variability for the “subarctic oceanic” copepod group.

Temperature-and-flow-field linked displacements of zooplankton species groups are not limited to the continental margin boundary current systems. In the NE Atlantic, Beaugrand et al. (2002) showed that during the past 50 years, there have been large-scale and progressive poleward displacements of the distributions of four copepod species assemblages (indicators of warm-temperate, temperate, cold-temperate, and subarctic environments, respectively). Batten and Freeland (2007) recently examined shifts in zooplankton species distributions in the oceanic Northeast Pacific by combining CPR data with geopotential anomalies derived from Project ARGO temperature and salinity profiles. The ARGO data had previously revealed low frequency north–south displacements of the zonal North Pacific Current (Freeland and Cummins, 2005; see also Cummins and Freeland, 2007). Multidimensional Scaling ordinations of rate of occurrence in CPR samples of selected zooplankton indicator species (Batten and Freeland, 2007) showed that a relatively strong faunal discontinuity could be identified, and that the location of this discontinuity closely tracked the displacement of the bifurcation between the Alaska and Central gyre circulations.

#### 4.3. Altered seasonality of *N. plumchrus*

A second important mode of zooplankton response to climate variation consists of phenological changes: differences in when within the year a given species is most abundant, and the seasonal timing of key steps in its life cycle. The copepods that form the “subarctic oceanic” species group described in the previous section (*N. plumchrus*, *N. flemingeri*, *N. cristatus*, and *E. bungii*) have distinctive life cycles: a relatively brief growing season in spring and early summer, followed by downward migration and a prolonged annual dormancy at mesopelagic depths (400–2000 m, Miller et al., 1984; Miller and Clemons, 1988). One consequence of this life history strategy, combined with their dominance of the regional mesozooplankton biomass, is that the annual peak of total mesozooplankton biomass in the upper layers of the Subarctic Pacific is intense but very narrow (Mackas and Tsuda, 1999). At any given location, the duration over which total biomass exceeds half the annual maximum is only about one to two months. At OSP and in much of the remainder of the subarctic NE Pacific, *N. plumchrus* is the most abundant within this group. For this species, we have observed large interannual and spatial variations in the timing window for its growth, development and onset of dormancy (Mackas et al., 1998; Bertram et al., 2001; Batten et al., 2003b). Similar seasonal timing shifts have been observed in the subarctic Atlantic (Edwards and Richardson, 2004) and in the western N. Pacific (Chiba et al., 2005). In the following subsections, we present a substantial amount of new timing data and additions

to previously published phenology time series (Sections 4.3.1 and 4.3.2), plus some preliminary evidence that *N. plumchrus* may produce a (small) second cohort in warm years (Section 4.3.3).

4.3.1. Evidence from net tows

Fig. 8 shows the timing variability of *N. plumchrus* in two regions: the southern Alaska Gyre (OSP and stations P16 and P20 along the seaward half on Line P) and along the Vancouver Island continental margin (the southern and northern Vancouver island monitoring stations shown as triangles in Fig. 1, plus P4 and P8 on the nearshore part of Line P). The peak-date estimates are shown both as 1957–2004 time series (Fig. 8a) and as a function of upper ocean temperature during the March–May growing season (Fig. 8b). From the late 1950s through the mid-1970s, the OSP time series shows a trend to later peak timing. The sign of this trend reversed in the mid 1970s, and the peak biomass of *N. plumchrus* gradually shifted earlier by 5–8 weeks both in oceanic areas (grey symbols in Fig. 8a) and along the BC continental margin (black triangles). Note that the interannual-decadal variability within each region is superimposed on an east–west and nearshore–offshore spatial gradient; the date of the biomass peak along the continental margin is consistently offset about 4 weeks earlier than at OSP. In both regions, the trend to earlier timing was interrupted briefly during and immediately following the 1999 La Niña, and peak timing was close to the regional long-term averages from 1999 to 2002. However, very early timing returned in 2003 and 2004 (and almost certainly also in 2005, although our net tow sampling dates in 2005 gave relatively poor resolution).

Both along the BC continental margin and in the southern part of the Alaska Gyre, variability of *N. plumchrus* life cycle timing is associated very strongly, and approximately linearly, with cumulative anomalies of upper-ocean temperature during the season in which the copepods are feeding and growing in the near-surface layer (Fig. 8b). Note that the timing offset between continental margin and offshore regions is mostly accounted for by the fact that spring-early summer temperatures are 2–3 °C warmer along the continental margin than further offshore (see Fig. 6). The x-axis records degree days over a 90 day time span, so the full range therefore corresponds to ~6 °C difference in average temperature and to more than 3 months difference in timing of the biomass peak.

4.3.2. Evidence from the CPR

The North Pacific CPR surveys in 1997 and 2000–2004 cover fewer years than the net tow time series discussed in the previous section, and have somewhat coarser taxonomic resolution (*N. plumchrus* and *N. flemin-*

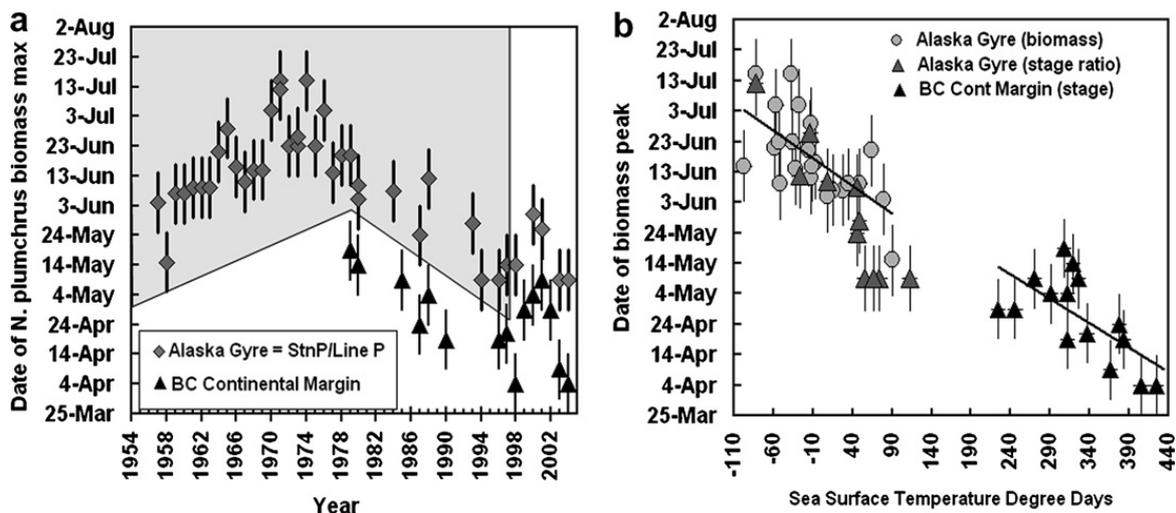


Fig. 8. Seasonal timing of the upper ocean biomass maximum of *Neocalanus plumchrus* from net tow samples in the Alaska Gyre (OSP and outer Line P) and along the Vancouver Island continental margin (updated from Mackas et al., 1998 and Bertram et al., 2001). (a) Estimated date of the biomass maximum vs. year. Timing is 3–5 weeks earlier along the Vancouver Island continental margin, but interannual-decadal fluctuations are strongly correlated. Shaded area indicates data previously published in Mackas et al. (1998). (b) Timing vs. cumulative warmth of the upper ocean during the March–May growing season (as degree days relative to a 6 °C baseline). Warmer water is strongly associated with earlier timing.

geri are not routinely discriminated in CPR samples) but span a much broader range of latitude and temperature. The CPR data (Figs. 9, 11 and 12) suggest strongly that timing trends similar to those at OSP and off Vancouver Island (Fig. 8) have occurred over much of the Alaska Gyre.

In an early analysis of CPR results from a single year (2000), Batten et al. (2003b) used stage composition in the *N. plumchrus/flemingeri* composite group to index developmental timing as a function of location along a transect from Prince William Sound to California. They found that the date at which 50% of the individuals were C5 copepodites occurred 5 weeks earlier at the south of its range (~45°N) than at the north (~60°N). Intermediate latitudes had intermediate timings.

The CPR samples from 2001 to 2004 have now been analyzed, and allow a more extensive comparison of developmental timing vs. location and year, and also of differences between alternative estimators of timing (time series of stage composition, of total *N. plumchrus/flemingeri* biomass, and of regionally-averaged upper ocean temperature). The newer data also include separate enumeration of “large” (>4.2 mm) and “small” C5 *Neocalanus* copepodites. The “large” C5 are assumed to be all or mostly *N. plumchrus*, and the “small” to be *N. flemingeri*. The new results (Figs. 9, 11 and 12) collectively support a south-to-north progression of *Neocalanus* developmental timing and also indicate that interannual variability of this timing is coherent over much (but not all) of the Gulf of Alaska. However, they also show some inconsistency among the three timing estimation methods.

Fig. 9 shows, for the three northernmost CPR sampling regions, the annual increases of percentage of “large” C5 *N. plumchrus/flemingeri* copepodites vs. survey date and year (within the 42–45°N latitude band, sampling began too late in most years to track the stage progression). Most years showed a monotonic increase in the fraction of C5 copepodites (including 2000, for which “large” and “small” C5 were not enumerated separately). The exception was 2004 (Fig. 10), when the upward trend was interrupted mid-season by relatively large numbers of C2 (at 45–50°N) or C3 (50–55°N). Within the 45–50°N band, the “% large C5” line in Fig. 9 crossed 50% twice in 2004 (~day 81 and ~day 130), and it remains unclear from the full set of stage composition data (Fig. 10) which date is closer to the annual biomass peak. Based on large total abundance on day 126, followed by a decline to very low abundance on day 152, we are confident that the peak must have

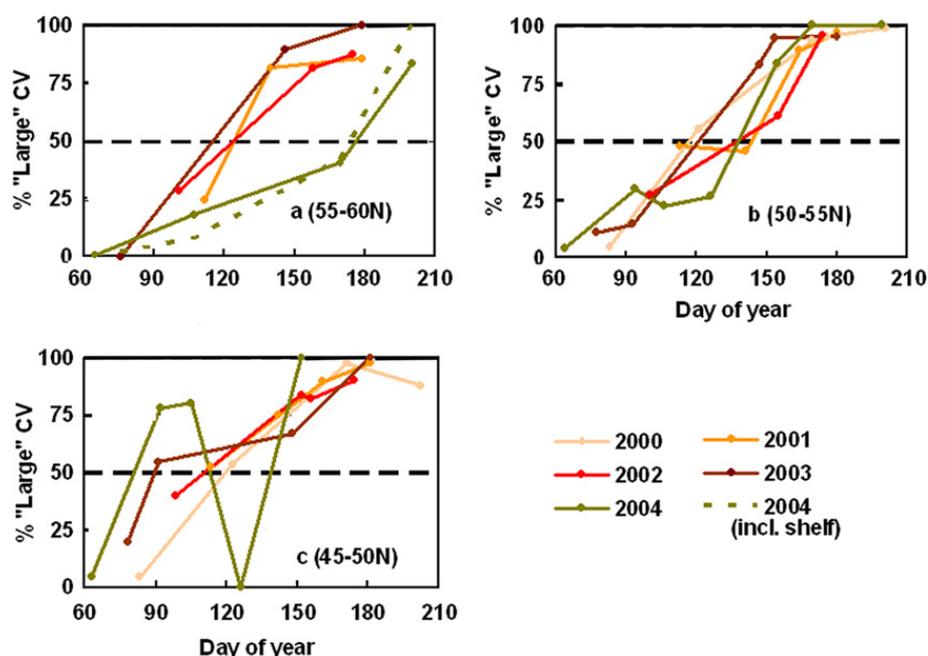


Fig. 9. CPR estimates of developmental timing based on seasonal progression of stage composition. Plots show for the three northern latitude bands, and for years 2000–2004, the average fraction of *N. plumchrus/flemingeri* that are “large” C5 copepodites vs. the median sampling date within that year and region. The “50%” date is used (Batten et al., 2003b; Mackas et al., 1998; this paper) as an estimator of the date of the biomass maximum in each region and year. Color coding by year matches the maps of survey line locations shown in Fig. 2. Date/stage estimates for the 42–45°N latitude band are summarized in Fig. 12 but are not detailed here because sampling of the southernmost region usually caught only the late stages of the seasonal progression.

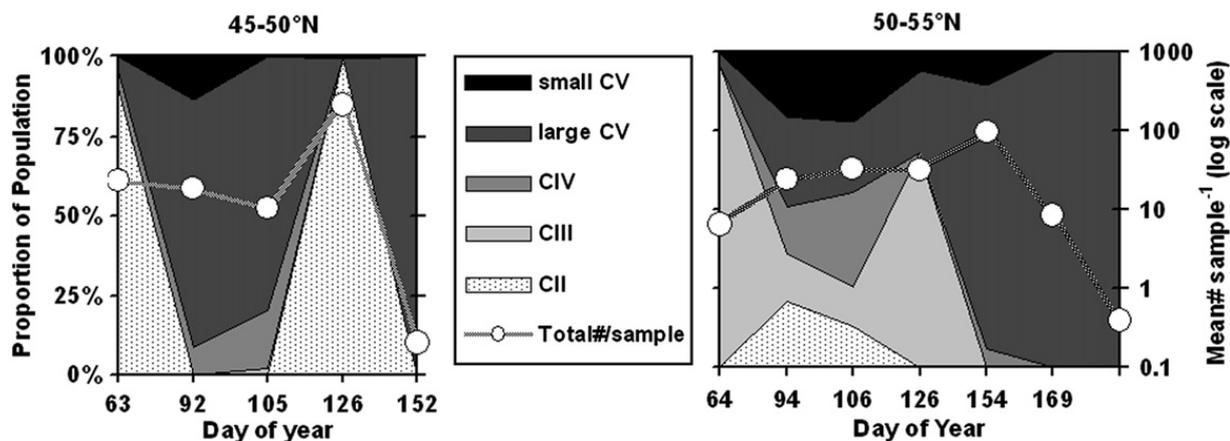


Fig. 10. Mid-season increase in abundance of early-stage *N. plumchrus/flemingeri* copepodites in CPR samples from 2004, after many had reached C5. This suggests a second annual cohort, contrary to the “normal” single generation per year. Net tow samples from 1998 and 2004 also found late re-occurrence of low numbers of C1–C3 *N. plumchrus* copepodites.

occurred between days 81 and 130, and in our overall summary of the phenology estimates (Fig. 13 below) have somewhat arbitrarily used the average of the two “50% large C5” dates for this latitude band and year. The sudden reappearance of large numbers of early copepodites partway through the annual development sequence raises another interesting question about *Neocalanus* life history timing: the maximum number of cohorts per year. We will return to this topic in Section 4.3.3.

Over the entire latitude range covered by the CPR surveys, the estimated dates at which half the population were “large C5” range from days 80 to 130 (20 March to 20 April) in the two southern latitude bands, and from days 115 to 176 (24 April–24 June) in the two northern bands. In all regions, timing of 50% C5 was relatively late in 2001 and 2002, and earliest in either 2003 or 2004.

Fig. 11 shows annual sequences of total *N. plumchrus/flemingeri* biomass vs. sampling date averaged from offshore CPR samples 48–55°N. The spatial domain for this analysis is similar to the stage-based estimates from 50 to 55°N (Fig. 9) but the latitude range is extended southward to include both the north–south and east–west CPR lines. Timing and duration of the biomass peaks differ among years: late (early–mid June) and broad in 2000 and 2001; early (mid–late May) and narrow in 2003 and 2004, and probably intermediate (although less well-determined by the sampling dates) in 2002. Although we had not commented on it in our earlier analyses, a similar association of early with narrow vs. late with broad biomass peaks is present in the earlier 1958–1981 OSP net tow data (cf. Figs. 3a and b).

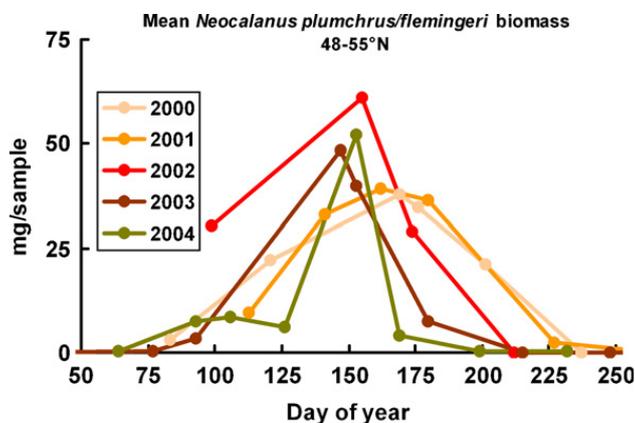


Fig. 11. CPR estimates of developmental timing based on total *N. plumchrus/flemingeri* biomass: average dry weight per sample vs. average sampling date for portions of CPR survey area located seaward of the continental slope and between 48 and 55°N. Color coding by year matches Figs. 2 and 9.

Fig. 12 summarizes all our *Neocalanus* timing estimates from offshore regions in the years 2000–2004 (stage composition from CPR and from DFO net tows along Line P, total biomass from CPR, and degree-day calculations using average monthly temperature within each latitude band and the temperature vs. timing regression line from Fig. 8b). The biggest component of the variability of developmental timing (from ~day 65 = early March in the south to ~day 175 = late June in the north) is associated with between-region differences in spring-early summer temperature. This temperature gradient is largely but not entirely latitudinal; nearshore areas in the northern part of the 55–60°N region can have warmer temperatures (Fig. 6) and earlier developmental timing (Figs. 9 and 12) than offshore areas located further south. During the 5 years of CPR sampling, interannual variability within each latitude band has spanned about 20 days (vs. ~65 days over the 50 year duration of the OSP time series shown in Fig. 8). Most of the date estimates agree to within their expected uncertainty ( $\pm 10$ –15 days for each variable, Figs. 3 and 8) with other methods applied to the same year and region. The exception is in the two northern latitude bands, where the dates of “50% large C5” from CPR samples are 30 or more days earlier than the corresponding estimates based on CPR biomass, stage-composition in Line P net-tows, or sea-surface temperature degree-days. One plausible explanation for the discrepancy is that size classification of the C5 copepodites did not adequately separate *N. plumchrus* and *N. flemingeri*. This explanation is consistent with several “knowns” for the region: In the Alaska Gyre, development of *N. flemingeri* leads that of *N. plumchrus* by about 1–1.5 stages  $\cong$  about 15–20 days (Miller, 1993a,b), *flemingeri* is larger in the northwest half of the Alaska Gyre than in the southeast half (Tsuda et al., 2001; Kobari et al., 2003), and the *flemingeri*:*plumchrus* abundance ratio increases greatly along the northern margin of the Gyre (K. Coyle, pers. comm.). Any misclassification of *N. flemingeri* as *N. plumchrus* would therefore lead to an overly early estimate of local *N. plumchrus* developmental timing, and misclassification is more likely in the more northerly samples. Other possibilities are that the relatively shallow and single-depth CPR sampling preferentially captures C5 over earlier stages, or *N. flemingeri* over *N. plumchrus*, or that copepods sampled from the Alaska continental margin did not develop locally, but instead spent much of their developmental history in warmer upstream regions from which they were transported by the strong along-shore current. At present, we lack sufficient North Pacific comparison sampling between CPR and net tows to know which of these explanations is correct. However, we now believe that the latitudinal range of developmental timing is at least as large, and probably larger, than was originally interpreted by Batten et al. (2003b) from CPR stage-ratio data.

The CPR data (especially the biomass-based developmental timing estimates shown in Figs. 11 and 12) also provide evidence that the strong and approximately linear correlation between interannual anomalies of local *N. plumchrus* developmental timing and local temperature (Fig. 8b) may be applicable throughout the Alaska Gyre. On this topic, it is noteworthy that the interannual variations in timing and spring season are coherent

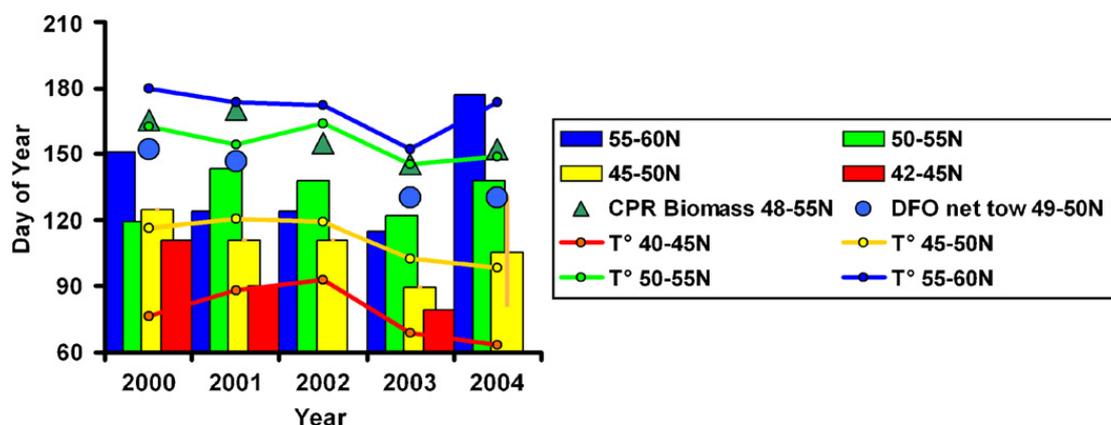


Fig. 12. Timing estimates for the *N. plumchrus* biomass maximum from CPR survey locations classified by year and latitude band. Column graphs show the interpolated dates (from Fig. 8) at which half the *N. plumchrus/flemingeri* are “large C5”. Triangles are the annual dates of the biomass maximum interpolated from Fig. 11. Colored lines are “degree day” estimates of the date of the biomass maximum calculated from the OSP date vs. temperature regression line shown in Fig. 8b, and spatially-averaged monthly sea-surface temperature grids downloaded from the PFEL website (<http://las.pfeg.noaa.gov>).

over large areas, but not necessarily over the entire basin. For example, Fig. 12 shows that the trend to warmer temperatures and earlier timing continued into 2004/2005 in the southeastern Alaska Gyre, but that in the north, 2004 was cooler and “later” than 2003.

#### 4.3.3. A second annual cohort?

Most previous analyses of *Neocalanus* life cycles in the North Pacific and Bering Sea (e.g. Miller et al., 1984; Miller and Clemons, 1988; Tsuda et al., 1999) have concluded that these copepods have one generation per year (or fewer in regions such as the Okhotsk and Japan/East Sea where winter and early spring surface temperatures are coldest) and that at least one dormant period precedes reproduction. The *Neocalanus* life history contrasts with the diversity of life history strategy exhibited by the dominant North Atlantic species *C. finmarchicus* (Conover, 1988), which has a single annual generation at the northern limit of its range, but multiple generations in areas where the water is warmer and/or food availability is higher and seasonally more prolonged. A difference in morphology that may explain the difference in life history is that adult female *C. finmarchicus* retain functional mouthparts, and usually feed before spawning. However, if warming temperatures will bring longer growing seasons to the high latitude Pacific and Bering Sea (as we suggested in Section 2), it is interesting to ask if *Neocalanus* might also be capable of some plasticity in the sequence of dormancy and reproduction. The 2004 CPR data from the 45 to 50°N and 50 to 55°N latitude bands (Fig. 10) show an anomalous sequence of stage composition. In both regions the initial increase in the proportion of C5 copepodites was interrupted in early May (along the same CPR survey line) by the appearance of a large percentage and large absolute abundance of earlier stage copepodites: C2 at 45–50°N and C3 at 50–55°N. By the next survey (~one month later), C5 were again numerically dominant in both regions. Similar departures from a monotonic stage progression also occur in time series from 42 to 45°N, but total numbers of *Neocalanus* in this latitude band are small for all stages, making the stage composition time series less reliable.

The 2004 sequences of *Neocalanus* stage composition and total abundance of copepodites shown in Fig. 10 strongly suggest the possibility of two separate cohorts of early copepodites in 2004, separated in time by about 2 months. There are at least four possible explanations:

- The two groups of early-stage copepodites had radically different upstream source regions (i.e. the first peak a warm source leading to early development, the second peak a much colder source leading to later development). However, we think this explanation is unlikely because the affected area was large (only strong and large-scale circulation anomalies would affect the entire region), yet the regional circulation pattern was quite stable from late winter through mid-summer 2004 (monthly stream function maps available at [http://www.pac.dfo-mpo.gc.ca/sci/osap/projects/argo/Dhgts\\_e.htm](http://www.pac.dfo-mpo.gc.ca/sci/osap/projects/argo/Dhgts_e.htm), and Cummins and Freeland, 2007).
- The two groups may correspond to the two different species (*N. flemingeri* early, *N. plumchrus* later). The higher proportion of “small C5” in the early to mid-season samples lends support to this. However, the majority of the C5 were “large” (hence probably *N. plumchrus*) in all time periods. A 50–60 day timing difference is also larger than has been previously observed for these species in the Alaska Gyre (Miller, 1993a,b), and the timing of the second peak is later than predicted for *N. plumchrus* based on observed surface temperatures in 2004 (Fig. 12).
- The overwintering generation (G0) of *N. plumchrus* produced two distinct batches of offspring (G1A, G1B). This interpretation requires that spawning by G0 was not only very prolonged (known to be true, Miller and Clemons, 1988), but also that rates of egg production and/or of survival of early juveniles were very intermittent, resulting in near zero recruitment of juveniles for an intervening period of a more than a month.
- Some of the initial spring generation (G1) matured immediately in early spring and spawned a second generation (G2) without passing through an intervening and prolonged dormant period. This interpretation is the most radical (as far as we know, the only unequivocal precursor is Smith and Vidal, 1986). However, we believe it is plausible, and that development from egg through C5 in relatively warm surface water would probably be fast enough allow a complete generation within the ~60 day time gap seen in Fig. 10. In 2004, the March–April–May average temperatures in the CPR survey area were 9.0, 9.8, and 11.8 °C in the 45–50°N latitude band, and 6.2, 7.0, and 8.3 °C in the 50–55°N latitude band (data from

<http://las.pfeg.noaa.gov>). Egg hatch times (EHT) of *N. plumchrus* are 4 and 5 days at 2 °C and 4 °C (Saito and Tsuda, 2000) but shorten to ~2.5 days at 7 °C (Fulton, 1973) and presumably less at higher temperatures. If sufficient food is available, subsequent naupliar and copepodite stage durations are proportional to the EHT for the same temperature. Saito and Tsuda (2000) estimate a proportionality factor of 8.3 for naupliar development (hatch–C1) and 10.7 for copepodite development to C5 (C1–C4). For a EHT of 2.5 days, these sum to 47.5 days, suggesting that at 7 °C a total egg-through-C5 duration of 55–65 days is possible. The required time span would be even shorter for average temperatures above 7 °C. However, a few caveats are required. Seasonal cycles from throughout the Pacific show that *N. plumchrus* disappears from the surface layer when and where water temperatures exceed 10–12 °C. The possibility of a G2 generation also requires that G1 C5 can bypass dormancy, and if they do so, that a prolonged additional time span within C5 is not needed to form eggs (Miller and Clemons, 1988 showed that *N. plumchrus* females sampled at depth are ready to spawn almost immediately after they molt from dormant C5, but that initial ovary development occurred within the C5 stage). Finally, we did not observe C6 *N. plumchrus* in any of the CPR samples.

At present, none of the above explanations is a clear “best fit” to the CPR observations shown in Fig. 10. However, we think that the latter two sequences (*N. plumchrus* G1A ⇒ G1B or G1 ⇒ G2) are more likely than the first two (large within-year change in advective history, or *Nflem*G1 ⇒ *Nplum*G1).

Seasonal surveys elsewhere in the subarctic Pacific and Bering Sea have produced scattered but qualitatively similar observations of delayed secondary peaks of early juvenile stages of *N. plumchrus* or *N. plumchrus/flemingeri* that are also suggestive of a second annual cohort. The most complete evidence comes from the Bering Sea. Two years of intensive sampling of the SE Bering Sea margin (Smith and Vidal, 1986) showed that development followed the normal single cohort pattern in 1980. However, in the “warm” year 1981, following the development of the main cohort in April–May, Smith and Vidal found some adult *Neocalanus* in the upper 60 m in June, abundant early copepodites (C1–C4) in July, and a few pre-dormant juveniles still present in the upper layer as late as October. Although the taxonomic discrimination between *N. plumchrus* and *N. flemingeri* by Miller (1988) had not yet been finalized at the time of their analysis, Smith and Vidal were aware that both species could be present, and concluded that the summer animals were entirely *N. plumchrus*.

Geinrikh (2002) recently re-analyzed earlier samples based on the revised taxonomy, and found relatively abundant C2 *N. plumchrus* in August–September 1950 samples from the western Bering Sea. She concluded that “reproduction took place in the summer as well” although she did not identify the parent generation.

Finally, our own data show that C2 and C3 *N. plumchrus* were frequently present in net tow samples from both the BC continental margin and the Alaska Gyre in summer and/or early autumn of 1997, 1998 and 2004 (Galbraith and Mackas, unpublished). All three of these were anomalously warm years (Fig. 5) in which the main peak of C5 abundance occurred earlier in the calendar year (early April along the continental margin, early May at OSP, see Fig. 8).

#### 4.4. Higher trophic levels

One of the major motivations for studying interannual variability of zooplankton is to know if and how climate response at the base of the pelagic food web is associated with variability of visible, harvested or otherwise charismatic predator species. Fig. 13 shows time series of survival and reproductive success for a suite of local predators. The choice of time series is partial and to some degree arbitrary, but provides broad evidence that environmental conditions were unfavorable for resident pelagic predators during most of the 1990s, favorable for a span of about 4–5 years following the 1999 La Niña event, but have trended toward unfavorable since 2002 or 2003.

##### 4.4.1. Coho salmon marine survival and first year growth

It is now well-established that ocean-phase survival of Pacific salmon stocks has varied significantly in recent decades, that much of this variance is at multi-year time scales and correlated with various indices of regional and larger scale ocean climate indices, and is also spatially-autocorrelated over alongshore

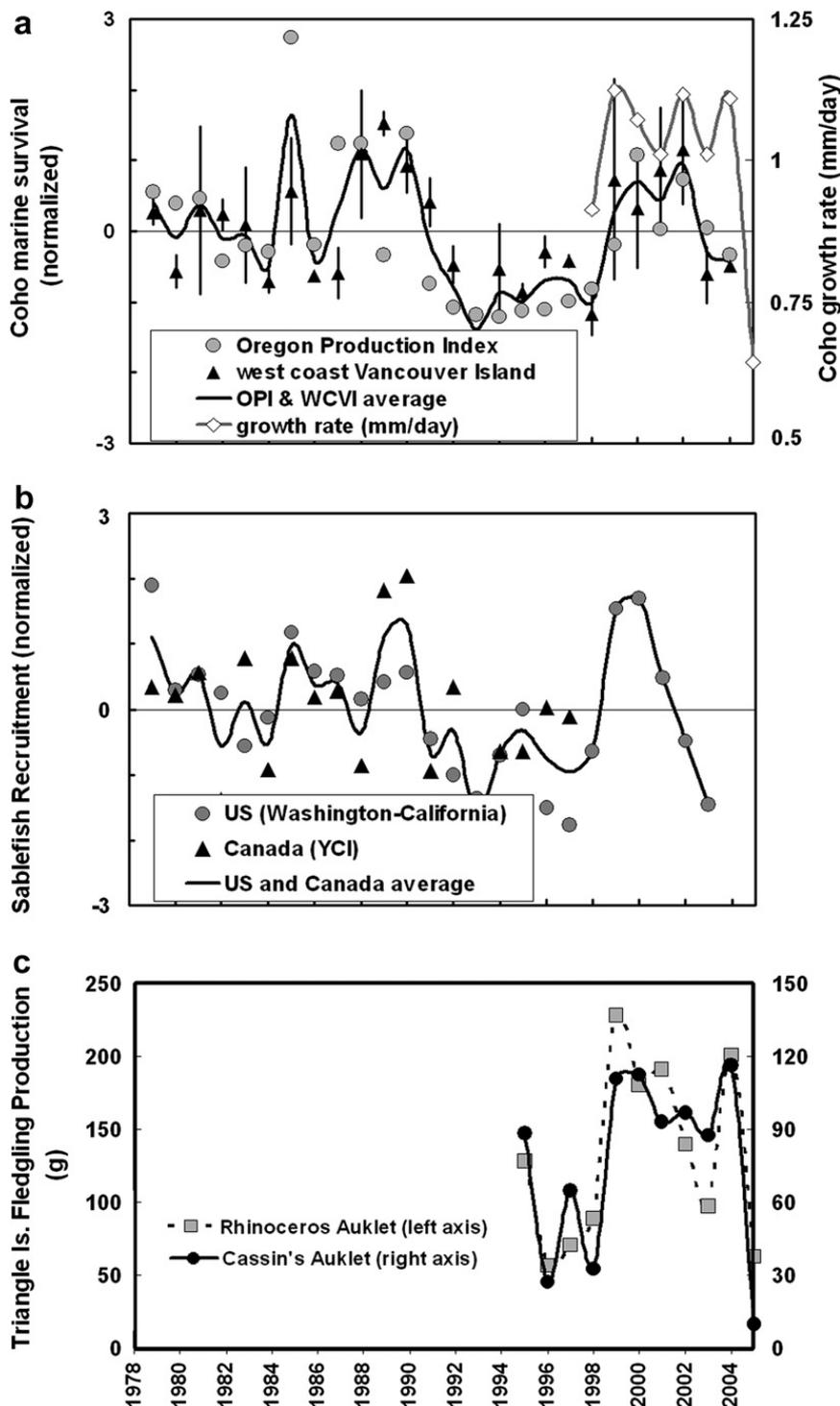


Fig. 13. Time series indexing the success of pelagic “predator” species that inhabit and exploit the waters off Vancouver Island: (a) marine survival of coho salmon and growth in their first ocean summer, (b) recruitment of sablefish, (c) reproductive success of Cassin’s and Rhinoceros Auklets at the Triangle Island seabird colony.

distances of several hundred kilometers (e.g. Mantua et al., 1997; Beamish et al., 2000; Cole, 2000; Koslow et al., 2002; Mueter et al., 2002; Pyper et al., 2002). For coho (*O. kisutch*) that inhabit the continental margin off Vancouver Island, Washington, and Oregon, normalized marine survival rates referenced to year of ocean entry (Fig. 13a) were “fair” during most of the 1980s (but above average for the 1979–2004 time span shown in the figure), below average from 1991 to 1998, above average 1999–2002, and now appear to be declining from 2003 to the present.

There are fewer data on coho growth rate during their first summer in the ocean, but measurements since 1998 (right hand end of Fig. 13a) show that variability in growth has tracked (or more probably, been a causal contributor to) variability in survival.

Juvenile coho quickly become piscivorous in the marine environment, and derive relatively little of their diet directly from copepods or other small zooplankton (Brodeur and Pearcy, 1990). Nevertheless, the low frequency fluctuations of coho survival and growth shown in Fig. 13a are very similar to the time series of copepod biomass anomalies (Fig. 7) and of the changes in copepod life cycle timing (Fig. 8).

#### 4.4.2. Sablefish recruitment

In contrast to coho salmon, the diet of larval and juvenile sablefish (*A. fimbria*) is dominated initially by copepod nauplii (McFarlane and Beamish, 1992), shifting to dependence on copepods and larger zooplankton as the larvae mature into juveniles (Grover and Olla, 1987, 1990). Sablefish year class strength is believed to be associated with interannual variations in the availability of copepods as food. King et al. (2000) used zooplankton biomass off Vancouver Island as one of the input criteria for a “report card” of expected sablefish recruitment in British Columbia, and Schirripa and Colbert (2006) reported a 1985–1999 correlation between sablefish recruitment off Washington and Oregon, and the copepod community composition anomalies (from Mackas et al., 2001; a subset of the data plotted in Fig. 7). Fig. 13b shows that variability of sablefish recruitment since 1999 has paralleled the upward and downward trends of zooplankton biomass and phenology, and of coho survival and growth. Sablefish recruitment was above average in 1999–2000, near average in 2001–2002, but in 2003 was much below average and similar to the poor recruitment observed in the mid-late 1990s.

#### 4.4.3. Seabird reproductive success

Measurements of annual average reproductive success of Cassin's and Rhinoceros Auklets at the Triangle Island seabird colony (Fig. 13c, data courtesy M. Hipfner and D. Bertram, Canadian Wildlife Service) also suggest poor conditions in the mid-late 1990s, relatively good conditions 1999–2001, and then a gradual deterioration after 2002 (2005 was the worst year recorded for Cassin's Auklets, and the second worst for Rhinoceros Auklets). The main difference between the seabird time series and the ‘fish’ time series in the previous sections is that both seabird species did relatively well in 2004. However, parallel measurements of diet showed that the mix of prey species was unusual in 2004 – the birds were able in 2004 to obtain sufficient food, but only by radically changing their foraging strategies (M. Hipfner, pers. comm.).

## 5. Interpretations

### 5.1. Correlations among the biological and temperature patterns and effects of spatial averaging

The matrix of product-moment correlations in Table 2 shows that the annual anomalies of zooplankton biomass, community composition, and life history timing anomalies (Figs. 7 and 8) have covaried moderately strongly (average  $r^2 \sim 0.3$ ) with each other, with temperature anomalies at several spatial scales (Fig. 5), and also with annual indices of recruitment and early stage survival of ‘predators’ such as coho salmon, sablefish, and colonial seabirds (Fig. 13). Comparison of the various time series and Table 2 suggests that there is an important “shared story” that connects these variables, and also that the interconnection has an alongshore spatial scale of several hundred kilometers (correlation of the predator responses with zooplankton and temperature is intensified when the predator time series are averaged regionally, rather than analyzed stock-by stock). Similar conclusions about spatial scale and the potential benefits of regional averaging were reached by Pyper et al. (2002) and Mueter et al. (2002) from region-wide association of temperature and salmon survival, and by Mackas et al. (2004) from comparison of zooplankton anomaly time series between Oregon and Vancouver Island.

We examined the resemblance among the physical and biological time series using a Principal Components ordination analysis (calculated by decomposition of the correlation matrix from Table 2). Fig. 14 shows the contributions of each of the different variables to the first three component axes. These three axes capture the great majority (77%) of the total variance/covariance of the normalized input data series. Axis 1 alone accounts for more than half (56%), and also shows a pronounced separation along this axis between two

Table 2  
Matrix of pairwise correlations among the variables shown as annual time series in Figs 5, 7, 8 and 13

Category	What was indexed	Variable	Abbrev.	BOREAL	SOUTH	SUBARC	NP_VI	NP_AG	CS_av	CS-Rob	CS-Carn	CS-OPI	CG	SR_av	SR-BC	SR-US	CAAU	RHAU	"PDO"	"VIC"	LineP	WCVI	
Zooplankton	Biomass/abundance anomalies	"Boreal Shelf" copepods	BOREAL		.24	.24	15	13	.24	.24	.24	.24	7	.23	.17	.23	10	10	.24	.24	.24	.24	
		"Southern" copepods	SOUTH	-.72		.24	15	13	.24	.24	.24	.24	7	.23	.17	.23	10	10	.24	.24	.24	.24	
		"Subarctic" copepods	SUBARC	.66	-.32		15	13	.24	.24	.24	.24	7	.23	.17	.23	10	10	.24	.24	.24	.24	
Zooplankton	Phenology ( <i>N.plunchnrus</i> timing)	Date of max - WCVI	NP_VI	.59	-.81	.35			.15	.15	.15	.15	7	.14	.8	.9	9	9	.15	.15	.15	.15	
		Date of max - AG	NP_AG	.60	-.64	.41	.88		.14	.14	.14	.14	5	.13	.9	.13	5	5	.14	.14	.14	.14	
Fish	Coho Marine Survival	BC-OPI average	CS_av	.57	-.63	.53	.57	.57		.26	.26	.26	7	.25	.19	.25	10	10	.26	.26	.26	.26	
		BC-Robertson Cr.	CS-Rob	.30	-.33	.38	.18	.20	.59		.26	.26	.26	7	.25	.19	.25	10	10	.26	.26	.26	.26
		BC-Carnation Cr.	CS-Carn	.52	-.60	.11	.58	.42	.73	.25		.26	.26	7	.25	.19	.25	10	10	.26	.26	.26	.26
		US-OPI area	CS-OPI	.47	-.52	.58	.48	.60	.90	.29	.51		.26	7	.25	.19	.25	10	10	.26	.26	.26	.26
Fish	Coho Growth Rate	WCVI coho	CG	.80?	-.69?	.84?	.38?	?	.65?	.85?	.13?	.50?		.6	0	.6	7	7	.7	.7	.7	.7	
Fish	Sablefish Recruitment	BC-US average	SR_av	.53	-.50	.45	.56	.54	.67	.52	.40	.58	.53?		.19	.25	10	10	.25	.25	.25	.25	
		BC		.37	-.22	.33	?	?	.57	.53	.44	.45	?	.85		.19	3	3	.19	.19	.19	.19	
		US		.56	-.55	.54	.67	.73	.64	.39	.36	.62	.53?	.89	.39		9	9	.25	.25	.25	.25	
Seabird	Reproduction	Cassin Auklet	CAAU	.65	-.61	.80	.36?	.42?	.62	.61	.12	.64	.89?	.62	?	.70		10	10	.10	.10	.10	.10
		Rhinoceros Auklet	RHAU	.71	-.61	.66	.41?	.55?	.60	.62	.22	.53	.72?	.86	?	.92	.85		10	10	.10	.10	.10
Temperature	NPae SST (detrended)	PC/EOF#1	"PDO"	-.27	.37	-.06	-.28	-.24	-.26	-.63	-.15	-.02	-.81?	-.38	-.12	-.31	-.60	-.53		.26	.26	.26	
Temperature	NPae SST (detrended)	PC/EOF#2	"VIC"	.23	-.19	.43	.22	.32	.51	.58	.22	.41	.49?	.43	.17	.48	.66	.81	-.15		.26	.26	
Temperature	Alaska Gyre	Line P anomaly	LineP	-.28	.52	-.10	-.36	-.48	-.61	-.73	-.45	-.37	-.47?	-.42	-.20	-.39	-.30	-.50	.45	-.51		.26	
Temperature	BC coast	Amphitrite Pt anomaly	WCVI	-.45	.61	-.26	-.64	-.43	-.31	-.33	-.21	-.21	-.63?	-.28	-.27	-.49	-.72	-.73	.44	-.39	.37		

Upper diagonal contains the number of overlapping years *N* for each pair of time series. Lower diagonal contains the product moment correlation coefficient *r*. Font indicates estimated significance level of each individual comparison (italic for  $p < 0.1$ , bold for  $p < 0.05$ , ? = few years of overlap). The significance levels are not corrected for multiple comparisons (i.e. by chance about 10% of entries will record as significant at  $p < 0.1$ ), but do assume a reduced number of effective degrees of freedom  $N^* \sim 0.7 * (N - 2)$  due to effects of serial autocorrelation. Gridlines indicate groupings of variables by category. Columns/rows with shaded background are "local" measures of coho survival and sablefish recruitment. Their normalized time series were averaged to produce regional composites used in the PCA analysis.

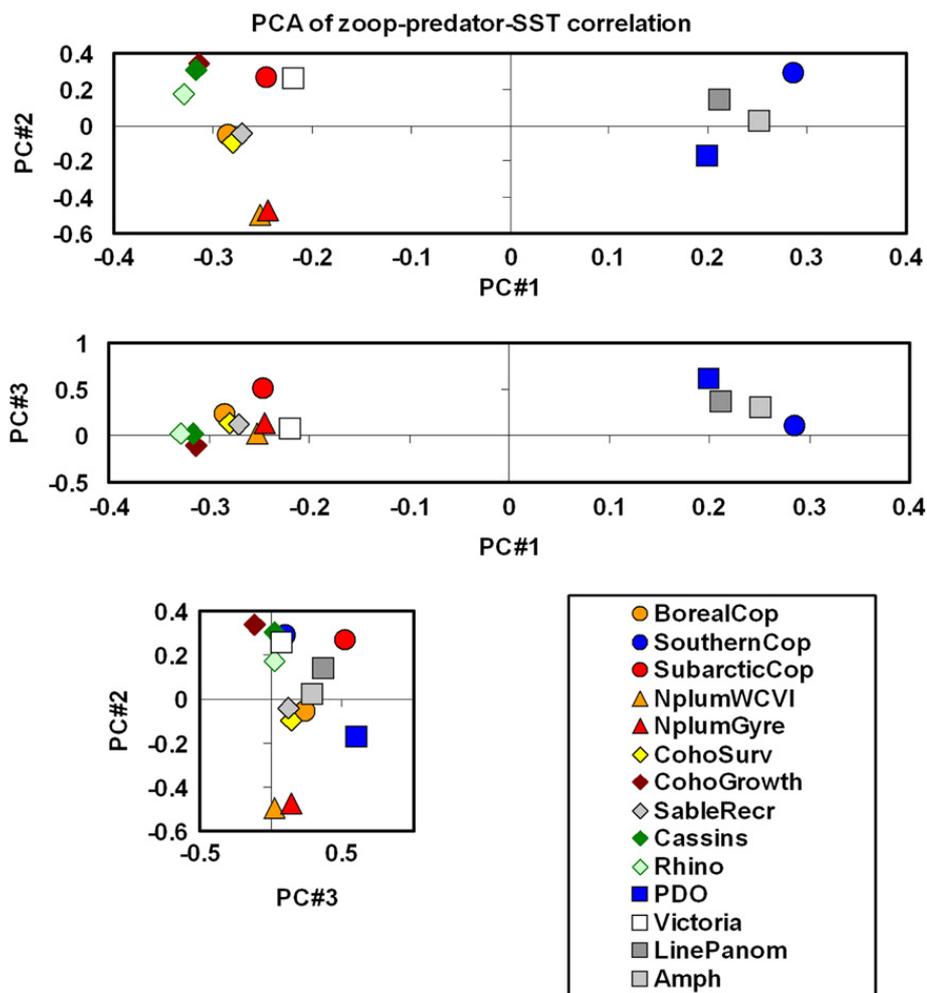


Fig. 14. Principal components ordination of zooplankton/temperature/upper trophic level correlations. Plots show eigenvector coefficients for each variable on the three leading component axes. Symbol shapes classify the variables by type: squares = temperature indices, circles = copepod biomass and species composition, triangles = copepod life cycle timing, diamonds = success of selected predator species. Axis 1 can be interpreted as a “warm” vs. “cool” contrast, and had strong weightings by all variables, although the response was stronger for the biological than for the physical variables. Component axes were scaled graphically to give a visual impression of the fraction of the total normalized variance/covariance “explained” by each component (55%, 13%, and 9%, respectively).

clusters of the input variables. The interpretation of this separation is also consistent. For the variables plotting on the left hand side of PC axis 1, positive anomalies are indicative of “cool water” and “high abundance/growth/survival by endemic northern species”. Conversely, positive anomalies of the variables plotting on the right hand side of Axis 1 indicate “warm water” and “favorable for warm-water southern-origin species”. Interestingly, although none of the input variables has a neutral weighting on axis 1, the biological variables show a stronger and more consistent “response” to this component (larger absolute values of their eigenvector coefficients) than do the temperature indices. Hare and Mantua (2000), McFarlane et al. (2000), Beaugrand (2004), and Hays et al. (2005) reported similar conclusions from their comparisons of “regime” responses by climatic and biological variables.

Time series of annual scores for the principal components can be generated from appropriately weighted sums of the input time series (Section 2.6). The three leading components are plotted in Fig. 15, with vertical scaling adjusted in proportion to eigen value to give a visual impression of their partitioning of the total variance/covariance of the input data. As noted in Section 2.6, the raw PC scores have also been weighted to compensate for missing variables, and are therefore less reliable before the mid-1980s and in 2005. However, it is clear that PC 1 strongly dominates the overall pattern in most years. The pairwise correlations of individual data series with the shared pattern captured by PC1 is also usually stronger (average  $|r| = 0.72$ , range 0.51–

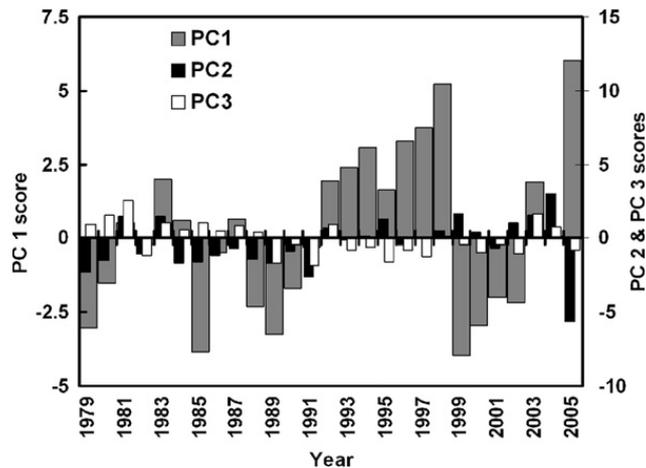


Fig. 15. Time series of the three principal components shown in Fig. 14. PC1 strongly dominates the total pattern, and shows the alternation between groups of years that were “cool and productive” vs. “warm and unproductive”.

0.86) than the pairwise correlations among the anomaly time series (Table 2). Our interpretation of the PC1 time series is that the ocean off Vancouver Island has alternated episodically between a set of linked conditions that can be summarized as “cool and productive” (1999–2002, and non-Niño years between 1979 and 1990) and conditions that can be summarized as “warm and less productive” (1992–1998, 2003–2005, plus El Niño years 1983 and 1987). Although 2005 data are incomplete (coho and sablefish recruitment and survival data are not yet available), a prediction based on the other contributors to the PC1 time series is that 2005 fish recruitment and early marine survival off Vancouver Island may prove to be about as poor as in 1997 and 1998.

We stress that “warm” vs. “cool” temperature is probably neither the sole nor the primary proximate cause of the observed biological variability. Instead, we suggest that temperature is serving as a proxy for anomalies of other physical variables and processes (vertical density stratification, intensity of upwelling and vertical mixing, direction of horizontal transport...) and also of the ecological characteristics of the dominant zooplankton. Although statistical associations of predator success with zooplankton community composition and phenology are often strong (Table 2), we do not yet know the precise linking mechanisms. One recent hypothesis (e.g. Rosen and Trites, 2000; Peterson and Schwing, 2003; Trudel et al., 2005; Wanless et al., 2005; Hooff and Peterson, 2006; Trudel et al., 2007) is that predator growth and survival are more closely linked to prey “availability” and quality as food than to total prey biomass. We know that the growing conditions and life history strategies of the “boreal shelf” and “subarctic oceanic” copepods promote relatively large individual body size plus extensive accumulation of lipid reserves. Both factors help make the high latitude zooplankton an energy rich food source, provided that the seasonality of their production and availability overlaps with the seasonal demand by their predators. Conversely, the southern-origin zooplankton tend to be less lipid rich and individually smaller, and may therefore be less available and useful to endemic predators. An attractive feature of the “good food vs. junk food” mechanism is that prey energy content/food value can propagate upward through successive trophic levels. Another plausible hypothesis is that the interaction of temperature, zooplankton, and vertebrate predators involves several different processes that differ in detailed mechanism (and perhaps fluctuate in relative importance) but correlate at an interannual time scale both with each other and with temperature. For the time period covered in our analysis, the proxy relationships of temperature with zooplankton composition, seasonal timing, and predator success all appear to have been relatively strong and reliable. However, new monitoring programs and methods (e.g. Argo drifters) are rapidly expanding the potential for large-scale time series measurements of these and other environmental variables and processes. Although our PC1 appears to capture a lot of the total interannual signal, we expect that its performance and reliability could be improved by incorporating a broader (and perhaps better) set of environmental index variables.

## 5.2. Environmental misinformation and timing match-mismatch

We close by returning to a topic we raised in Section 3: how increasingly positive temperature anomalies could directly affect the trophic timing match-mismatch of mid- and high-latitude pelagic ecosystems. Zooplankton in these regions are very strongly, and for the most part successfully, adapted to a large amplitude seasonal cycle of temperature and productivity (Fig. 4). The serious dilemma (and potential for large changes in growth and survival) comes when a highly successful strategy for dealing with strong and predictable variability at the seasonal time scale (e.g. reproduction timed to the annual seasonal cycle of primary productivity) encounters and conflicts with unpredictable and spatially-extensive variability at a longer time scale (e.g. a progressively earlier date at which the mixed layer temperature exceeds some threshold value). Short term temperature variability in the ocean is strongly damped by the large heat capacity of the ocean. Compared to terrestrial systems (in which instantaneous air temperature is a risky predictor of either the current date, or of temperature a week or month in the future), the within-year onset of temperature increase of the upper ocean is well-correlated with other important aspects of environmental seasonality (e.g. increasing insolation, stratification, and primary productivity). Demographic timing of zooplankton in both the Northeast Pacific (Figs. 8 and 12) and the Northeast Atlantic (Greve et al., 2004, 2005) is very strongly correlated with (regulated by?) the temperature that the juvenile zooplankton encounter during early spring. Such a calendar-setting mechanism works well for synchronizing reproduction and growth with beneficial environmental conditions, provided that the association of temperature and environment also remains stable. However, our data suggest that the zooplankton synchronization may be with the actual temperature, rather than with the cumulative warming from the temperature minimum of the previous winter (arguably a more reliable proxy for stratification and insolation). A shifting baseline temperature could therefore produce timing offsets relative to the seasonality of their food supply (controlled more by light and vertical stratification) and of their predators (often controlled by migration from different locations).

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