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Changes in oceanic zooplankton populations in the north-east Pacific associated with the possible climatic regime shift of 1998/1999

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Abstract

There is increasing evidence that the winter of 1998–1999 saw a shift in the ecosystem structure of the north-east Pacific. The Continuous Plankton Recorder sampled plankton along a transect from Alaska to California in 1997, the warm period preceding the regime shift, as well as the subsequent cool period of 2000 and 2001. Analyses of mesozooplankton biomass and species composition show significant changes in the plankton communities of the open Gulf of Alaska and the Alaskan shelf, consistent with the changing environmental conditions. Boreal calanoid copepod species showed lower abundances in the warm period while subtropical species showed higher abundances and a more northerly distribution. During the colder period, boreal species had higher abundances and subtropical species were less abundant on the northern part of the transect. Differences were greatest between the years of 1997 and 2001, with 2000 appearing as a ‘transition’ year. The communities in the open Gulf of Alaska appear to be as responsive to climate change as shelf ecosystems, whose responses have been reported elsewhere. The composition changes have implications for higher trophic levels that forage in the open ocean, and for the forcing of the downwelling ecosystem of the Alaskan continental shelf ecosystem by events offshore.

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1. Introduction

At multi-decadal scales, marine ecosystems display low-frequency variability with periods of relative stability lasting one or two decades interrupted by a sudden transition to a new ‘regime’. Although the concept of regime shifts

has been discussed for several decades, interest has increased during the 1990s and into this century. One reason is that ecosystems contain species of commercial importance whose abundance, distribution and productivity differ from regime to regime. In addition, although time series of physical atmospheric and ocean-surface variables are generally available, corresponding time series of biological variables to examine the ecosystem response to regime shifts are much rarer and only now reaching sufficient lengths for analysis. It has

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been suggested that biological variables provide a more diagnostic signal of regime shifts than climate indices (Ebbesmeyer et al., 1991; Hare and Mantua, 2000) since the ecosystem may filter out some of the noise and clarify the signal. Probably the most famous regime shift in the eastern north Pacific occurred in the late 1970s, although it was not recognised as such for about another decade (Ebbesmeyer et al., 1991). There is some evidence for a shift in the late 1980s (e.g., IRI, 2002; Welch et al., 2000) and increasing evidence for a similar event in 1999 (Bograd et al., 2000; Schwing and Moore, 2000).

Zooplankton are thought to be sensitive indicators of regime shift type events because (in contrast to commercial fish species for which many data exist) they have short life spans and assessments of their abundance are unaffected by fishing effort. The north-east Pacific has few time series of zooplankton. Those that do exist (in southern California, Oregon and British Columbia) have for the most part been collected in shelf or slope waters. Open-ocean time series are even rarer, and in fact are limited to the data collected at Ocean Station Papa, the extremities of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) sampling, and the recent Continuous Plankton Recorder sampling that forms the focus of this study. Regime shift type changes have been previously identified in all four north-east Pacific time series, primarily as changes in zooplankton biomass (Brodeur and Ware, 1992; Roemmich and McGowan, 1995; Mackas, et al., 2001; Peterson, et al., 2001). Studies also have been published detailing the taxa, principally calanoid copepods, whose abundances have co-varied with changing oceanographic conditions (Mackas et al., 2001; Peterson et al., 2001; Mackas et al., 2004). The Oregon and British Columbia time series have several species in common; linked as these two regions are by the equatorward California current and the poleward slope current, this is not surprising. The species that showed a response can be separated into two groups which tended to show opposing responses to climatic variability: (1) species characteristic of boreal regions and (2) copepods of the southern California region. Responses to decadal variability in southern

California have been more equivocal, nevertheless a response to identified regime shifts was noted in some species (Rebstock, 2002).

During July and August 1997 a Continuous Plankton Recorder (CPR) was towed along a transect from Prince William Sound, Alaska to Long Beach, California as a pilot study. Repeated sampling along this transect then took place five times in 2000 and five times in 2001 between March and September. The pilot study carried out in 1997 was during a time of anomalously warm conditions for the north-east Pacific when 1997/1998 saw the strongest El Niño on record. Additionally, two indices of climate variability in the north Pacific reached extreme values; the Pacific Decadal Oscillation (PDO) was in a positive phase (PDO index available at <http://tao.atmos.washington.edu/pdo/>, see Mantua et al., 1997), the Northern Oscillation Index (NOI) was strongly negative (NOI index available at <http://www.pfeg.noaa.gov>, see Schwing et al., 2002). Sampling in 2000 and 2001 was during a time of cooler than average conditions, and the PDO and the NOI indices were reversed from their pre-1998 phase. It appears that the El Niño of 1997/1998 marked the transition to a new regime in the North Pacific, beginning in 1999 (Schwing and Moore, 2000).

Although lengthier time series are generally needed to detect a regime shift, the CPR sampling provided us with the opportunity to examine the CPR data with respect to these warm and cool periods. One objective was to determine whether or not the CPR, which is a large-scale sampling system, was a useful tool in detecting climate-related ecosystem change in the north Pacific. A second objective was to determine whether the open-ocean plankton showed as extensive a response as the shelf communities already described in the literature.

2. Materials and methods

The CPR is a mechanical plankton sampler that is towed behind merchant ships at a depth of around 7 m. It has been extensively deployed in the North Atlantic, and a full description of its

operation is given in Warner and Hays (1994). A square 1.2-cm aperture at the front of the device allows seawater to enter and plankton are filtered onto a continuously moving band of silk gauze with a mesh size of 270 μm . A second piece of gauze covers the filtering gauze once it has passed across the entrance tunnel, and the resulting ‘sandwich’ is rolled onto a spool in a storage tank that contains formaldehyde solution. Once the deployment is complete, the roll is unwound and cut into discrete samples, each representing 18 km. Assuming 100% filtration, this is equivalent to about 3 m³ of seawater per sample. Plankton retained on the gauze are identified and enumerated at the Sir Alister Hardy Foundation for Ocean Science according to a standard set of procedures (Warner and Hays, 1994), with taxonomic resolution that varies from life stages of key species to phyla level. Individuals smaller than about 2 mm are counted in a subsample (representing 0.02 of the sample), while organisms larger than 2 mm are counted with no subsampling. The method of counting zooplankton is a compromise between accuracy of enumeration and speed of processing. Abundances are estimated in categories, shown in Table 1, and an ‘accepted mean’ for each category is then taken to be the abundance of that organism. The ‘accepted mean’ was derived from calculations of the true mean

Table 1
The categories employed in CPR sample processing, and the accepted values of abundance

Actual abundance	Category	Accepted value
1	1	1
2	2	2
3	3	3
4–11	4	6
12–25	5	17
26–50	6	35
51–125	7	75
126–250	8	160
251–500	9	310
501–1000	10	640
1001–2000	11	1300
2001–4000	12	2690

For organisms less than 2 mm that are counted in a subsample the accepted values are further multiplied by 49 to give the abundance per sample.

number in each category when detailed counts on many samples were made. The limits of the accuracy of these accepted values are discussed in Rae (1952). Rae concluded that when the data are used to find a mean population density of an organism over a large area or for any month by averaging the available observations, then little accuracy is lost through using categories instead of finite estimates.

The route in the North Pacific from Alaska to California (Fig. 1) was operated by an oil tanker, which completed the journey in approximately 5–6 days. The five deployments in each year were spaced about 5 weeks apart to cover the main mesozooplankton biomass season of late March to September (Table 2). The number of samples processed varied because of other studies using these data, but on each transect all consecutive shelf samples were processed for plankton abundances. The coarsest resolution for oceanic samples was every fourth sample processed, but on some transects alternate samples were processed with the remainder being archived. There was thus a maximum of 72 km between the midpoints of

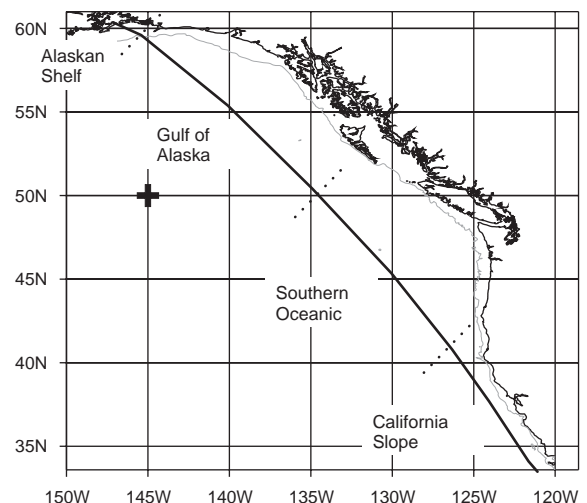


Fig. 1. The typical location of the route from Prince William Sound, Alaska, USA to Long Beach, California, USA. Variability in deployment position was minimal. The position of Ocean Station P, where many previous studies have been carried out, is shown by a ‘+’ for reference. Regional divisions used in the analyses are indicated by dashed lines. The 500 m isobath is also shown.

Table 2
The dates for each transect that was sampled

1997	2000	2001
	21–26 March	22–27 April
	29 April–5 May	20–25 May
	17–22 June	27 June–2 July
21 July–6 August	19–24 July	10–16 August
	23–29 August	21–25 September

processed ocean samples, with each sample representing an 18-km track.

The eastern North Pacific as sampled by the CPR can be subdivided into four regions, determined by the topography and the main currents: the Alaskan shelf, the Gulf of Alaska (bounded to the north by the Alaskan Coastal Current and to the south by the northern diversion of the North Pacific Current into the Alaska Current), the oceanic region to the south of the Alaska Gyre (bounded by the southern diversion of the north Pacific Current into the California Current), and the upwelling region of the Oregon and California slope and shelf (Fig. 1). The abundance of the mesozooplankton (organisms from 200 μm to a few mm, the size range most quantitatively sampled by the CPR) was determined for each of these four areas for each sampling period. Although abundance can be considered as a proxy for biomass, changes in species composition can result in changes in biomass irrespective of abundance. A switch from small to large taxa can result in an increase in biomass even if abundances also decline. To examine whether or not the mesozooplankton biomass reflected the same interannual and regional variability, we estimated the mesozooplankton biomass of each sample. This was achieved by multiplying the abundance of each taxon by a taxon-specific individual dry weight value and summing the values for each sample. The dry weight values were derived from actual measurements that have been made of individual organism's length and dry weight (Planque and Batten, 2000). If measurements were not available for a particular taxon, dry weights were calculated from the published

length of the organism and the taxonomically closest organism's measured length to weight ratio. Mean biomass per area, per transect was then calculated. Differences between years for each region were examined using a non-parametric *t*-test for sample means.

Species composition changes were examined in two ways. Since organisms are identified at a range of taxonomic levels, the whole mesozooplankton community could only be examined at a coarse taxonomic resolution. Taxonomic groups were created, such as large and small copepods, pteropods, larvacea, etc., by summing the abundances of the component taxa where necessary. Secondly, since most copepods were identified at least to genus and most to species level, and because other studies had noted changes in the relative numbers of boreal and sub-tropical calanoid copepods (Mackas et al., 2004), we looked for similar changes in the CPR data. Abundance of each copepod species (or genus if

Table 3
Copepod species/genera identified from CPR samples

Northern species	Southern species
<i>Acartia longiremis</i>	<i>Acartia danae</i>
<i>Acartia</i> spp.	<i>Calanus pacificus</i>
<i>Calanus marshallae</i>	<i>Candacia armata</i>
<i>Candacia colombiae</i>	<i>Candacia bipinnata</i>
<i>Centropages bradyi</i>	<i>Candacia ethiopica</i>
<i>Eucalanus attenuatus</i>	<i>Clausocalanus</i> spp
<i>Eucalanus bungii</i>	<i>Corycaeus</i> spp. (note, cyclopoid not calanoid)
<i>Eucalanus elongatus</i>	<i>Euchirella pseudopulchra</i>
<i>Heterorhabdus tanneri</i>	<i>Euchirella rostrata</i>
<i>Neocalanus cristatus</i>	<i>Mecynocera clausi</i>
<i>Neocalanus plumchrus</i>	<i>Mesocalanus tenuicornis</i>
<i>flemingeri</i>	
<i>Oncaea</i> spp.	<i>Metridia pacifica</i>
<i>Paraeucaeta elongata</i>	<i>Nannocalanus minor</i>
<i>Pseudocalanus</i> spp.	<i>Pleuromamma abdominalis</i>
	<i>Sapphirina</i> spp.
	<i>Scolecithrix</i> spp.
	<i>Undeuchaeta bispinosa</i>
	<i>Undeuchaeta major</i>
	<i>Undeuchaeta plumosa</i>

Northern species are those whose abundance correlated positively with latitude, southern species correlated negatively on all samples between 40°N and 59°N.

the highest level identified) was correlated with latitude for all samples collected on the transects, except those samples collected over the continental shelf/slope (north of 59°N and south of 40°N). By separating the coastal samples, this eliminated the more neritic species that occurred at both extremes of the transect and which could confuse an analysis of species composition. Species that correlated positively with latitude were termed ‘northern species’, and those that correlated negatively were termed ‘southern species’ (Table 3). Southern and northern indices were then calculated for each sample by summing the abundances of the respective species on each sample (not all species occurred on each sample). Mean values of each index were calculated for each 1° band of latitude along the entire transect.

3. Results

Although only one transect is available from the warm regime, there are noticeable differences in the abundance and biomass of zooplankton between the warm and cool periods (Fig. 2). At no time in the cool period were mean abundances as high as they were in 1997 except on the Alaskan shelf. Biomass, however, reached comparable or higher levels. The two oceanic areas show a similar pattern with abundances lower in 2000 than in 1997 and lower again in 2001, while biomass is similar in 1997 and 2000 but slightly higher in 2001. The Alaskan shelf is showing an opposite signal to the oceanic areas despite gaps in the data—both abundances and biomass were very low in summer 1997, and higher in the summers of 2000 and 2001. Both abundance and biomass were

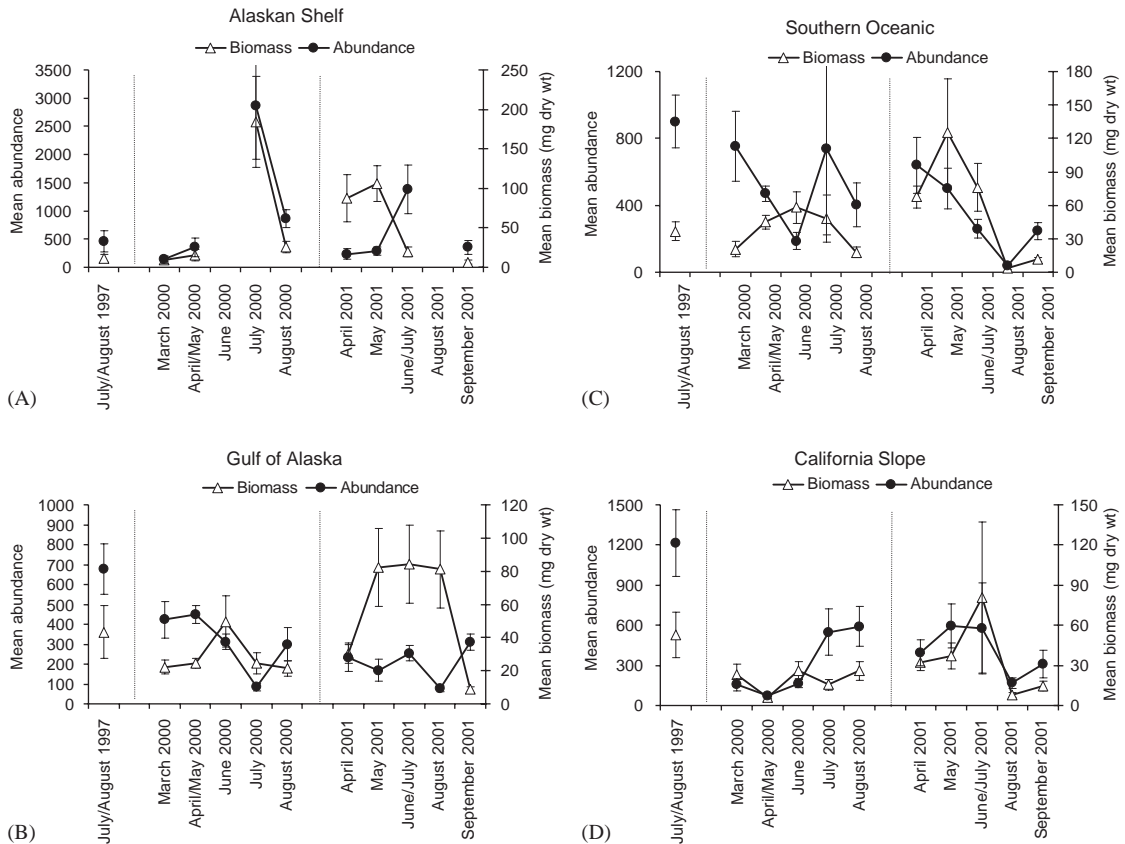


Fig. 2. The mean abundance and biomass per sample, for each region, on each sampled transect. Each sample is equivalent to about 3 m³ seawater filtered. Error bars are ± standard error. Dashed lines separate the 3 years of study.

more variable in the California slope area, probably owing to the heterogeneity generated by upwelling and offshore jets (also seen in rapid fluctuations in recorded SST for this region).

By focussing on the comparable sampling periods in each year (21 July–6 August in 1997, 19 July–29 August in 2000, and 27 June–16 August in 2001) we can detect where significant differences occurred between the warm and cool periods, and within the two sampled years of the cool period, in terms of mesozooplankton abundance and biomass (Table 4). Even allowing for the likelihood of some type-1 errors, given the number of inter-comparisons made, it is clear that abundances between the warm and cool periods are generally significantly different while abundances within the cool years are similar (except for the California slope region where the abundance was significantly different in each year). Biomass, however, is not significantly different between the two periods (with the exception of the Alaskan shelf). A significant change in abundance without a significant change in biomass implies that there must have been a change in the species composition.

The abundance of broad taxonomic groups for the summer period of each year is shown in Fig. 3 (note that the two oceanic areas have been

combined). The open ocean (centre panel) is where we see the most striking contrast between years, with a decrease in abundance and an increase in biomass (Fig. 2). This is explained by the changes in species composition (Fig. 3). During summer 1997 small copepods were very numerous, 4–5 times more numerous than in the cooler summers of 2000 and 2001. *Oithona* was the dominant genus in summer 1997, it was the second most abundant genus in 2000, and the third in 2001. During summer 2000 and 2001 *Paracalanus* was the dominant genus (and the second most abundant genus in 1997). *Pseudocalanus* was not common in summer 1997 but was more dominant in summer 2000 and 2001. *Clausocalanus* was also commonly found in all 3 years.

Conversely, larger copepods were at least as abundant in 2000 as in 1997, but 2–3 times more abundant in 2001 than in 1997. The dominant species in summer 1997 was *Calanus pacificus*, then *Neocalanus plumchrus* and *N. cristatus*. These three species were also the dominant species in 2000 and 2001, although *N. plumchrus* was more abundant than *C. pacificus*. For 2001 at least, this is explained by the slightly earlier summer sampling. *N. plumchrus*, which is the dominant species in spring, begins downwards migration to overwin-

Table 4

The results (*p* values, two tailed test) of non-parametric *t*-tests for mesozooplankton sample means

		1997 & 2000	1997 & 2001	2000 & 2001
Alaskan shelf	<i>n</i>	3 & 17		
	Abundance	<i>0.024</i>		
	Biomass	<i>0.021</i>		
Gulf of Alaska	<i>n</i>	16 & 32	16 & 42	32 & 42
	Abundance	<i>0.002</i>	<i>0.001</i>	0.780
	Biomass	0.229	0.103	<i>0.002</i>
Southern oceanic	<i>n</i>	16 & 29	16 & 55	29 & 55
	Abundance	0.309	<i>0.0003</i>	0.130
	Biomass	0.816	0.794	0.662
California slope	<i>n</i>	17 & 29	17 & 41	29 & 41
	Abundance	<i>0.028</i>	<i>0.001</i>	<i>0.018</i>
	Biomass	0.091	0.141	0.976

Samples from July and August from each region (rows) were compared for each pair of years (columns). Both abundance and biomass values were compared. The Alaskan shelf portion of the transect was not sampled in August 2001, so no comparison was made between this year and the other years. Significant results are in italics, *n* refers to the number of samples in each year.

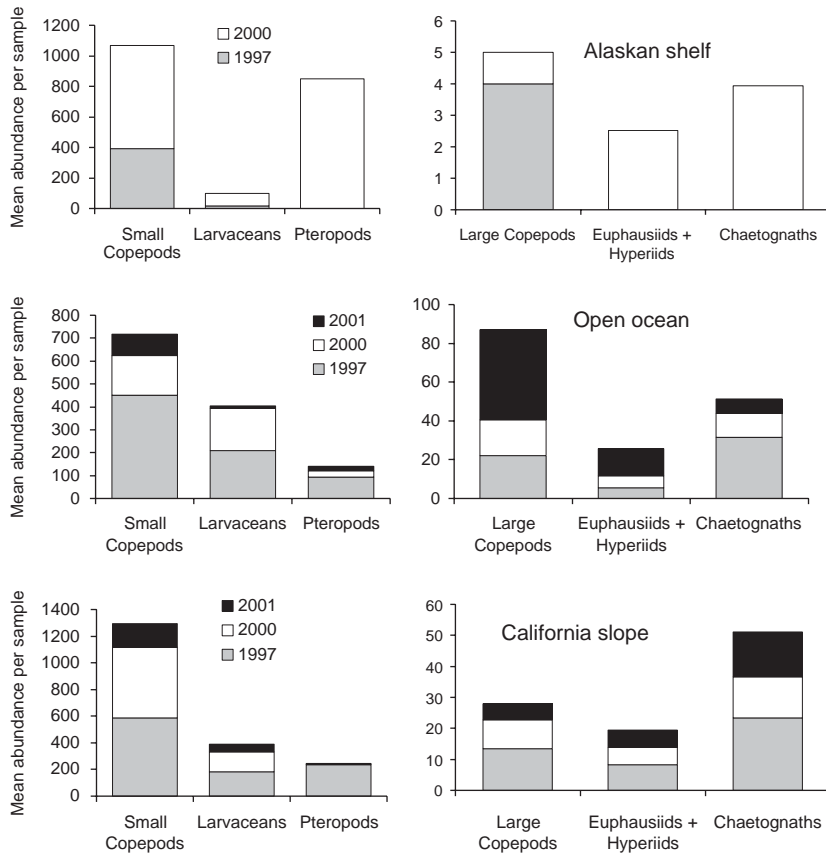


Fig. 3. The mean abundance per sample of major taxonomic groups of mesozooplankton in the three years for the Alaska shelf, the oceanic section of the transect (the Gulf of Alaska and southern oceanic sections combined) and the California slope.

tering depths in summer, and so earlier sampling is likely to find more of this species still in surface waters.

Larvaceans, another numerically dominant but low biomass group, were also abundant in 1997 and less so in the cooler period. The larger crustacea caught by the CPR, the euphausiids and hyperiids, were more abundant in 2001 than in 1997, with 2000 abundances similar to those in 2001. These data suggest that environmental change caused a change from small to large species in the open ocean. 2000 appears to be something of a transition year, with differences between 2001 and 1997 more noticeable.

The analysis for the Alaskan shelf region (upper panel, Fig. 3) has to be treated with caution as only three samples are available from summer

1997, compared to 17 in July/August 2000 (2001 is not considered because sampling was not complete on the August transect). However, it is clear that the patterns in the copepod community of the Alaskan shelf are opposite to those of the open ocean. Abundances of small copepods doubled from 1997 to 2000, but large copepods (although few in number) declined between the warm period and the cool. *Paracalanus* was by far the dominant small copepod genus in both years, followed by *Oithona*, and *Neocalanus plumchrus* dominated the large copepods in both years. On the Alaska shelf, euphausiids, hyperiids and chaetognaths, which were almost absent in 1997, were present in 2000 and presumably contributed to the increased biomass seen in this year.

The California slope region (lower panel, Fig. 3) shows a decline in abundance of all groups between 1997 and 2000 and a further decrease in 2001. Small copepods were dominated by *Paracalanus* in all 3 years, with *Oithona*, *Clausocalanus*, *Acartia danae* and *Pseudocalanus* also common. *Calanus pacificus* was the dominant large copepod in 1997 and 2000. However, *Nannocalanus minor* was the second most abundant species in 1997 but was not found at all in 2000 or 2001. *Calanus marshallae* was the second most abundant species in 2000. Although only found in samples collected at night, *Metridia pacifica* was common and increased in abundance from 1997 to 2000 and again in 2001 when it became the dominant species.

The indices of southern and northern copepods are shown in Fig. 4 and clearly support the idea that there has been a shift in the oceanic copepod community since the El Niño of 1997/1998. Abundances of southern copepods were much higher in the Gulf of Alaska in summer 1997, and abundances of northern species were much lower along the entire transect. The occurrence of northern species at the southern end of the transect probably reflects the upwelling of cold water that occurs off the California coast. Northern species were particularly abundant on the Alaskan shelf in

the cool period, and much more frequent in the oceanic areas. The California slope region shows little change in the index values between the two regimes.

4. Discussion

The potential regime shift that occurred in 1998/1999 is clearly evident in the CPR data from the Alaskan shelf to about 42°N. For the region of the transect to the south of this point, in the slope waters off California, the results describe inter-annual variability with little evidence for a step-wise shift. This supports the findings of Rebstock (2001) who found stable copepod community structure over a 49-year period and Rebstock (2002) where evidence of regime shift type responses was found in only some copepod species using the extensive time series of data from the CalCOFI. Mackas et al. (2004) describe simultaneous changes in zooplankton community composition anomalies from three continental margin regions covering a 850-km distance along the eastern margin of the northeast Pacific from northern British Columbia to Oregon. Our results suggest that the plankton communities of the

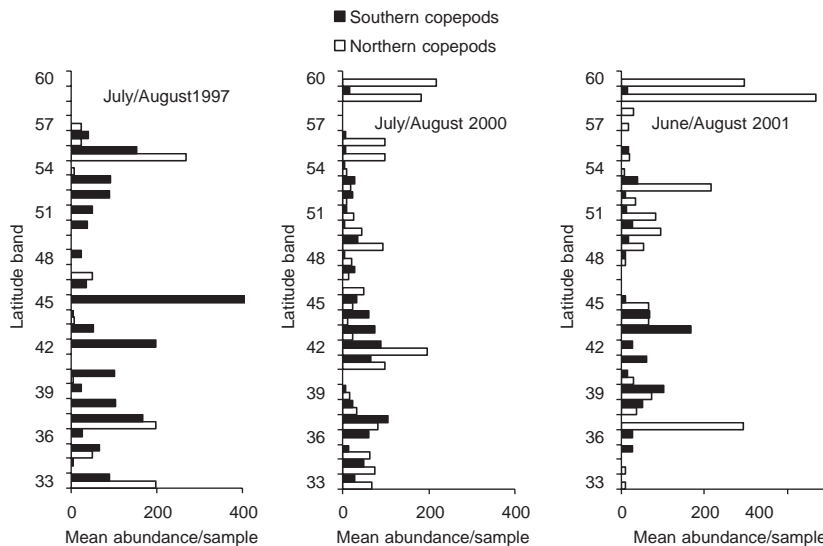


Fig. 4. Southern and northern copepod abundance index values (see text for derivation) for 1° bands of latitude.

oceanic Gulf of Alaska are as responsive to climate change as these more coastal temperate regions.

During August 1997 surface-water temperatures in the Gulf of Alaska were about 1–2°C warmer than the long-term average (Freeland, 1998) and in 2000 and 2001 about 1°C lower than average along much of the transect (Freeland and Batten, 2002). The CPR data suggest that the anomalously warm oceanic water contained large numbers of small species, chiefly copepods, and that these were species of a more southerly origin. The Alaskan shelf had very low numbers of copepods in the warm regime. The implication is that rather than northern species being replaced by southern species (as appeared to happen in the Gulf of Alaska), northern species simply failed to do well on the sub-Arctic shelf. After the regime shift, the oceanic areas saw a return to larger organisms, and colder boreal species of copepods became more abundant. The Alaskan shelf saw a large increase in small boreal copepod species (such as *Acartia* and *Pseudocalanus*) leading to higher recorded zooplankton abundance and biomass in the cool period. We have restricted our description to the mesozooplankton, but it should be noted that the CPR sampling mechanism is most suited to hard-shelled organisms such as crustacea. Gelatinous zooplankton are very rarely identifiable in the samples, and so we cannot comment on changes in such fauna.

Physical processes undoubtedly played a role in determining the spatial extent of the boreal and subtropical species, since each regime has associated atmospheric and ocean current modes. The NOI is strongly negative in El Niño years (Schwing et al., 2002) and was mostly negative through the 1990s until 1998; it has been generally positive since. When the NOI is negative there is anomalously low pressure at the north Pacific Subtropical High, weaker trade winds and probably a weaker southward flow of the California Current (Lynn and Bograd, 2002). This implies that northern origin species will not be advected so far south (the pattern seen in Fig. 4 left hand panel). There was also substantial advection of warm water northwards along the West Coast during 1997, which would allow southern origin species to extend further north (Peterson et al., 2002).

Work by Mackas et al. (2001) on the time series of zooplankton off the west coast of British Columbia suggests that this region is probably a 'pulse point', representing the most northern extension of California Current zooplankton on the shelf in the warm regime. Southern zooplankton showed a weak but consistent positive correlation with the strength of poleward currents; stronger poleward currents occur when the NOI is negative. There are several mechanisms by which zooplankton are advected off the shelf, such as seaward Ekman transport (Mackas, 1992) and mesoscale anticyclonic eddies that form along the eastern continental margin of the Gulf of Alaska in winter (Mackas and Galbraith, 2002; Batten and Crawford, unpublished data). These eddies are thought to be more pronounced in El Niño years, and furthermore, Batten and Crawford (unpublished data) show that as the eddies decay and entrained zooplankton are released, subsequent spread via surface currents can occur over large areas of the Gulf of Alaska.

It is also probable that physiological mechanisms will play some role, such that subtropical species physiologically adapted to warm water will do better at the higher latitudes in warm years, and that northern species, adapted to cooler temperatures, will do worse. The spatial extent and success of southern species in northern waters is thus likely to be the result of enhanced advective processes increasing their northward transport and bringing along a more favourable thermal environment.

The changes described here have implications for higher trophic levels. Firstly, larger prey items are more energetically rewarding to predators and secondly the mesozooplankton biomass levels appear to have increased (or remained the same) across all areas since the regime shift. More food therefore appears to be available in the larger size fractions. Evidence for the relevance of these changes to upper trophic levels can already be found in the returns of Pacific salmon, which have shorter generation lengths than most other animals, and therefore respond more quickly to climatic changes. The returns of adult chinook and steelhead salmon to the Columbia River in

2001 reversed from near historic lows to reach the highest and second highest recorded levels, respectively, since record keeping began in 1938 (Wakefield, 2001). These animals entered the ocean 2 years earlier (in 1999), just after the climate changed. Adult returns of Columbia River Coho showed a similar response but starting 1 year earlier (in 2000), consistent with their shorter marine life cycle. Adult returns of Fraser River pink salmon also turned around and may have reached the highest levels of the preceding century in 2001 (even-year runs of pink salmon are almost absent from the Fraser).

In summary, it is clear that the CPR is a suitable instrument with which to monitor large-scale plankton dynamics in the north Pacific, particularly the regions far from shore, which are difficult to monitor through traditional sampling programs. We have shown that these open-ocean regions are as responsive to climate change as coastal environments. Given that many commercial species, such as Pacific salmon, make extensive use of the open ocean environment, monitoring of this ecosystem is necessary if we are to predict the impacts of climate change on these resources.

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