Common signals between physical and atmospheric variables and zooplankton biomass in the Subarctic Pacific

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There is increasing evidence that zooplankton inter-annual variability is related to changes in the physical and atmospheric environments. Here, we analyse and compare the inter-annual variations of zooplankton biomass and of two environmental properties – surface temperature and surface salinity – at Station P, Gulf of Alaska (50°N 145°W). This 1956–1980 data set was gathered by Canadian weatherships, with a frequency of approximately 1 month. Spectral analysis shows that the annual cycle dominates the variations of zooplankton biomass, as well as temperature and salinity. However, most of the inter-annual variability in all three properties is contained in frequency bands corresponding to periods near 12–24 years, ∼6 years, ∼29 months, and ∼14.5 months. These frequencies correspond to those found in well-known oscillations in the atmosphere–ocean system. In this article we summarize some of the results of our work, compare our results with others reported in the literature and discuss possible mechanisms for the relationships between zooplankton, salinity, and temperature.

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Key words: climate–ocean interactions, copepod, Gulf of Alaska, inter-annual variations, North Pacific, Quasi Biennial Oscillation, salinity, SST, time series, zooplankton biomass.

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Introduction

Zooplankton biomass is highly variable in space and time (Haury *et al.*, 1978; Steele, 1985; Wroblewski *et al.*, 1975; Mullin, 1979; Mackas *et al.*, 1985; Steele and Henderson, 1992), but it is known to undergo similar changes across large oceanic regions on the inter-annual time scale (Garrod and Colebrook, 1978; Chelton *et al.*, 1982), suggesting the existence of low-frequency environmental changes that affect the planktonic standing stocks over large areas.

Since most marine species have planktonic life stages and/or depend on plankton as a food source at some stage, changes in planktonic abundances can have widespread effects on whole ecosystems. As zooplankters are under the influence of their surrounding element, it is natural to seek to relate their variations quantitatively to changes in the physical environment or, more generally, to climate changes. In the last decade, several studies in the Atlantic (Southward, 1984; Radach, 1984; Colebrook, 1986; Dickson *et al.*, 1988; Aebischer *et al.*, 1990; Cushing, 1990; Taylor, 1995; Fromentin and Planque, 1996) and Pacific (Miller *et al.*, 1985; Brodeur and Ware, 1992; Francis and Hare, 1994; McFarlane and Beamish, 1992; Mackas, 1995) oceans have suggested relationships between zooplankton inter-annual variations and variations in physical or atmospheric properties.

In this article we summarize some of the results of our work on time-series analysis of the mesozooplankton biomass, temperature, and salinity series measured for 24 years at Station P, in the Gulf of Alaska, and compare our results with others reported in the literature. The basic question we seek to answer is "*why does zooplankton biomass vary from year to year?*". To this end, the following specific questions are addressed:

- How does mesozooplankton biomass vary over the period of observation and are there identifiable patterns?

- If so, are these patterns also found in the physical environment?
- Are they found in atmospheric variables as well?
- If there are common patterns of variability, are they causally related, and, if so, what are the mechanisms involved?

Data and analyses

Station P is located in the open ocean (4200 m depth) at 50°N 145°W. Mesozooplankton biomass (wet weight in mg m^{-3}; daytime vertical hauls from 150 m to the surface) was measured using methods described by LeBrasseur (1965), Fulton (1983), and Frost (1983). A number of biological, chemical and physical parameters (including chlorophyll *a*, oxygen, nutrients, temperature, salinity, and mixed layer depth) were also measured (Frost, 1983; Tabata *et al.*, 1986). The monthly time series of zooplankton, sea surface temperature (SST), and salinity are shown in Fig. 1.

The time series were analysed using standard techniques of spectral analysis (e.g., Platt and Denman, 1975; Bloomfield, 1976) to identify the frequencies at which significant variations occur. Spectra were calculated using a standard Fast Fourier Transform algorithm as implemented at the Center of Coastal Studies, Scripps Institution of Oceanography. The time series were detrended before transformation, and tapered. Spectra with two degrees of freedom are presented (Figs 2 and 3) in order to obtain maximum resolution. The average noise level shown was calculated by subtracting the variance of the 12-month period and its harmonics (since these periods represent well-known, non-random signals) from the total variance, assuming that all remaining fluctuations in the data represent a white noise process, and dividing by n. The 95% level of significance was calculated by using the theorem that for a noise process the sample spectrum estimates at a given frequency are distributed about the population spectrum according to the chi-square distribution, divided by the number of degrees of freedom (Bloomfield, 1976, pp. 195–196). Details about the bandpass filter used for the analysis of the Quasi Biennial Oscillation (QBO) signals are reported in Conversi and Hameed (1997).

Results

Although very different, the time series of raw data of mesozooplankton biomass, temperature, and salinity (Fig. 1) are all dominated by the annual signal, and all three show inter-annual variability, i.e. some years are 'high' while others are 'low'. The difference is not only in the shapes of the time series, but also in the magnitudes of their variability: while zooplankton biomass varies 100-fold, from less than 5 mg m^{-3} (the minimum winter value; Jan 1980) to more than 480 mg m^{-3} (the maxi-

mum spring value; May 1958), temperature varies three-fold, from 4.5°C (March 59) to 14.5°C (in August 1979), and salinity varies by less than 1.5%, from 32.41 (in October 1980) to 32.88 (in May 1958). Yet spectral analysis of the three variables (Fig. 2) shows that, in addition to the expected annual peak, there are common patterns not visible in the raw time series.

The common features among all three variables in the inter-annual part of the spectra (enlarged in Fig. 3) are:

- A long-term peak (12 years in zooplankton, 24 years in SST and salinity). Note, however, that the resolution at the low-frequency end of the spectrum is very low, e.g. an 18-year variation (e.g., Royer, 1993) could fall in either the 24- or the 12-year category. Since it is difficult to discern the periodicity at this time scale, this type of variation will henceforth be referred to as "interdecadal band".
- A near 6-year (72 month) peak.
- A near 2.3 years (29 month) peak.
- A near 14/15-month peak.

In addition, salinity has a significant peak at 41 months (3.4 years) and at 20.5 months, and temperature has a significant peak at 22 months. Note also (Fig. 2) the harmonics of the annual signal in the zooplankton spectrum, at 6 and 4 months, and the 6-month harmonic in the SST spectrum. These harmonics account for a good part of the intra-annual variability in these properties and are present because the annual cycles are not sinusoidal (not shown). The annual cycle of salinity follows an almost perfect sinusoid and the spectrum has no significant harmonics.

The next question was whether these peaks were somehow associated. Cross spectral and bandpass filter analysis indicated the presence of a phase relationship between temperature and zooplankton at the 2.3-year periodicity, i.e. changes in temperature at the quasi-biennial time scale precede changes in zooplankton by ∼4 months (Conversi and Hameed, 1997). There is a phase relationship also between salinity and zooplankton at the 6-year (72 months) periodicity, with changes in salinity preceding changes in zooplankton by nearly 11 months. A phase relationship showing a change in a physical variable preceding a change in a biological variable is of interest because it may indicate the presence of a causal relationship between the two systems (e.g. changes in temperature/salinity – or in the water masses that they represent – influencing inter-annual changes in zooplankton biomass).

Discussion

We address the questions posed in the introduction sequentially:

How does mesozooplankton biomass vary over the period of observation and are there identifiable patterns?

Zooplankton biomass variations are dominated by the annual signal and by its harmonics (Fig. 2a). The inter-annual variations (Fig. 3a), although smaller than the annual variation (17% of the total variability vs. 58%), fall mostly within four frequency bands – near the inter-decadal band and at periods of ∼6 years, ∼29 months, and ∼14 months. We shall see later that the variance in these frequency bands is also found in physical and atmospheric variables.

If there are identifiable patterns, are they also found in the physical environment?

SST and salinity inter-annual variations both have significant energy at the inter-decadal band and at periods of ∼6 years, ∼29 months, and ∼15 months (Figs 2 and 3). Thus, spectral analysis shows that most of the inter-annual variations in all three variables tend to fall into common cycles, suggesting that this may be more than a simple coincidence. Mysak *et al.* (1982), analysing 40–80 years of data in the Gulf of Alaska, found coherent *5–6 year* signals in sea level, SST, and salinity measured at coastal stations, and also in cross spectra of sockeye salmon catch and herring recruitment (data from open waters) with physical variables (sea level and salinity). Their results suggest that the 6-year cycle in physical and biological variables has a wide spatial scale, possibly encompassing a large portion of the Gulf of Alaska. And on a larger, Pacific Ocean scale, Favorite and McLain (1973) found movements of anomalously warm or cold surface water in the North Pacific gyre from Japan to US, with a period of 5–7 years. Mysak *et al.* (1982) also found *2.3-year* signals in sea level and SST and the sockeye catch off the Gulf of Alaska. This last signal was also found by Tabata (1989) in the 27-year SST record at Station P; Tabata noted its possible association with the atmospheric QBO.

Are these found in atmospheric variables as well?

A survey of the literature shows that similar periodicities are found in several atmospheric variables (Table 1). A *6-year* variation is found in the Southern Oscillation Index (Burroughs, 1992), as well as in the North Atlantic Oscillation, which is the seesaw of atmospheric pressure between subtropical and high latitude regions of the North Atlantic (Hurrell and van Loon, 1995). In addition, an oscillation of nearly 6 years has long been noted in a large number of other variables, including tree rings (Liritzis and Kosmatos, 1995), and in the Baltic ice cover and sedimentary deposits (Lamb, 1972). A similar periodicity has also been found in marine biota outside the Pacific; for example the 5-year cycle in diatom abundance at Narragansett Bay (Smayda, 1998).

Hameed *et al.* (1995) have suggested that the ∼6-year oscillation is linked to the Pole Tide and the annual cycle through non-linear interactions in the climatic system.

The *29-month* period found here is in the range of periods attributed to the QBO, which was originally identified in the 26-month quasi-periodic reversal of tropical stratospheric winds (Reed *et al.*, 1961). A similar signal (25–30 months) has also been detected in the troposphere, sea level pressure, air and SSTs (Landsberg *et al.*, 1963; Trenberth, 1975; Currie and Hameed, 1988; Labitzke and van Loon, 1992). This has been proposed as the explanation for the alternation of weak and strong El Niños (Rasmusson *et al.*, 1990; Kane, 1992; Angell, 1992; Gray *et al.*, 1992). A detailed analysis of the specific QBO signal in the temperature and zooplankton time series at station P, its phase relationship, and its possible meaning was made in a previous study (Conversi and Hameed, 1997), and indicates that a climatic signal is possibly present in the oceanic biota.

Finally, the *14-month* periodicity observed is similar to that found in another oscillation, the Pole Tide, also known as Chandler wobble. Originally found in 1891, following analysis of astronomical data by Chandler, as an oscillation of the earth's surface about the rotation axis with a period of ≈14 months (Lambeck, 1980), the Pole Tide has been observed in variations of the sea level (Miller and Wunsch, 1973; Currie, 1975) and atmospheric pressure (Maksimov, 1952; Bryson and Starr, 1977). Its amplitude is particularly large at high northern latitudes (Maksimov, 1952; Hameed and Currie, 1989), which may explain why the peak at ∼14 months is the strongest in the inter-annual range of frequencies in the zooplankton data (Fig. 3a).

In a previous study (Hameed and Conversi, 1995) we discussed the presence of this signal in the North Pacific Index of Trenberth and Hurrell (1994) and in the zooplankton biomass at Station P. Further work on the phase relationship between these signals in the air–water–biota compartments needs to be done in order to identify a possible link.

In addition to the above signals, which are common to all three variables, the 41-month (3.4-year) periodicity found in salinity coincides with another common phenomenon in climatic data, called the Quasi Triennial Oscillation (Hameed *et al*., 1995). And the 20.6-month peak found in salinity, close to the 22-month peak in SST, is also found in the North Pacific Index (Hameed and Conversi, 1995). This period, being the difference frequency between the annual cycle and the QBO, represents the non-linear characterization of ocean variability in this region.

If there are common patterns of variability, are they causally related and, if so, what are the mechanisms involved?

This last question is more difficult to answer. Several possibilities can be invoked, and at this point they are
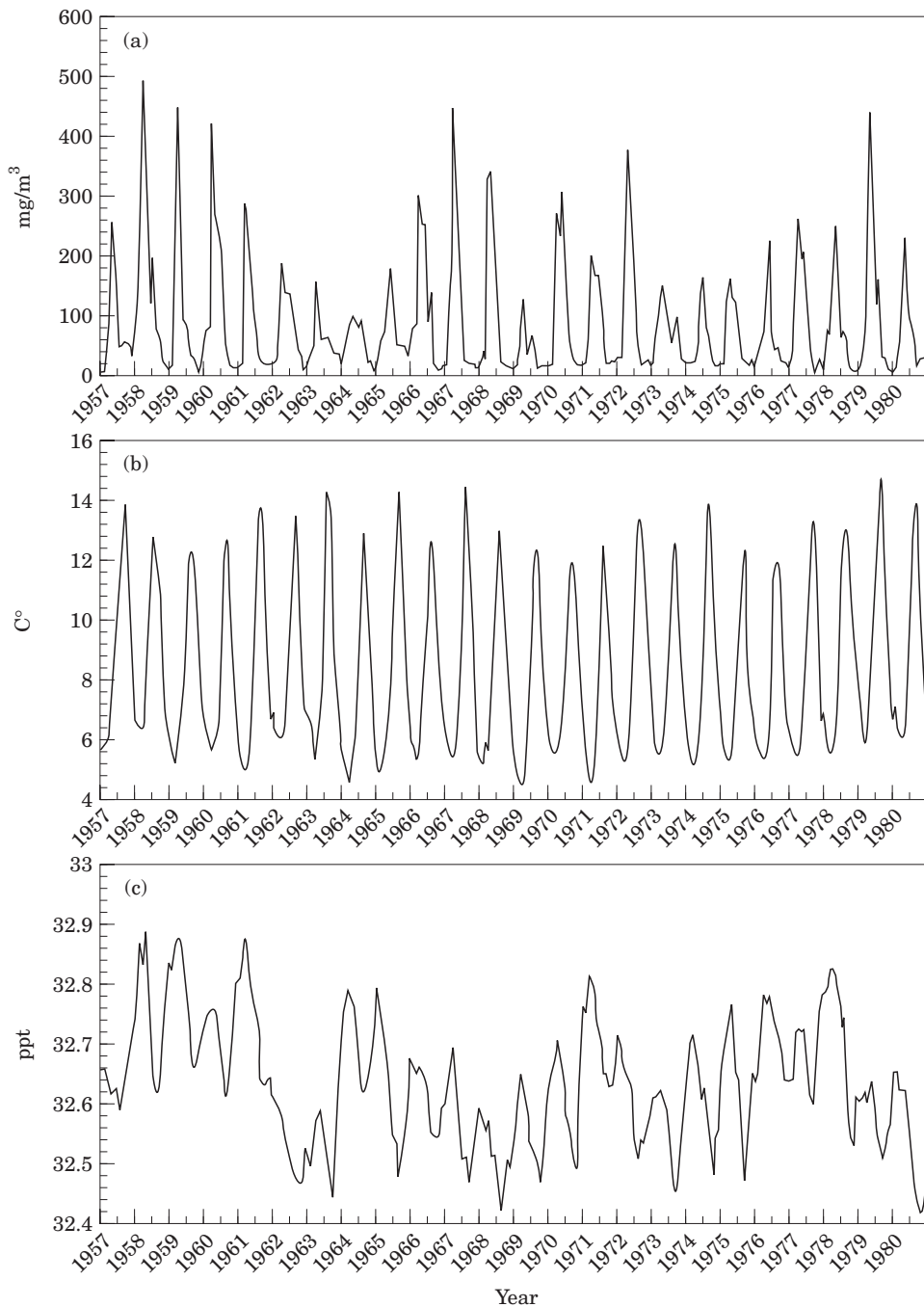
Figure 1. Times series of raw data: (a) Mesozooplankton biomass at station P (mg m^{-3} wet weight); (b) sea surface temperature (SST, °C); (c) surface salinity.

simple speculations. Since the relationship between zooplankton and SST was positive, we have postulated (Conversi and Hameed, 1997) that slight inter-annual changes in SST at the QBO range affect the growth rates of copepods (the major component of Station P zooplankton biomass) directly, and indirectly by affecting the growth rates of their prey. This is based on indications that copepod growth rates and those of their prey, phytoplankton, and microzooplankton, are positively affected by an increase in temperature (Huntley and Lopez, 1992; Eppley, 1972), and on the consideration that, at the severely low temperatures of the
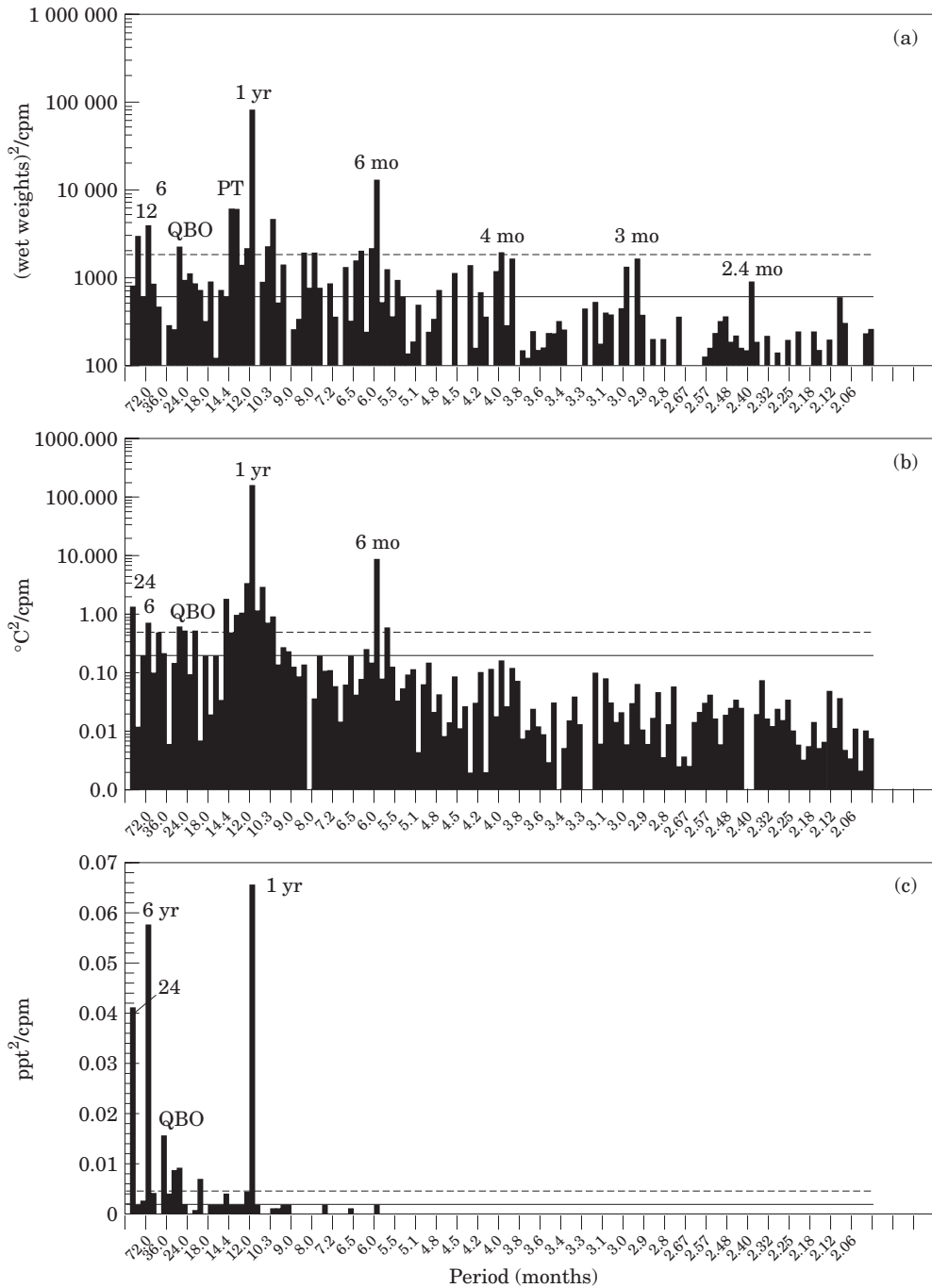
Figure 2. Spectra (2 degrees of freedom): (a) Mesozooplankton biomass (log scale); (b) SST (log scale); and (c) surface salinity (linear scale because of zero values). See text for explanation of the 95% significance level. QBO indicates the frequency of the Quasi Biennial Oscillation, PT of the Pole Tide. Noise (——); 95% significance level (– – –).

Subarctic Pacific, even small temperature changes are likely to have major repercussions on the biota, particularly because the Subarctic Pacific is not nutrient limited (Miller *et al.*, 1991). According to this hypothesis, subtle changes in SST from year to year would result in same-sign changes in the zooplankton biomass, the magnitude of which depending on whether the season of the anomaly is crucial for the copepod development.
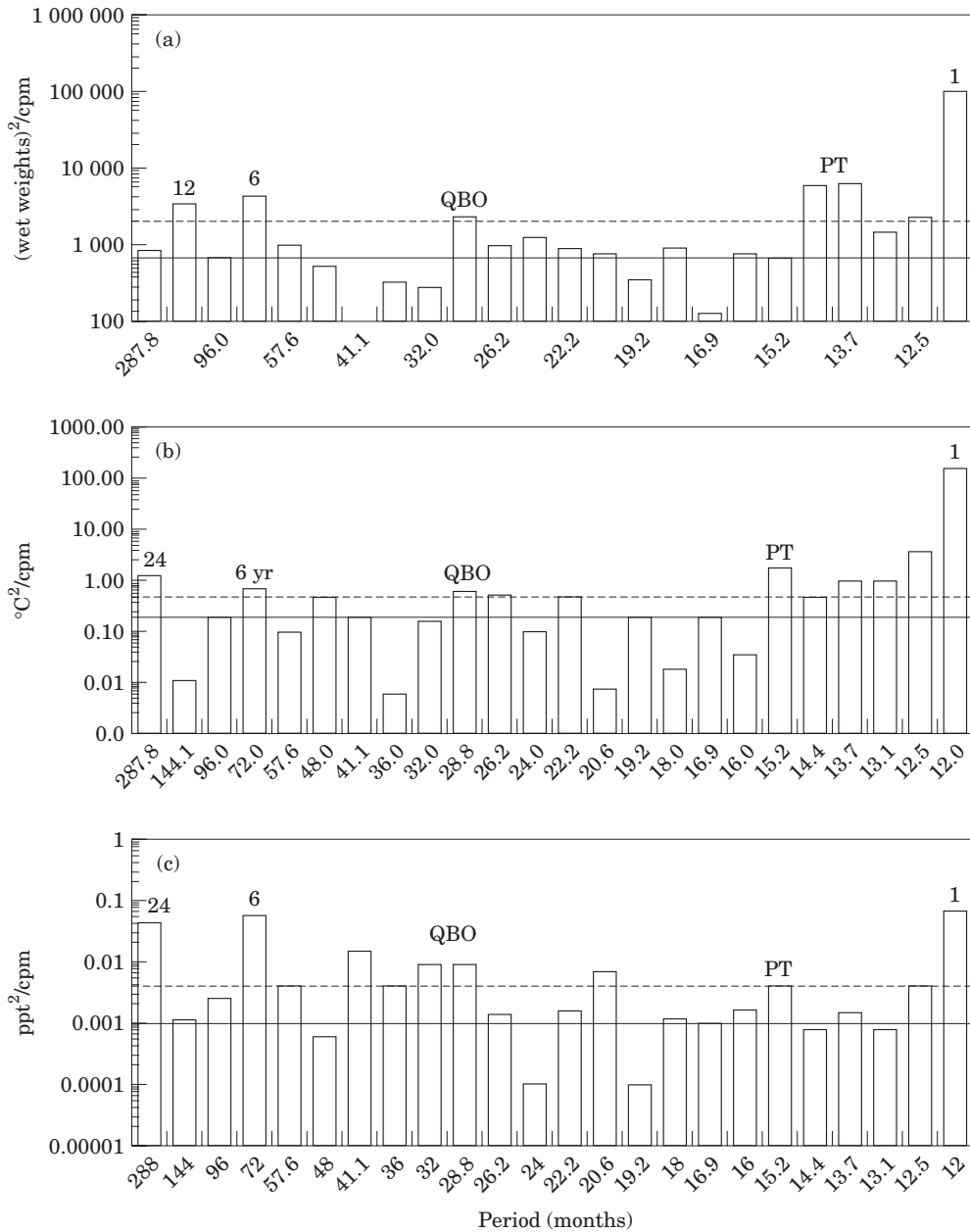
Figure 3. Enlargement of the inter-annual part of the spectra: (a) Mesozooplankton biomass; (b) SST; and (c) surface salinity. (See also legend of Fig. 2.) Noise (——); 95% significance level (– – –).

The above hypothesis does not address the effect of salinity. Another hypothesis would be that inter-annual changes in SST and salinity are due to shifts in the latitude of the West Wind Drift. This would seem likely since low amplitude oscillations have been found in the Kuroshio Current (McPhaden, 1994; Kawasaki, 1984; Qiu and Joyce, 1992; Qiu and Lukas, 1996), which feeds the West Wind Drift. Station P is near the outer edge of the Alaskan gyre and is likely to be influenced by shifts

in the latitude of the West Wind Drift/Transition Zone (Parslow, 1981). The West Wind Drift has higher salinity and temperature than the Subarctic Current (Parslow, 1981) and probably supports different zooplankton communities (and associated biomass). On the other hand, zooplankton biomass is known to increase at convergence areas (Kingsford and Suthers, 1994; Thibault *et al.*, 1994). Thus it is plausible that higher temperatures and salinities from the lower-latitude water

Table 1. Common signals in oceanic, atmospheric and environmental variables in the Gulf of Alaska (GoA) and elsewhere.

5- to 6-year signal	
Sea level, salinity (GoA)	Mysak *et al.* (1982)
SST (GoA)	Favorite and McLain (1973); Mysak *et al.* (1982)
Sockeye catch/herring recruitment (GoA)	Mysak *et al.* (1982)
Southern Oscillation Index	Burroughs (1992)
North Atlantic Oscillation	Hurrell and van Loon (1995)
North Atlantic pressure	Burroughs (1992)
South American rainfall	Burroughs (1992)
Baltic ice cover	Lamb (1972)
Paleo-strata	Lamb (1972)
Tree rings	Liritzis and Kosmatos (1995)
Diatoms, Narragansett Bay	Smayda (1998)
2.3-year signal (quasi biennial oscillation)	
Sea level (GoA)	Mysak *et al.* (1982)
SST (GoA)	Mysak *et al.* (1982); Tabata (1989)
Sockeye catch (GoA)	Mysak *et al.* (1982)
Tropical stratospheric winds	Reed *et al.* (1961)
Sea level press, SST (Southern Hemisphere)	Trenberth (1975)
Southern Oscillation Index	Rasmusson *et al.* (1990); Kane (1992); Angell (1992); Gray *et al.* (1992)
14-month signal (pole tide)	
North Pacific Index	Hameed and Conversi (1995)
Atmospheric pressure	Maksimov (1952); Bryson and Starr (1977)
Sea level	Miller and Wunsch (1973)

masses contribute to higher zooplankton biomass, and that slow, inter-annual shifts in the current system would result in changes of the same sign in salinity, temperature, and zooplankton, which is what we find.

The latter hypothesis is more appealing from a global perspective, since inter-annual changes in the atmosphere–ocean system are expected to affect the oceanic circulation. Mysak *et al.* (1982) put forward a different hypothesis; namely, that the presence of the ~6-year cycle in the physical properties was due to northward-propagating baroclinic Kelvin waves.

Conclusions

Inter-annual changes in zooplankton, SST, and salinity at Station P fall into common bands of periodicity. A literature survey indicates that similar periodicities are also found in several other oceanic and atmospheric variables. It seems unlikely that these co-occur by co-incidence only. Rather, they appear to represent links between the physical and the biological systems at the inter-annual scale. The mechanisms involved are still unclear and could involve large circulation shifts as well as direct effects of some of the physical properties on the biota. The results presented may provide grounds for hypothesis-testing through modelling.

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References

Aebischer, N. J., Coulson, J. C., and Colebrook, J. M. 1990. Parallel long-term trends across four marine trophic levels and weather. Nature, 347: 753–755.

Angell, J. K. 1992. Evidence of a relation between El Niño and QBO, and for an El Niño in 1991–1992. Geophysical Research Letters, 19(3): 285–288.

Bloomfield, P. 1976. Fourier analysis of time series: An introduction. John Wiley and Sons, New York. 258 pp.

Brodeur, R. D., and Ware, D. M. 1992. Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. Fisheries Oceanography, 1: 32–38.

Bryson, R. A., and Starr, T. B. 1977. Chandler tides in the atmosphere. Journal of the Atmospheric Sciences, 34: 1975–1986.

Burroughs, W. J. 1992. Weather cycles – real or imaginary? Cambridge University Press, New York. 207 pp.

Chelton, D. B., Bernal, P. A., and McGowan, J. A. 1982. Large-scale interannual physical and biological interaction in the California current. Journal of Marine Research, 40(4): 1095–1125.

Colebrook, J. M. 1986. Environmental influences on long-term variability in marine plankton. Hydrobiologia, 142: 309–325.

Conversi, A., and Hameed, S. 1997. Evidence for quasi biennial oscillations in zooplankton biomass in the subarctic Pacific. Journal of Geophysical Research, 102: 15 659–15 665.

Currie, R. G. 1975. Period, Qp, and amplitude of the Pole Tide. Geophysical Journal of the Royal Astronomical Society, 43: 73–86.

Currie, R. G., and Hameed, S. 1988. Evidence of quasi-biennial oscillations in a general circulation model. Geophysical Research Letters, 15(7): 649–652.

Cushing, D. H. 1990. Recent studies on long-term changes in the sea. Freshwater Biology, 23(1): 71–84.

Dickson, R. R., Kelly, P. M., Colebrook, J. M., Wooster, W. S., and Cushing, D. H. 1988. North winds and production in the eastern North Atlantic. Journal of Plankton Research, 10(1): 151–169.

Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. Fishery Bulletin, 70: 1063–1085.

Favorite, F., and McLain, D. R. 1973. Coherence in transpacific movements of positive and negative anomalies of sea surface temperature, 1953–60. Nature, 244: 139–143.

Francis, R. C., and Hare, S. R. 1994. Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. Fisheries Oceanography, 3: 279–291.

Fromentin, J. M., and Planque, B. 1996. *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series, 134: 111–118.

Frost, B. W. 1983. Interannual variation of zooplankton standing stock in the open Gulf of Alaska. *In* From Year to Year, pp. 146–157. Ed. by W. S. Wooster. Sea Grant, University of Washington, Seattle, WA.

Fulton, J. 1983. Seasonal and annual variations of net zooplankton at Ocean Station "P", 1956–1980. Canadian Data Report of Fisheries and Aquatic Sciences, 374: 1–65.

Garrod, D. J., and Colebrook, J. M. 1978. Biological effects of variability in the North Atlantic Ocean. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 173: 128–144.

Gray, W. M., Sheaffer, J. D., and Knaff, J. A. 1992. Hypothesized mechanism for stratospheric QBO influence on ENSO variability. Geophysical Research Letters, 19(2): 107–110.

Hameed, S., and Conversi, A. 1995. Signals in the interannual variations of zooplankton biomass in the Gulf of Alaska. *In* Holocene cycles: climate, sea levels, and sedimentation, pp. 21–27. Ed. by C. W. Finkl. Coastal Education and Research Foundation, Charlottesville.

Hameed, S., and Currie, R. G. 1989. Simulation of the 14-month Chandler wobble in a global climate model. Geophysical Research Letters, 16(3): 247–250.

Hameed, S., Currie, R. G., and LaGrone, H. 1995. Signals in atmospheric pressure variations from 2 to 70 months: Part I, simulations by two coupled ocean-atmosphere GCMs. International Journal of Climatology, 15: 853–871.

Haury, L. R., McGowan, J. A., and Wiebe, P. H. 1978. Patterns and processes in the time–space scales of plankton distributions. *In* NATO Conference on Marine Biology, Erice, Italy, November 1977 – Spatial patterns in plankton communities, pp. 277–327. Ed. by J. H. Steele. Plenum Press, New York, NY.

Huntley, M. E., and Lopez, M. D. G. 1992. Temperature-dependent production of marine copepods: a global synthesis. American Naturalist, 140: 201–242.

Hurrell, J. W., and van Loon, H. 1995. Decadal trends in North Atlantic Oscillation and relationships to regional temperature and precipitation. *In* Proceedings of the 6th International Meeting on Statistical Climatology, 19–23 June 1995, Galway, Ireland, pp. 185–188.

Kane, R. P. 1992. Relationship between QBOs of stratospheric winds, ENSO variability and other atmospheric parameters. International Journal of Climatology, 12: 435–447.

Kawasaki, T. 1984. Why do some fishes have wide fluctuations in their numbers? A biological basis for fluctuations from the viewpoint in evolutionary biology. FAO Fisheries Report No. 291, Rome, 1065–1080.

Kingsford, M. J., and Suthers, I. M. 1994. Dynamic estuarine plumes and fronts: importance to small fish and plankton in coastal waters of NSW, Australia. Continental Shelf Research, 14: 655–672.

Labitzke, K., and van Loon, H. 1992. Some influences responsible for the interannual variations in the stratosphere of the northern hemisphere. *In* The role of the stratosphere in global change, pp. 267–283. Ed. by M. Chanin. Springer-Verlag, New York.

Lamb, H. H. 1972. Climate, present, past and future. Methuen and Co., London. 613 pp.

Lambeck, K. 1980. The Earth's variable rotation: geophysical causes and consequences. Cambridge University Press, Cambridge. 449 pp.

Landsberg, H. E., Mitchell, J. M., Crutcher, H. L., and Quinlan, F. T. 1963. Surface signs of the biennial atmospheric pulse. Monthly Weather Review, 91: 549–556.

LeBrasseur, R. J. 1965. Seasonal and annual variations of net zooplankton at Ocean Station P, 1956–1964. Fisheries Research Board of Canada – Manuscript Report Series (Oceanographic and Limnological). No. 202.

Liritzis, I., and Kosmatos, D. 1995. Solar-climate cycles in a tree-ring record from the Parthenon. *In* Holocene cycles: climate, sea levels, and sedimentation, pp. 73–78. Ed. by C. W. Finkl. Coastal Education and Research Foundation, Charlottesville.

Mackas, D. L. 1995. Interannual variability of the zooplankton community off southern Vancouver Island. *In* Climate change and northern fish populations, pp. 603–615. Ed. by R. J. Beamish. National Research Council of Canada, Ottawa.

Mackas, D. L., Denman, K. L., and Abbott, M. R. 1985. Plankton patchiness: biology in the physical vernacular. Bulletin of Marine Sciences, 37(1): 652–674.

Maksimov, I. V. 1952. On the "pole tide" in the sea and the atmosphere of the earth. Doklady Akademii Nauk USSR, 86: 673–676.

McFarlane, G. A., and Beamish, R. J. 1992. Climatic influence linking copepod production with strong year-classes in sablefish, *Anoplopoma fimbria*. Canadian Journal of Fisheries and Aquatic Sciences, 49: 743–753.

McPhaden, M. J. 1994. The eleven-year El Niño? Nature, 370: 326–327.

Miller, C. B., Batchelder, H. P., Brodeur, R. D., and Pearcy, W. G. 1985. Response of the zooplankton and ichthyoplankton off Oregon to the El Niño event of 1983. *In* El Niño North, pp. 185–187. Ed. by W. S. Wooster and D. L. Fluharty. Washington Sea Grant, Seattle.

Miller, C. B., Frost, B. W., Wheeler, P. A., Landry, M. R., Welshmeyer, N. A., and Powell, T. M. 1991. Ecological dynamics in the subarctic Pacific, a possibly iron-limited system. Limnology and Oceanography, 36(8): 1600–1615.

Miller, S. P., and Wunsch, C. 1973. The pole tide. Nature Physical Science, 246: 98–102.

Mullin, M. M. 1979. Longshore variation in the distribution of plankton in the Southern California Bight. CalCOFI Report, 20: 120–124.

Mysak, L. A., Hsieh, W. W., and Parsons, T. R. 1982. On the relationship between interannual baroclinic waves and fish populations in the northeast Pacific. Biological Oceanography, 2(1): 63–103.

Parslow, J. S. 1981. Phytoplankton–zooplankton interactions: data analysis and modelling (with particular reference to Ocean Station P [50°N 145°W] and controlled ecosystem experiments). Ph.D. dissertation, University of British Columbia, Vancouver. 400 pp.

Platt, T., and Denman, K. L. 1975. Spectral analysis in ecology. Annual Review of Ecology and Systematics, 6: 189–210.

Qiu, B., and Joyce, T. M. 1992. Interannual variability in the mid- and low-latitude western North Pacific. Journal of Physical Oceanography, 22: 1062–1079.

Qiu, B., and Lukas, R. 1996. Seasonal and interannual variability of the North Equatorial Current, the Mindanao Current, and the Kuroshio along the Pacific western boundary. Journal of Geophysical Research, 101: 12 315–12 330.

Radach, G. 1984. Variations in the plankton in relation to climate. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 185: 234–254.

Rasmusson, E. M., Wang, X., and Ropelewski, C. F. 1990. The biennial component of ENSO variability. Journal of Marine Systems, 1: 71–96.

Reed, R. J., Campbell, W. J., Rasmussen, L. A., and Rogers, D. G. 1961. Evidence of a downward-propagating, annual wind reversal in the equatorial stratosphere. Journal of Geophysical Research, 66(3): 813–818.

Royer, T. C. 1993. High-latitude oceanic variability associated with the 18.6 year nodal tide. Journal of Geophysical Research, 98(C3): 4639–4644.

Smayda, T. 1998. Patterns of variability characterizing marine phytoplankton, with examples from Narragansett Bay. ICES Journal of Marine Science, 55: 562–573.

Southward, A. J. 1984. Fluctuations in the "indicator" chaetognaths *Sagitta elegans* and *Sagitta setosa* in the Western Channel. Oceanologica Acta, 7: 229–239.

Steele, J. H. 1985. A comparison of terrestrial and marine ecosystems. Nature, 313: 355–358.

Steele, J. H., and Henderson, E. W. 1992. A simple model for plankton patchiness. Journal of Plankton Research, 14 (10): 1397–1403.

Tabata, S. 1989. Trends and long-term variability of ocean properties at ocean station P in the Northeast Pacific Ocean. Geophysical Monographs, 55: 113–131.

Tabata, S., Thomas, B., and Ramsden, D. 1986. Annual and interannual variability of steric sea level along Line P in the northeast Pacific Ocean. Journal of Physical Oceanography, 16: 1378–1387.

Taylor, A. H. 1995. North–south shifts in the Gulf Stream and their climatic connection with the abundance of zooplankton in the UK and its surrounding seas. ICES Journal of Marine Science, 52: 711–721.

Thibault, D., Gaudy, R., and Lefevre, J. 1994. Zooplankton biomass, feeding and metabolism in a geostrophic frontal area (Almeria–Oran front, western Mediterranean) – significance to pelagic food webs. Journal of Marine Systems, 5: 297–311.

Trenberth, K. E. 1975. A quasi-biennial standing wave in the southern hemisphere and interrelations with sea-surface temperature. Quarterly Journal of the Royal Meteorological Society, 101: 55–74.

Trenberth, K. E., and Hurrell, J. W. 1994. Decadal atmosphere–ocean variations in the Pacific. Climate Dynamics, 9: 303–319.

Wroblewski, J. S., O'Brien, J. J., and Platt, T. 1975. On the physical and biological scales of phytoplankton patchiness in the ocean. Mémoires de la Société royale des Sciences de Liège, 7: 43–57.