

Seasonal variations of mesoplankton biomass in the upper layer of the Bering Sea; understanding biomass oscillations in the ocean

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Data on the mesoplankton biomass in the upper layer (down to 100 m) of the western part of the Bering Sea and the adjacent regions of the north-west Pacific were fitted to a periodic regression. The biomass values (wet weight) change from 74 mg m^{-3} in winter to 770 mg m^{-3} in summer, the annual average value being 240 mg m^{-3} . These changes closely agree with the seasonal biomass oscillations in the north-east Pacific at Weather Station "P" (50°N , 145°W), which were determined on the basis of long-term observations. These results were used to analyse data derived mainly from published literature to produce equations that describe the pattern of seasonal zooplankton biomass oscillations in the World Ocean. The result confirms the intuitive ideas of planktonologists: phases of these oscillations are approximately opposite in the two hemispheres, and the phase shift from the Poles to the Equator reaches about two months in the Northern Hemisphere and at least three months in the Southern Hemisphere.

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Introduction

To get a better insight into the structure and functioning of oceanic ecological systems, knowledge of the distribution of the biomass of pelagic animals is required. Most importantly, the biomass of mesoplanktonic animals (body length approximately 0.20–20 mm) is needed, since they are the food items of many fish species and, concurrently, are important consumers of primary production (Tseitlin, 1986).

The oceanic mesoplankton biomass values change not only in space but also in time (Banse, 1964; Vinogradov, 1968). Measurements taken at different latitudes demonstrate that there are prominent seasonal oscillations in zooplankton biomass in the superficial layers of the oceans, both in the Northern and Southern Hemispheres, and that phases of these oscillations are approximately opposite in the two hemispheres (Bogorov, 1941). Some authors have suggested that, moving equatorwards from polar latitudes within each hemisphere, the maximum biomass values can be observed progressively earlier in the seasonal cycle (Voronina, 1984; Heinrich, 1993). A similar progression

can be seen in data from satellites on the distribution of phytoplankton pigments in the Northern Hemisphere (Banse and English, 1994).

Seasonal fluctuations of zooplankton biomass have only clearly been observed at temperate and polar latitudes. In the tropics, the seasonal biomass pattern is not so well defined, supposedly being obscured by diurnal oscillations and large localized variations. The latitude-dependent changes in amplitude of the seasonal oscillations of the sea-surface temperature (Stepanov, 1974) are consistent with the intuitive concepts of planktonologists on zooplankton biomass variability. However, there are situations where the descriptive expression of a natural law is insufficient and there is a need to express it mathematically. Such a necessity has arisen in a project to map global zooplankton biomass values where there is a clear need to correct raw data. This has led the authors to study seasonal biomass fluctuations at different latitudes and to generalize the results, updating those from the zooplankton biomass mapping of Reid (1962), for the Pacific, and of Bogorov *et al.* (1968), for the World Ocean (the latter modified somewhat by Vinogradov and Shushkina in 1985).

Table 1. Distribution of the biomass from 0 to 100 m; number of observations by months.

Month No.	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
	6	0	0	18	7	33	1	12	18	17	0	7

These authors used raw data mainly from the summer at temperate and high latitude zones but from the whole year in the tropics. Since the summer biomass values in temperate and high latitudes are several times greater than observed in winter (Foxton, 1956; McAllister, 1961; LeBrasseur, 1965; Heinrich, 1993), annual biomass values cannot be compared between regions without considering the seasonal effect.

In this study, periodic regression (Bliss, 1958) was used to describe mathematically the seasonal variations of mesoplankton biomass in the upper layer of the Bering Sea and adjacent regions of the North-west Pacific. These results, in addition to those derived from analysis of published data, were used to produce an equation describing the pattern of seasonal zooplankton biomass oscillations in the global ocean at a wide range of latitudes.

Materials and methods

To test the periodic regression method we used wet weight biomass values of zooplankton samples from five cruises of R/V "Vityaz" (1950–1953) to the Bering Sea and nearby areas of the north-west Pacific. The sampling stations were positioned primarily between 50 and 60°N, and to the west of the 180° longitude. The distribution of the biomass from 0 to 100 m as observations per month is given in Table 1. The position of the plankton stations was given by Tseitlin *et al.* (1994).

The samples were taken with a vertical closing Juday net with mesh size 178 µm and mouth area 0.1 m². The layers sampled were 0–10, 10–25 (or 0–25), 25–50, and 50–100 m. Sometimes the total samples from 0–50 or 0–100 m were taken. The sampling depth of each tow was calculated from wire length and angle.

In the laboratory, the animals were counted in the whole sample, or in a subsample of 1/5 to 1/20, depending on the plankton abundance. The length of chaetognaths, amphipods, euphausiids, and decapods was measured with an eye-piece micrometer.

Zooplankton biomass calculation was made with the information system "PLANKTON" (Kitain and Rudjakov, 1994), based on individual weights tabulated by Lubny-Herzik (1953) and on the regression formulae of weight on length of plankters (Kamshilov, 1951; Krilov, 1968; Chislenko, 1968).

Since plankton abundance estimates may be adjusted to a Gaussian distribution by logarithmic transformation (Barnes, 1952; Roesler and Chelton, 1987), the calculations were made on logarithmically transformed

biomass data (to the base 10); the data were then fitted to the periodic regression (Bliss, 1958):

$$\log(B) = a + b \cos(\pi t/6) + c \sin(\pi t/6). \quad (1)$$

where B = biomass, a = mean log of B (antilogarithm of a is annual geometric mean biomass value), t = time in months (midnight of 31 December roughly corresponds to 0), b and c = cosine and sine amplitudes. Square root of the sum of b^2 and c^2 is oscillation amplitude (half of the oscillation range), whose antilog is the factor by which the maximum or minimum biomass value exceeds the annual mean biomass level; b and c are invariable with biomass unit.

In practice, the multiple regression was fitted where $\log(B)$ was the dependent variable, $\cos(\pi t/6)$ and $\sin(\pi t/6)$ were independent variables, and time t was equal to month minus one plus day divided by 32. For example, for 31 December $t = 12 - 1 + 31/32 = 11.97$ and for 1 January $t = 1 - 1 + 1/32 = 0.03$.

The estimates of planktonic biomass have been derived from a range of different techniques taken with various sampling devices, expressed in values of wet and dry weight, displacement and settling volume, calculated through individual animal weights, estimated using the length of specimens of different species, and integrated from the surface to different depths down to 150 m. The independence of b and c from biomass unit, given by logarithmic transformation of biomass values, made it possible to pool such heterogeneous data sets, considering the relative biomass oscillations about the mean level of unity. To construct the global scale pattern of seasonal oscillations, sine and cosine amplitudes b and c of Equation (1) were considered as functions of geographical latitude using a polynomial fitting:

$$P = k_0 L^0 + k_1 L^1 + k_2 L^2 + \dots \quad (2)$$

where L = latitude (degrees), and P denotes b or c from Equation (1).

Results and discussion

The periodic regression fitted to the Bering Sea and the North-west Pacific biomass data (mg m⁻³) gave parameter estimations of: $a = 2.38$, $b = -0.488$, $c = 0.108$ (Fig. 1, dashed line). The seasonal oscillations were well defined: the summer biomass values (776 mg m⁻³) were approximately 10 times greater than those of winter (74 mg m⁻³), the annual average value being equal to 240 mg m⁻³. The biomass attained its maximum in May–June, and its minimum in December–January.

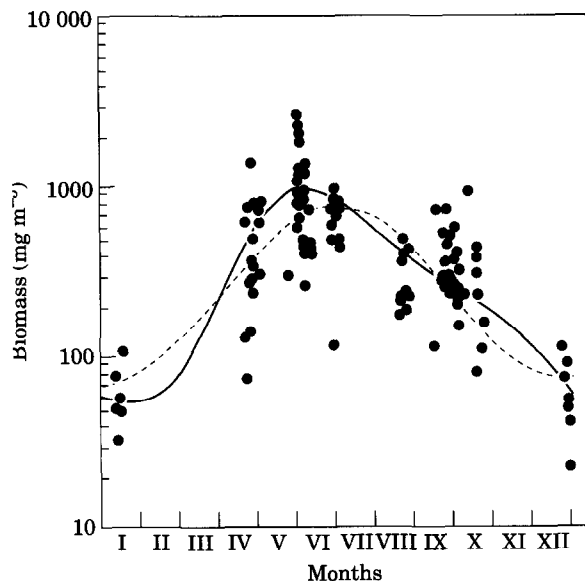


Figure 1. Seasonal variations of zooplankton biomass (wet weight) (0–100 m layer) in the Bering Sea and adjacent regions of the North-west Pacific from 50°N to 60°N (points and dashed line). Solid line represents Weather Station “P” data from Figure 2.

A study of seasonal biomass alterations seems valid only over limited longitudinal zones. Nevertheless, splitting the zone 50–60°N into two, from 50 to 55°N and from 55 to 60°, resulted in a very close agreement of parameters of formula (1) estimates, with statistically non-significant differences (Student’s *t*-test modified by Bliss (1958) was used).

The observational data used here have a serious inadequacy, namely, a very uneven seasonal distribution. Three months were not covered by observations, and the winter observations accounted for only 11% of the total measurement in number. The results were therefore compared with the results derived from analysis of a more complete data set, the zooplankton biomass measurements at the Weather Station “P” (50°N, 145°W), which cover the years 1956–1964. These data were collected regularly, and there were 30–70 measurements for each calendar month. The latitude of WS “P” corresponds to the southern border of the zone under consideration, so that at least a limited comparison of results is possible.

We used 603 biomass measurements (mg m^{-3}) from LeBrasseur (1965). As this data set was much greater than that we had for the area covered by “Vityaz” stations, it was reasonable to augment Equation (1) with the second harmonic terms:

$$\log(B) = a + b_1 \cos(\pi t/6) + c_1 \sin(\pi t/6) + b_2 \cos(\pi t/3) + c_2 \sin(\pi t/3). \quad (3)$$

The observation points and the regression curve are given in Figure 2. The estimates of the Equation (3)

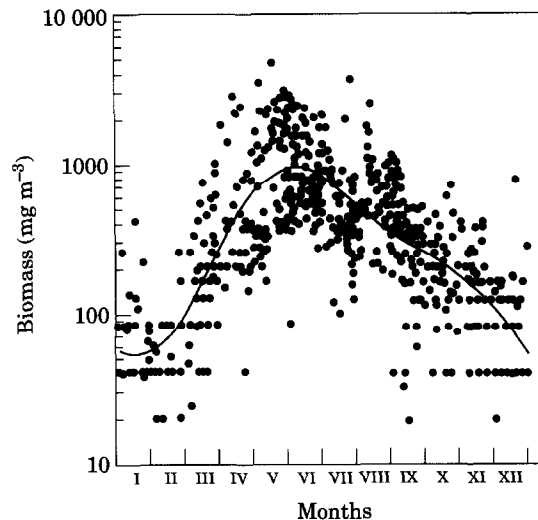


Figure 2. Seasonal variations of zooplankton biomass (wet weight) in the 0–150 m layer at Weather Station “P”.

parameters were: $a = 2.39$, $b_1 = -0.542$, $c_1 = 0.038$, $b_2 = -0.038$, $c_2 = -0.162$.

There was close agreement between the annual mean value and the first harmonic terms and the corresponding values derived for the Bering Sea and adjacent regions of the North-west Pacific. The coincidence seems surprising since the biomass values at WS “P” were taken in the larger layer 0–150 m, samples were collected with larger mesh size (330 μm), and the method of biomass calculation was different.

A good agreement between parameter estimates for the first harmonic terms suggests a closer agreement of seasonal changes in both regions concerned. In Figure 1 the solid line represents the curve from Figure 2, without adjustment. The figure shows a better fit of Equation (3) with parameters estimated on the WS “P” data set to the “Vityaz” data array: the rates of the biomass increase and decrease are explicitly different and the chances are better than even that the biomass attains its maximum in May and not in June.

The last example is particularly remarkable as it shows how informative extensive data sets can be. Unfortunately, such a large data set has never been obtained since. In the published literature, most seasonal observations only cover one or two years, are irregular, with large gaps, and are often taken less than once per month. For this reason, the global scale patterns of seasonal biomass oscillations were restricted to the first harmonic only and all data sets available were fitted to Equation (1).

Calculated results (Table 2) show that the oscillations around the mean are lowest in the Equatorial zone. At higher latitudes the rates of increase differ between the two hemispheres, being lower in the Southern Hemisphere. In order to visualize these trends, the latitudinal

Table 2. Latitude (L, South negative), coefficients (b) and (c), amplitude ($A = \sqrt{b^2+c^2}$), locality and the source of data.

L	b	c	A	Locality and data source
72	-0.397	-0.129	0.417	Skarsvåg, Norway (Wiborg, 1978)
71	-0.541	-0.139	0.559	Ingøy, Norway (Wiborg, 1978)
69	-0.298	-0.236	0.380	Barents Sea, off Murmansk (Zelikman, 1977)
68	-0.632	-0.044	0.634	Eggum, Norway (Wiborg, 1978)
68	-0.141	-0.158	0.212	Skrova, Norway (Wiborg, 1978)
66	-0.404	0.018	0.404	Weather station "M", 2°E (Wiborg, 1978)
63	-0.395	0.164	0.428	Ona, Norway (Wiborg, 1978)
61	-0.410	0.091	0.420	Sognes, Norway (Wiborg, 1978)
59	-0.383	0.096	0.395	Utsira, Norway (Wiborg, 1978)
55	-0.488	0.108	0.500	Bering Sea ¹
50	-0.542	0.038	0.543	Weather station "P", 145°W (LeBrasseur, 1965)
39	-0.322	-0.027	0.323	Weather station "X", 153°E (Marumo, 1955a)
36	-0.220	0.069	0.231	Off California (Bernal, 1979)
35	-0.108	0.158	0.191	Station "E", 48°W (Fish, 1954)
32	-0.078	0.160	0.178	Station "S", 65°W (Deevey, 1971; Deevey and Brooks, 1971)
32	-0.167	0.190	0.253	Off California (Bernal, 1979)
30	-0.188	0.013	0.188	Off California (Bernal, 1979)
30	-0.141	0.091	0.168	Off California (Bernal, 1979)
29	0.047	0.238	0.243	Off California (Bernal, 1979)
29	-0.062	0.215	0.224	Weather station "T", 135°E (Marumo, 1955b)
25	-0.175	-0.054	0.183	Off California (Bernal, 1979)
18	0.159	-0.107	0.192	Jamaica (Moore and Sunder, 1979)
18	0.177	-0.059	0.187	Jamaica (Moore and Sunder, 1979)
14	-0.027	0.208	0.210	Off West Africa (Postel, 1990)
13	0.018	0.020	0.027	Barbados (Moore and Sunder, 1977)
10	-0.041	0.017	0.044	Eastern Pacific (Blackburn <i>et al.</i> , 1970)
9	-0.112	0.139	0.179	Off Panama (Forsberg, 1963)
-2	-0.061	-0.117	0.132	Atlantic 1°N-5°S, 10°W (Gruzov, 1971)
-5	0.138	-0.114	0.179	Off Peru (Carrasco and Lozano, 1989)
-10	0.027	0.016	0.031	Off Peru (Carrasco and Lozano, 1989)
-16	0.218	-0.163	0.272	Off Peru (Carrasco and Lozano, 1989)
-21	0.074	-0.059	0.095	Eastern Indian Ocean (Tranter and Kerr, 1969)
-23	0.079	-0.030	0.085	Off Namibian Coast 17°-29°S ²
-34	0.109	0.081	0.136	Benguela Upwelling (Andrews and Hutchings, 1980)
-34	0.177	0.063	0.188	Vicinity of Sydney (Tranter, 1962)
-34	0.132	-0.063	0.146	Vicinity of Sydney (Tranter, 1962)
-36	0.098	-0.104	0.143	Off New Zealand (Jillett, 1971)
-40	0.250	0.090	0.266	Subantarctic Zone (Foxton, 1956)
-42	0.186	-0.074	0.200	Off New Zealand (Bradford, 1972)
-60	0.136	0.198	0.240	Antarctic Zone (Foxton, 1956)
-69	-0.027	0.258	0.259	39°E (Fukuchi <i>et al.</i> , 1985; Watanabe <i>et al.</i> , 1986) ³
-69	0.042	0.072	0.083	39°E (Fukuchi <i>et al.</i> , 1985; Watanabe <i>et al.</i> , 1986) ⁴

¹Data presented in this article.²Data kindly placed at our disposal by A. G. Timonin (P. P. Shirshov Institute of Oceanology, Russian Academy of Sciences).³Data for 0-150 m.⁴Data for 0-50 m.

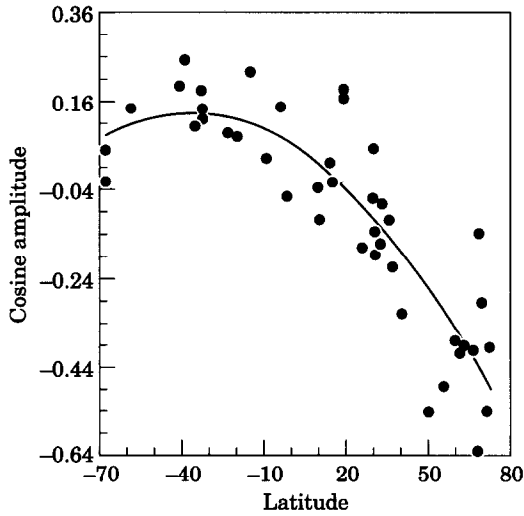


Figure 3. Cosine amplitude (b) versus latitude.

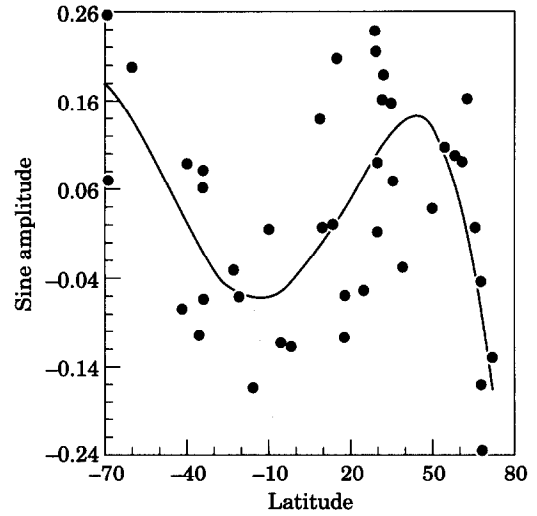


Figure 4. Sine amplitude (c) versus latitude.

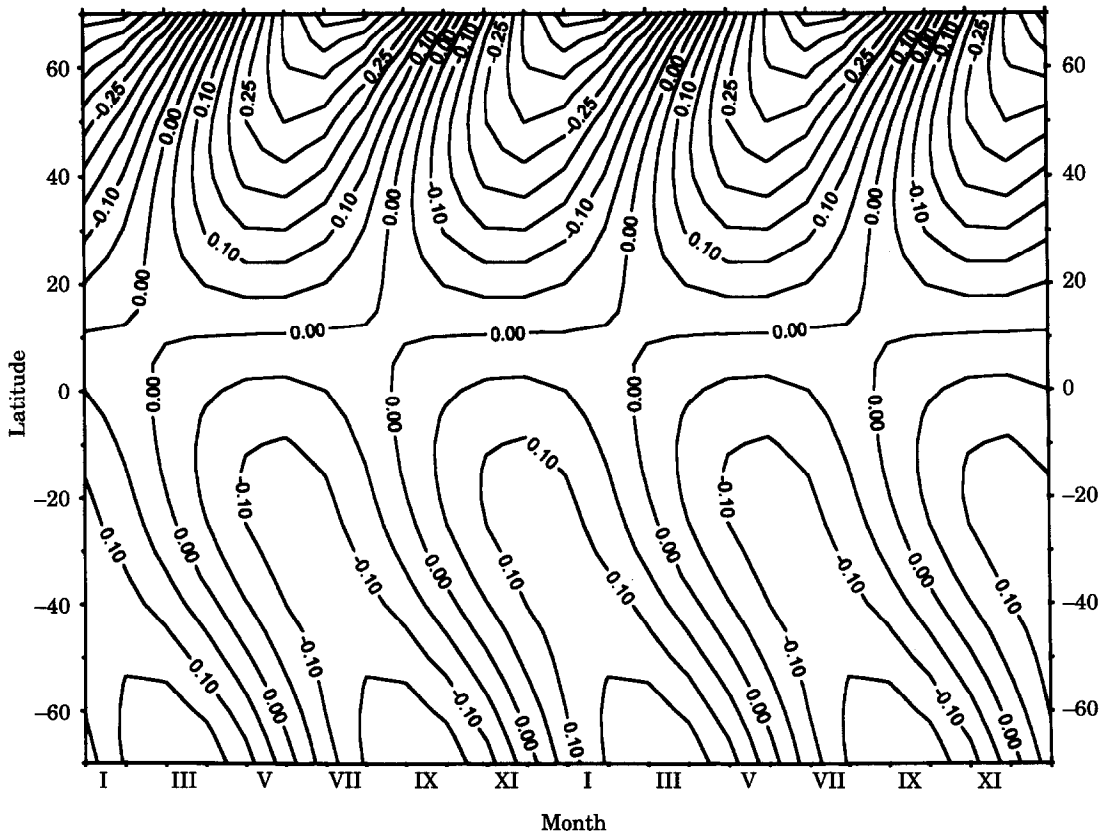


Figure 5. The logarithmic biomass oscillations at different latitudes (South negative) relative to the mean level of zero. As an example, at 70°S at the end of March the biomass is 1.5 times that of the annual mean level (antilogarithm of 0.17) and by the beginning of June it drops to the annual mean level (antilogarithm of zero equals unity). Note the phase shift from the Equator to the Poles, which reaches three months in the Southern Hemisphere.

changes in the b and c coefficients were derived using a polynomial approximation, in which all terms are significant at $p < 0.05$:

$$b = 0.0504 - 3.934 \cdot 10^{-3} L - 5.1 \cdot 10^{-5} L^2 \quad (4)$$

$$c = -4.216 \cdot 10^{-2} + 3.198 \cdot 10^{-3} L + 1.03 \cdot 10^{-4} L^2 - 1.085 \cdot 10^{-6} L^3 - 1.786 \cdot 10^{-8} L^4. \quad (5)$$

The quality of the fit can be judged from Figures 3 and 4, where the dissimilarity of data used and local differences in the longitude dependence of biomass values (such as the difference between nearshore and offshore regions) show up in full measure. The topography of the surface, specified by Equation (1) with $a = 0$ and b and c substituted by Equations (4) and (5), is given in Figure 5. Note that the phase shift from the Poles to the Equator reaches about two months in the Northern Hemisphere and at least three months in the Southern Hemisphere. The surface is quasi-symmetrical to about 10°N and not to about the Equator, which is in good agreement with the latitude of the minimal seasonal oscillations in water temperature, determined by Stepanov (1974) at 5°N . As with phytoplankton pigment seasonality (Banse and English, 1994), the amplitude is much higher in the North relative to the southern hemisphere at similar latitudes. Martin V. Angel (pers. comm.) suggests that "this may be a result of the differences in the areas of continental land masses between the two Hemispheres resulting in greater ranges in sea-surface temperatures occurring in the North, which must influence the patterns of stratification".

It is anticipated that a secondary biomass maximum may sometimes occur, particularly at temperate latitudes (see Figs 1, 2) supposedly in response to the autumnal productivity maximum (Bogorov, 1941; Tseitlin *et al.*, 1994). A better description of the seasonal oscillations may therefore be produced by using second or even higher harmonics. The real picture is much more complicated than this rather simple representation. For example, there are substantial differences in amplitude and the phase angle of the fluctuations observed in the different regions of the California Current (Roesler and Chelton, 1987). Evidence indicates that the seasonal cycles run differently in nearshore and offshore areas (Heinrich, 1993), specifically in upwelling areas (Andrews and Hutchings, 1980). Table 2 and Figures 3 and 4 show how strongly the biomass oscillations vary even in neighbouring Norwegian fjords. However, there are insufficient data sets available at present on which to base more sophisticated formalizations. This deficit is particularly pronounced for the Central Arctic regions, for which only fragmentary information has been available (Kosobokova, 1982) until recently.

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