Climate and Chlorophyll a: Long-Term Trends in the Central North Pacific Ocean

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Since 1968 a significant increase in total chlorophyll a in the water column during the summer in the central North Pacific Ocean has been observed. A concomitant increase in winter winds and a decrease in sea surface temperature suggest that long-period fluctuations in atmospheric characteristics have changed the carrying capacity of the central Pacific epipelagic ecosystem.

IN THE PAST DECADE THERE HAS BEEN an increasing scientific emphasis on large-scale, "global" processes, recently spawning several large-scale marine-oriented programs. Understanding long-term temporal trends, on the scale of tens of years, is critical to the design and interpretation of these studies (*1*); yet, aside from selected physical measurements at the ocean-air interface, little is known of variations in the major ocean basins on these scales. Recent recognition of the importance of ocean-atmosphere interactions has left us in the ironic position of knowing more about the association between near-surface conditions in the North Pacific and crop production in central North America than between near-surface conditions and production in the subsurface ecosystem.

The central North Pacific (CNP) is one of the largest epipelagic environments (*2*), extending roughly 15 million square kilometers. For more than 20 years, we have studied the planktonic ecosystem of the CNP. Preliminary surveys were conducted in the region in 1964 and 1966, and intensive sampling began in 1968. We have accumulated one of the few long-term physical, chemical, and biological data sets from an open ocean environment. Of the biological parameters, the most complete set is that of chlorophyll a, an index of phytoplankton biomass (*3*). We have documented a significant increase in the amount of chlorophyll a in the water column.

The chlorophyll data came from the region between 26.5° to 31°N and 150.5° to 158°W, the center of which lies about 650 km north of Hawaii. To avoid possible seasonal effects, we have eliminated four midwinter (January through March) data sets from our analyses (*4*). The remaining data were collected on 17 cruises between May and October, representing 12 of the 19 years. During these months the euphotic zone is thermally stratified and the phytoplankton exhibits the two-layered structure characteristic of summer months (*5*). Chlorophyll a was extracted from discrete water samples collected at 5- to 20-m intervals above 200 m (*6*). Data have been integrated vertically to estimate total chlorophyll a per square meter. The data are often nonnormal (*7*), and nonparametric analyses have been used.

Since 1968, total chlorophyll a has nearly doubled (Fig. 1). Because of our procedural consistency (*6*), we are convinced that the interannual changes in our chlorophyll a data are not due to procedural bias. Our data are insufficient to determine whether the chlorophyll a increase has been continuous over time (Kendall nonparametric correlation of chlorophyll a and time: $\tau = 0.70$, $P < 0.01$) or a more rapid change from a rather stable mean value between 1968 and 1973 (95% confidence interval: 11.22 to 13.82 mg/m^2) to a higher mean value since 1980 (19.83 to 24.25 mg/m^2). Regardless, chlorophyll a values since 1980 are significantly greater than those before 1974 (rank sum test, $P < 0.001$). Although, over smaller scales of space and time, a factor of 2 is not a remarkable variation in most marine ecosystems, the persistence of high chlorophyll a concentrations in the CNP since 1980, contrasted with the relatively low heterogeneity within single years, makes this increase highly significant. The change in total chlorophyll a is primarily due to increases in concentration and thickness of the subsurface maximum layer, generally found between 95 and 120 m (Fig. 2). During the interval between 1968–1973 and 1980–1985 the integrated chlorophyll a through the 5-m stratum containing maximum concentrations increased from 3.32 to 6.50 mg/m^2 ($P < 0.05$). In contrast, chlorophyll a in the near-surface layer (0 to 5 m) increased only from 1.52 to 1.79 mg/m^2 ($P > 0.20$).

Neither our other biological data nor our nutrient data show a similar change over the sampling period (*8*), but these data sets are less complete than the chlorophyll set, making changes more difficult to detect. However, an extensive data set of other environmental parameters routinely observed by ships is available. These data provide a proxy indication of changes in the upper ocean. There is a marked annual cycle in atmospheric activity over the North Pacific, with the mid-latitude westerlies and storm tracks reaching their most southerly extent in winter. We have focused on winter (December through February) as the season when atmospheric forcing most strongly affects a communication between the near-surface waters and those below. The sea level pressure (SLP) field (*9*) and its spatial gradients are good indicators of storminess and wind over the ocean, and the seasonal mean of SLP indicates the season's overall conditions (*10*). North of 25°N, average values of winter SLP during 1980 to 1985 (high chlorophyll years) were strikingly lower than during 1968 to 1973 (low chlorophyll years). This decrease was greatest to the north of the study area, resulting in an

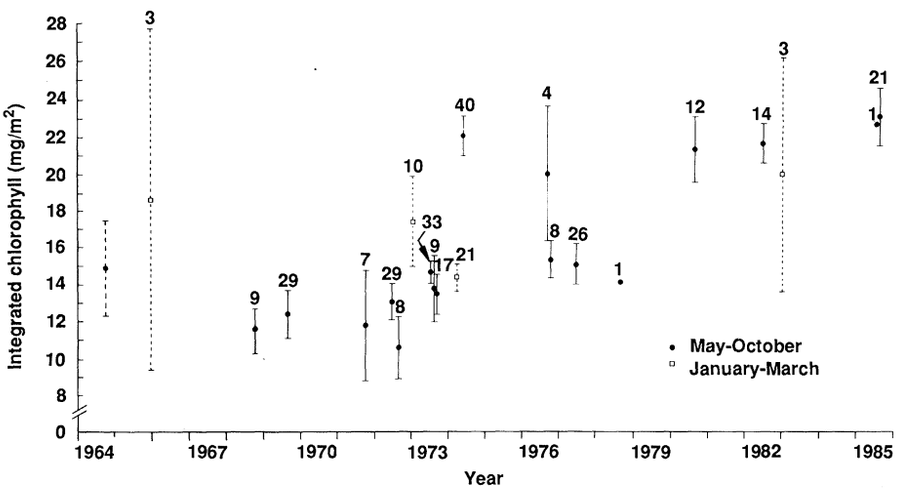

Fig. 1. Observations of integrated chlorophyll a in the CNP. Bars indicate the 95% confidence intervals of the mean $\bar{x} \pm t\sqrt{s^2/n}$; the number of observations is shown above each bar. Winter values (open squares) and values before 1968 are excluded from our analyses. Definitions: t, 97.5 percentile of t statistic with $n - 1$ df; s^2, the variance of the observations.

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intensification of the north-south gradients of SLP (Fig. 3), which can be interpreted as an increase in the strength of the westerly (west-to-east) winds. The difference between SLP fields between the two time periods is highly significant. If the winds are approximately geostrophic, the average westerly winds over the sampling domain were at least 3 m/sec stronger during the winters of the 1980–1985 period. This local difference is a symptom of a change over the entire basin, from which we can infer more vigorous storminess over much of the CNP.

Sea surface temperature (SST) differences between the same periods (Fig. 3) show a large area of cooler SST near the study site and to the north and west of it during the later period. Studies of SST changes on the scale of decades have shown them to be related to atmospheric conditions (*11*). The maximum differences in SST lie along the zone of maximum enhanced westerly winds and probably result from more active winter storminess, which has been documented for vigorous winters within the 1980–1985 period (*12*). An 8-year trans-Pacific bathythermograph survey between 30° and 50°N, the region of strongest SST anomalies, shows a negative temperature anomaly at 300 m since 1979 (*13*). Our temperature data show a cooling tendency ($P \sim 0.20$) throughout the upper 100 m, but there does not appear to be a concomitant change in salinity. The mechanisms of increased latent and sensible heat extraction from the ocean, north-to-south Ekman drift, and wind mixing may have played a role in cooling the upper ocean (*14*). Time series of derived wind and SST (Fig. 4) indicate that these properties have varied significantly from year to year and forcing mechanisms have probably operated episodically.

We postulate that these environmental fluctuations have resulted in significant long-term changes in the carrying capacity of the CNP epipelagic ecosystem. In this oligotrophic environment, the majority of nutrients in the upper 150 m are bound in organic material. Thus, an increase in the standing stock of phytoplankton must result from a reapportionment of nutrients among organic components, from a decrease in nutrient flux out of the euphotic zone, or from an increase in nutrient input. The latter would occur if increased surface cooling combined with increased winter wind stress to increase vertical mixing and enhance upward transport of new nutrients into the euphotic zone. Even if climatic forcing factors operate episodically, the biological consequences appear to be more persistent.

During the summer, the concentration and vertical distribution of chlorophyll a observed at our study site extend throughout the CNP (*15*). Also, SLP and SST characteristics occur over very large spatial scales (*10*). The increase in chlorophyll a observed at our study site may represent an increase in total organic carbon over an enormous area. A clear description of these large-scale fluctuations will only emerge from more extensive, long-term environmental and biological monitoring of surface and subsurface parameters.

Our observations have important implications for a variety of other studies. The increase in primary productivity reported by the Plankton Rate Processes in Oligiotrophic Oceans (PRPOOS) study at our study site (*16*) appears to reflect, at least partially,

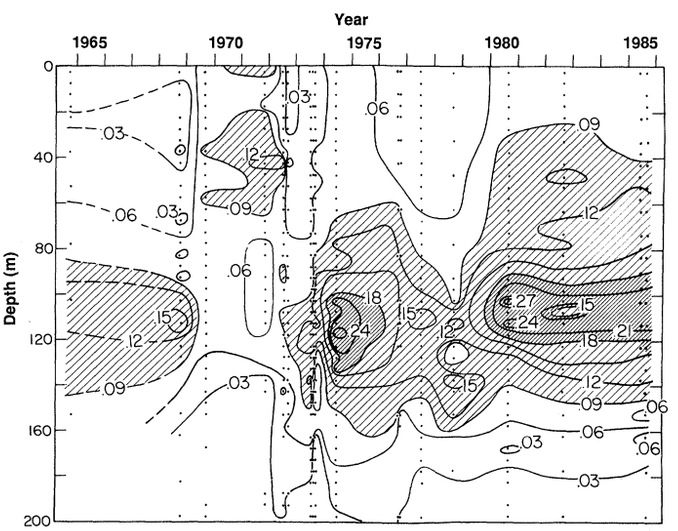

Fig. 2. Temporal change of the vertical distribution of chlorophyll a (in milligrams per cubic meter) in the CNP. Dots indicate that one or more samples were collected from that depth.

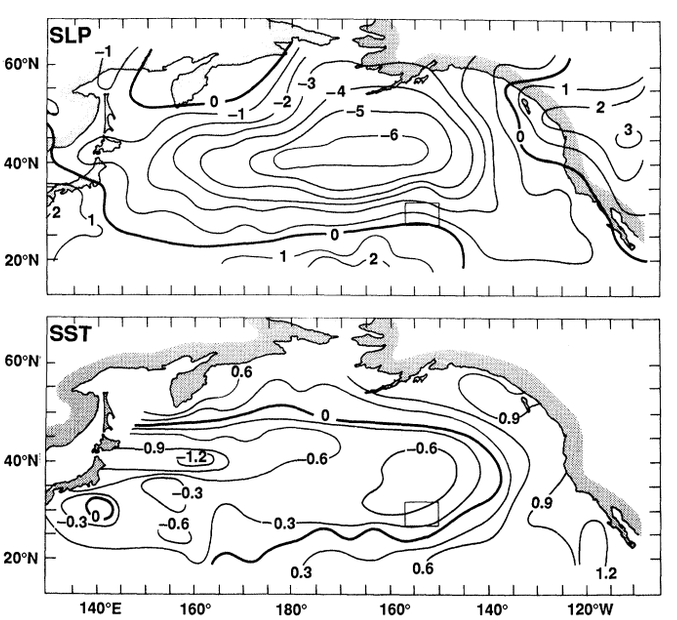

Fig. 3. Changes in SLP (**top**) and SST (**bottom**) over the North Pacific. Differences are winter values averaged over 1980–1985 minus winter values averaged over 1968–1973. The rectangles indicate the study region. For SLP, contour lines are labeled in millibars (0.1 kPa = 1 mb); SST labels are in degrees Celsius.

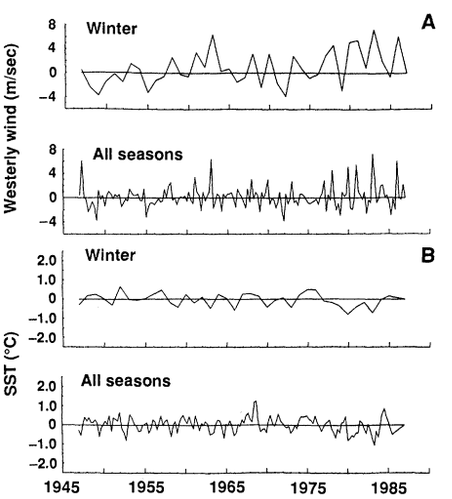

Fig. 4. Time series of anomalous west-to-east component of surface winds (**A**) and SST anomaly (**B**), centered on the study region [for (A), 20° to 35°N, 140° to 170°W; for (B), 25° to 30°N, 150° to 160°W]. Winds were calculated from the geostrophic formula applied to seasonal SLP distributions. Anomalies were calculated relative to the base period from 1947 to 1972.

true interannual differences rather than previous methodological bias. We need to re-evaluate both the assumption of steady state that underlies models of carbon or nutrient flux through the euphotic zone and our studies of community structure and dynamics.

REFERENCES AND NOTES

1. E. T. Sundquist, *Geophys. Monogr. Am. Geophys. Union* **32** (1985).
2. J. L. Reid, E. R. Brinton, A. Fleminger, E. L. Venrick, J. A. McGowan, in *Advances in Oceanography*, H. Charnock and G. Deacon, Eds. (Plenum, New York, 1978), pp. 65–130.
3. J. D. H. Strickland, in *Chemical Oceanography*, J. P. Riley and G. Skirrow, Eds. (Academic Press, London, 1965), vol. 1, pp. 478–610. The ratio of phytoplankton carbon to chlorophyl a is variable. The value is primarily determined by the light regime, and the maximum variability takes place in the vertical direction [J. H. Steele, *J. Mar. Res.* **22**, 211 (1964)]. Since we have no evidence to suggest a change in either incoming radiation or the transmission coefficient in the upper 200 m, we conclude that the chlorophyll a increase mirrors an increase in phytoplankton carbon and nitrogen.
4. We are uncertain about the existence of seasonality in chlorophyll a concentration. We can detect no consistent relation between the 12 summers and 4 winters for which we have chlorophyll a data [T. L. Hayward, E. L. Venrick, J. A. McGowan, *J. Mar. Res.* **41**, 711 (1983)]. However, chlorophyll a shows a negative correlation with the number of days since 1 May ($P < 0.10$), indicating a compensating increase during the winter months. The high value in 1974 is our only datum from May, but seasonality does not completely explain the value. Removing seasonality does not reduce the long-term change or alter our conclusions.
5. R. W. Eppley, E. H. Renger, M. M. Mullin, E. L. Venrick, *Limnol. Oceanogr.* **18**, 534 (1973); E. L. Venrick, *Ecology* **52**, 129 (1982).
6. In 1964, chlorophyll a was measured with the spectrophotometer. On all other expeditions, it was determined fluorometrically. We have included the 1964 data in our figures but do not include them in the statistical analyses because of possible bias introduced by the procedural change. With a single exception, our analytical procedure has remained constant since 1968. In 1980 we switched from grinding the filter, followed by a short-term extraction, to extraction for a period of 1 to 3 days without grinding. The latter procedure recovers an average of 8% less chlorophyll a [E. L. Venrick and T. L. Hayward, *Calif. Coop. Oceanic Fish. Invest. Rep.* **25**, 74 (1984)]. We have not corrected our recent data for this bias; adjustment would augment the observed chlorophyll a increase. The second set of data from 1985 was provided by the PRPOOS study. These samples were collected with H/A Millipore filters, and the data have been adjusted to our values (our samples were collected with GF/C filters), by subtracting 0.017 mg/m^3 from each sample for a total correction of 3.4 mg/m^2 for each integrated value (E. L. Venrick, S. L. Cummings, C. A. Kemper, *Deep Sea Res.*, in press).
7. D'Agostino's test; J. H. Zar, *Biostatistical Analysis* (Prentice-Hall, Englewood Cliffs, NJ, ed. 2, 1984), pp. 95–96.
8. T. L. Hayward, *Deep Sea Res.*, in press.
9. J. Namias, *Calif. Coop. Oceanic Fish. Invest. Atlas* **22**, 1 (1975).
10. ———, *Mon. Weather Rev.* **104**, 1107 (1976); R. E. Davis, *J. Phys. Oceanogr.* **6**, 249 (1976); D. R. Cayan and J. O. Roads, *Mon. Weather. Rev.* **112**, 1276 (1984).
11. A. V. Douglas, D. R. Cayan, J. Namias, *Mon. Weather Rev.* **110**, 1851 (1982).
12. J. Namias, *ibid.* **106**, 270 (1978).
13. L. D. Talley and W. B. White, *J. Phys. Oceanogr.*, in press.
14. R. L. Haney, *ibid.* **15**, 787, (1985).
15. R. Marumo, Ed., *Preliminary Report of the Hakuho Maru Cruise KH-69-4* (Ocean Research Institute, University of Tokyo, Tokyo, 1970); E. L. Venrick, J. A. McGowan, A. W. Mantyla, *Fish. Bull.* **71**, 41 (1971); J. A. McGowan and P. M. Williams, *J. Exp. Mar. Biol. Ecol.* **12**, 187 (1973); T. L. Hayward and J. A. McGowan, *J. Plankton Res.* **7**, 147 (1985); E. Shulenberger, *Deep Sea Res.* **25**, 1193 (1978); E. L. Venrick, *ibid.* **26A**, 1153 (1979); unpublished data (collected April–June 1985 on Scripps Institution of Oceanography expedition TPS-24).
16. R. A. Kerr, *Science* **232**, 1345 (1986).

17. The CNP project was supported by the Marine Life Research Group of Scripps Institution of Oceanography and partially by the Office of Naval Research and the National Science Foundation. The climatological research was supported by the Climate Dynamics Program of the Atmospheric Science Division, National Science Foundation grant ATM 84-07891, and by the State of California Department of Boating and Waterways. Data from PRPOOS were provided by R. Eppley. We thank J. Namias for his long-standing support of one of the authors (D.R.C.), for providing a climate data archive, and for advice on this report. Because of the long duration of this project, we must condense our acknowledgements into a single expression of thanks to the many other individuals who helped us at various stages.

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Trophic Stimulation of Cultured Neurons from Neonatal Rat Brain by Epidermal Growth Factor

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Epidermal growth factor (EGF) is a potent polypeptide mitogen originally isolated from the adult male mouse submaxillary gland. It also acts as a gastrointestinal hormone. EGF-immunoreactive material has recently been identified within neuronal fibers and terminals in rodent brain. In the present study, EGF was found to enhance survival and process outgrowth of primary cultures of subneocortical telencephalic neurons of neonatal rat brain in a dose-dependent manner. This effect was observed with EGF concentrations as low as 100 picograms per milliliter (0.016 nanomolar) and was dependent on the continuous presence of EGF in the medium. Similar effects were observed with basic fibroblast growth factor, but several other growth-promoting substances, including other mitogens for glial elements, were without effect. Thus EGF, in addition to its mitogenic and hormonal activities, may act as a neurite elongation and maintenance factor for select neurons of the rodent central nervous system.

POLYPEPTIDE GROWTH FACTORS ARE hormonelike agents that contribute substantially to the regulation of both hypertrophic and hyperplastic responses of eukaryotic cells, particularly in vertebrates (*1*). Neuronotrophic factors, a subset that acts on neurons of the peripheral and central nervous systems, primarily enhance neurite outgrowth and maintain cell viability (*2*). Nerve growth factor (NGF), a neuronotrophic agent with well-defined activity in the peripheral nervous system (*3*), is synthesized in the target region and acts via specific membrane-bound receptors located on the neuron (*4*). More recently, NGF has been identified within the central nervous system (CNS) and has been proposed to act as a trophic factor for a particular subset of neurons there (*5*). Other agents that act as trophic factors for the diverse types of CNS neurons have been identified, but have not been extensively characterized (*2*).

Epidermal growth factor (EGF) is a polypeptide mitogen for a number of cell types (*6*). It inhibits gastric acid secretion, a finding that has lead to the alternative designation, urogastrone (*7*). Recently, EGF immunoreactivity (*8*) and precursor messenger RNA (mRNA) (*9*) have been identified within the mammalian brain; the presence of EGF within the CNS is, however, the subject of controversy (*10*). EGF binding sites occur in brain tissue (*11*), and EGF stimulates the proliferation and differentiation of glial cells (*12*). In the present study we show that EGF also promotes the survival, and stimulates process outgrowth, of neonatal rat CNS neurons in vitro.

Dissociated cell cultures were derived from the subneocortical telencephalon of neonatal rats (*13*); this region contains areas that exhibit EGF immunoreactivity in the adult (*8*). The addition of mouse EGF (10 ng/ml) to these primary cultures resulted in a 15-fold increase in the number of surviving cells with a neuronal morphology (*14*) (Fig. 1A and Table 1). EGF also increased the number of processes and the degree of

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