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Environmental heterogeneity and plankton community structure in the central North Pacific

by T. L. Hayward[1], E. L. Venrick[1] and J. A. McGowan[1]

ABSTRACT
Spatial and temporal patterns of heterogeneity in nutrients (PO_4, NO_3), integrated water column chlorophyll, integrated water column primary production, and macrozooplankton biomass in the central North Pacific are described on spatial scales ranging from less than one to several thousand kilometers and on temporal scales from one day to 12 years. Fluctuations in these properties represent an index of the biological response of the ecosystem to physical forcing on various scales. These patterns are an important aspect of ecosystem structure because environmental perturbations may affect the outcome of biological interactions between populations. Heterogeneity in each property was low on all scales. Diel changes were evident only in macrozooplankton biomass, and no seasonal cycles were detected. This is consistent with a low overall level of physical forcing, little advection from outside the system into it, and lack of seasonal changes in nutrient flux to the euphotic zone. The central North Pacific shows relatively low heterogeneity, especially on mesoscales (tens to hundreds of kilometers), when compared to other pelagic ecosystems, suggesting that environmental disturbances do not have a major effect upon macrozooplankton and nekton populations.

1. Introduction

Environmental heterogeneity, in the form of spatial patchiness, temporal cycles, disturbances, etc., is an important aspect of ecosystem structure. The effects of such heterogeneity depend upon both its magnitude and its spatial and temporal scales (Haury *et al.*, 1978). To some extent, the relative importance of physical forcing on a particular scale can be inferred directly from the magnitude of the biological response on that same scale. Thus if seasonality is important, physical changes on seasonal scales and the related biological responses should be greater in magnitude than spatial patchiness or temporal fluctuations on other scales.

Environmental heterogeneity, however, may affect ecosystem structure in a more subtle manner because its effects also depend upon the interaction between physical scales of heterogeneity and biologically significant scales, such as generation times or ambits. The effects of a particular scale of heterogeneity may thus vary for different types of organisms with different characteristic biological scales. Environmental disturbances, for example, have been proposed as a potential mechanism for mainte-

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nance of diversity under conditions where competitive exclusion should otherwise lead to lower diversity (Hutchinson, 1961; Richerson *et al.*, 1970; Connell, 1978). The scales of disturbance necessary to permit coexistence in this manner would clearly differ for phytoplankton, with generation times of days and ambits of tens of meters or less, and macrozooplankton, with generation times of weeks to months and ambits over this time of at least tens of kilometers. The outcome of other interactions, such as zooplankton feeding or predation (Mullin and Brooks, 1976; Dagg, 1977), may also depend upon the interrelation between scales of environmental structure and the ecological scale upon which the process takes place.

The ambit of a planktonic organism depends both upon its movements in the water and motion of the water. The effects of patchiness in the ocean, thus, also depend greatly upon mixing and stirring, and the size, intensity, and persistence (or degree of diffusion) of patches (Levin, 1974; Casewell, 1978). Hence a description of the relative heterogeneity of different spatial and temporal scales, and a comparison of such patterns with biologically important scales, may lead to a better understanding of the effect of environmental heterogeneity upon ecosystem structure.

In addition, sampling programs are based upon assumptions about the nature of patchiness. Rate processes in the oligotrophic open ocean, for example, may be estimated assuming that the ecosystem is close to steady state, and measurements from different cruises or stations may be compared assuming that spatial and temporal changes are small. Patchiness, spatial gradients, and temporal cycles will increase the uncertainty in such attempts. A description of heterogeneity on different scales may help in the design of more effective sampling schemes.

This type of description has been difficult for planktonic ecosystems, especially in the open ocean, because there are few data sets with which to evaluate the role of large-scale (hundreds to thousands of kilometers or several years) and mesoscale (tens to hundreds of kilometers or weeks to months) processes in structuring oceanic ecosystems, and compare their effects to those of small-scale (less than one to tens of kilometers) processes. Large-scale and mesoscale patterns, however, seem likely to be important due to the large ambits and long generation times of macrozooplankton and nekton. In this paper we describe data collected over a 13-year period (1968–1980) on 17 cruises to the eastern part of the North Pacific central gyre. This report summarizes this large data set in a consistent format in an attempt to compare large-scale environmental heterogeneity with smaller scales.

The gyre habitat was originally chosen for study based upon physical and biogeographic evidence that the plankton community in this area is relatively isolated from the rest of the North Pacific and because the upper layers appear to be relatively homogeneous with respect to physical and biological properties (McGowan, 1974, 1977). It has since become apparent that the western part of the gyre (west of 180° longitude) is more heterogenous than the eastern part (Kenyon, 1978; Shulenberger, 1978; Venrick, 1979). We confine our comparisons in this report to the eastern part where more data are available.

Table 1. List of cruises and types of data collected. N—nutrients, C—chlorophyll, P—primary production, Z—macrozooplankton biomass.

Cruise	Date	N	C	P	Z
Summers					
CLIMAX I	Sept. 1968	X	X	X	
CLIMAX II	Aug. 1969	X	X	X	X
ARIES IX	Oct. 1971	X	X	X	X
CATO I	June 1972	X	X	X	X
C' BOG	Aug. 1972	X	X	X	
TASADAY I	June 1973	X	X		X
TASADAY II	July 1973	X	X		
CLIMAX VII	Aug. 1973	X	X	X	
DRAMAMINE II	May 1974	X	X	X	
AG76-1	Aug. 1976		X		X
AG76-3	Sept. 1976		X		X
INDOPAC XV	June 1977	X	X	X	X
MARIANA II	Aug. 1978				X
FIONA	Aug. 1980	X	X	X	X
Winters					
FCRG 71-2	Nov. 1971	X	X	X	
SOUTHTOW XIII	Feb. 1973	X	X	X	X
TASADAY XI	Mar. 1974	X	X	X	X

Several cruises were made to the same general locale near 28N, 155W (the "CLIMAX" area) and there were additional E-W and N-S transects. Although these cruises were not intended as a time series, nutrients (NO_3, PO_4), chlorophyll, primary production, and macrozooplankton biomass, among other properties, were measured with comparable techniques on many of them. We use fluctuations in these four properties as general indices of environmental heterogeneity and associated biological responses in an attempt to answer the following questions: (1) What is the magnitude of heterogeneity on different spatial and temporal scales, how do different scales compare with each other, do the different properties have similar patterns, and what causes these patterns? (2) How do such patterns affect the structure of the ecosystem, and what role do disturbances play? (3) How does the central North Pacific compare to other oceanic ecosystems?

2. Methods

The cruises considered in this study are listed in Table 1. Heterogeneity on different scales was estimated as follows.

Small-scale spatial and temporal variability was estimated from replicate samples collected at the same station during a 24- to 48-hour period. This represents spatial and temporal heterogeneity ranging from measurements which immediately follow each other to periods of 48 hours and spatial distances of up to a few tens of km. Chlorophyll

casts were taken at intervals ranging from a few minutes to several hours. For productivity, there was only one cast per day, except on one cruise, FIONA, where two replicate casts were collected sequentially and incubated simultaneously each day. Samples for macrozooplankton were generally collected twice each day, once near noon and once near midnight. On several cruises, sets of three replicate tows were taken sequentially near noon and midnight.

Mesoscale spatial and temporal variability was estimated by the difference between stations on a single cruise. Stations were separated by spatial intervals of tens to hundreds of km and by periods of a few days.

Large-scale temporal fluctuations at the CLIMAX area were estimated from the differences between cruises which occurred over a period of months to 12 years. Large-scale spatial variations within the gyre were examined along a N-S transect between 24N and 44N along 155W in 1980 (FIONA).

Because of the unbalanced nature of the data set, we do not emphasize statistical significance between scales of heterogeneity. We are concerned instead with qualitative differences in the magnitude of heterogeneity on different scales and comparisons with the patterns observed in other pelagic environments. We have tried to use simple indices of heterogeneity such as ranges, coefficient of variation (C.V.), or the amplitude of a cycle in order to facilitate comparison with data sets from other areas collected with different sampling schemes. Spatial and temporal heterogeneity are confounded to varying degrees on all scales in this analysis.

Nutrients were measured with an autoanalyzer by methods summarized in Strickland and Parsons (1972). The nutrient data are presented as depth distributions and vertical sections.

Chlorophyll was measured with a fluorometer after filtering the sample onto GF/C filters and extracting in 90% acetone according to the method of Yentsch and Menzel (1963) as modified by Holm-Hansen *et al.* (1965). Chlorophyll data are presented as water column totals integrated from the surface to 200 m.

Primary production was determined by ^{14}C uptake in simulated *in situ* experiments. Samples were collected from six depths, corresponding to predetermined levels of light penetration (expressed as a percent of the surface irradiance and estimated from the relationship $K = 1.54/\text{Secchi depth}$), were sampled. Two light and one dark bottle from each depth were then incubated from noon to approximately sunset in sea water cooled incubators which simulated *in situ* light levels. The samples were filtered through HA Milipore filters, fumed in HCl, and counted with a scintillation counter. Productivity at each depth was estimated by the average of the two light bottles corrected for dark uptake. Primary production data are presented as water column totals integrated from the surface to the depth reached by approximately 1% of surface irradiance.

These data are presented as ^{14}C uptake per approximately half-day experiment. The incubation times are shown, but the data have not been normalized to a standard time.

This is because uptake may not be linear over the incubation period, especially near the end of the day where there is little sunlight. Some of these data have also been presented as hourly rates in past publications. The conclusions in this report would not be affected by the method of data presentation.

Macrozooplankton was sampled with either a 1 m diameter ring net or a 3 m Isaacs-Kidd midwater plankton trawl, both equipped with a 0.505 mm plankton mesh and a flow meter. The nets were towed obliquely from the surface. The meter net reached a depth of 200 m and was towed for 21.5 minutes, typically filtering 400–800 m^3. The plankton trawl reached 200 to 400 m and tows were typically one hour in duration, filtering 20,000 to 50,000 m^3. Macrozooplankton biomass data are presented as wet displacement volume per 1000 m^3 water filtered, after removal of large organisms. The estimates of biomass from the meter net were consistently about 3 times larger than the plankton trawl and, therefore, data from each net are considered separately. These techniques and sampling schemes are described in more detail in various cruise data reports (Scripps Institution of Oceanography, 1974, 1975, 1978).

In previous studies, we examined the relative magnitudes of experimental and sampling errors for estimates of chlorophyll, primary production and macrozooplankton biomass (Venrick, 1978; Hayward and Venrick, 1982, and unpublished data). We are convinced that these sources of variability do not substantially affect our results. Moreover, since our comparisons are confined to data collected by the same procedures throughout the study, any biases associated with specific techniques will not affect our conclusions. However, potential biases should be considered when comparing the absolute values of these data with data from other systems obtained by different procedures.

3. Results

a. Vertical distributions

Figure 1 illustrates typical summer and winter vertical distributions of various properties at the CLIMAX area. The samples on each cruise were taken over about a four- to six-day period on an 18.5 by 111 km grid at 28–30N, 155W. These plots illustrate depth distributions and small-scale spatial and temporal variability in these properties.

In summer there is typically a mixed layer about 40 m deep with a broad thermocline below. Nitrate and PO_4 concentrations in the mixed layer and upper thermocline are always very low, usually well below 0.5 mg-at NO_3-N/m^3 and 0.1 mg-at $PO_4 - P/m^3$, although rare individual samples in the mixed layer on some cruises were up to double these values. A strong nutricline starts between about 100 and 150 m. Chlorophyll has a strong subsurface maximum well within the thermocline, between about 100 and 120 m. Primary production shows considerable scatter, but
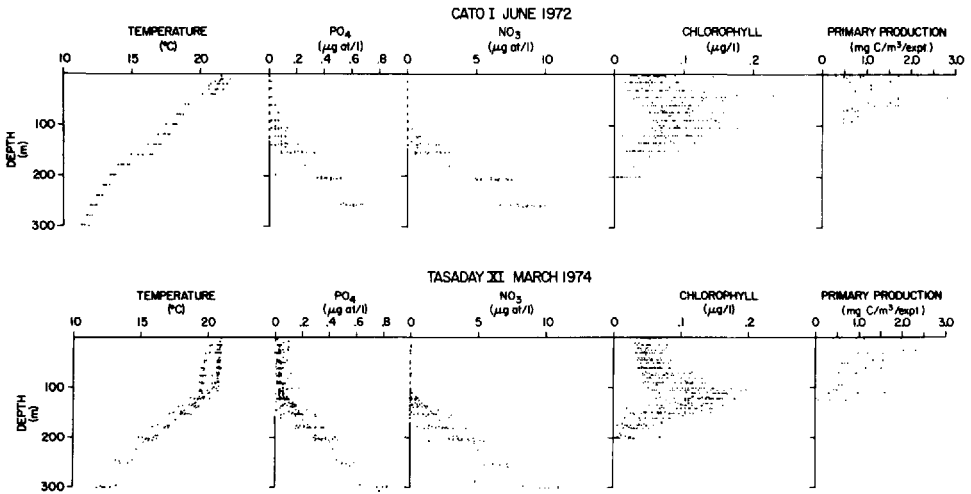
Figure 1. Summer and winter depth distributions of the properties at the CLIMAX area.

there is usually a subsurface maximum varying between about 25 and 50 m. Most production takes place above 100 m. The depth of the 1% light level varies from about 90 to 120 m.

In winter the mixed layer is more variable in depth, extending as deep as 140 m at some spots, although it may be as shallow as 40 m in nearby casts (Fig. 2). Concentrations of NO_3 and PO_4 are low in the upper layers (as in summers). There is a strong nutricline at the same depth as in summer. Winter mixing apparently does not extend deep enough to mix measurable quantities of nutrients into the upper euphotic zone, thereby altering the shape of the nutricline (McGowan and Hayward, 1978). There may be a strong chlorophyll maximum at the same depths as in summers. However, during at least one winter (1973), no chlorophyll maximum was apparent, presumably because mixing was sufficiently deep and persistent to disrupt it (Venrick, in preparation). As in summers, winter primary production is variable, with a tendency for a subsurface maximum. Most production takes place in the upper 100 m. The depth of the 1% light level remains between about 90 and 120 m.

It is possible that there are seasonal changes in the vertical distributions of these properties elsewhere within the central gyre, especially to the north. Past transects, however, show little evidence of this (McGowan and Williams, 1973).

b. Spatial and temporal distributions

Nutrients. Sampling on several transects has shown that the depth distributions of NO_3 and PO_4 throughout the eastern part of the gyre are similar to those at the CLIMAX area (Fig. 3, NorPac Committee, 1960; Reid, 1965; McGowan and Williams, 1973).
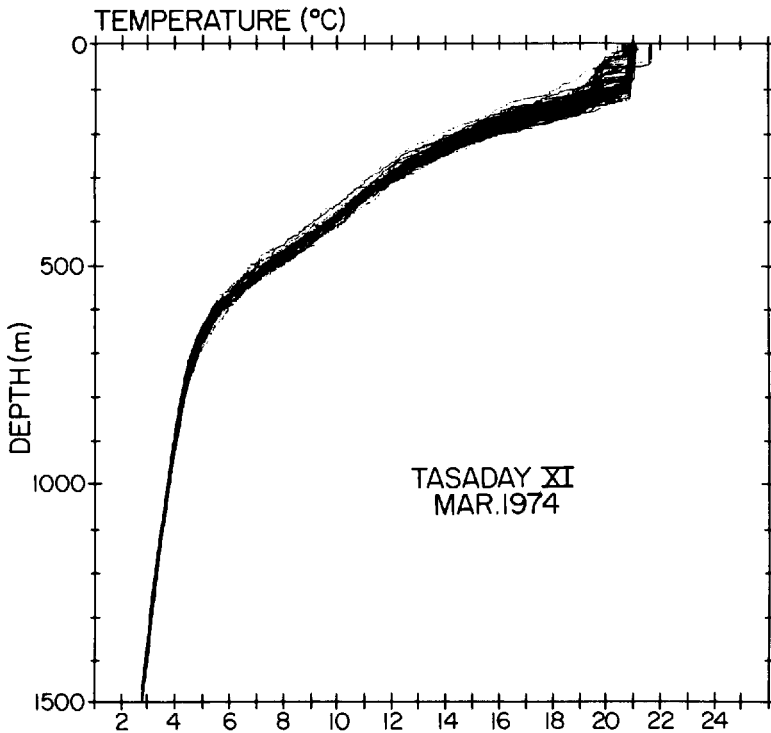
Figure 2. Winter structure of the thermocline. This plot was made by overlaying STD casts from the CLIMAX area.

We have never seen a major perturbation such as a winter overturn or high nutrient concentrations in the mixed layer. The nutricline shoals to much shallower depths in the Transition Zone and Subarctic (north of about 38–40N, Fig. 3). Within the central North Pacific there are also small spatial and temporal changes in the depth and slope of the nutricline. It is difficult to quantify this variability in nutricline shape in a simple index. These changes may also affect production, but, as is shown in the following sections, the observed variability in production is small.

Chlorophyll. There was little heterogeneity in vertically integrated chlorophyll on any scale. For each of 16 cruises, the range of all measurements on a cruise was within half to double the cruise mean. The range of mean values between cruises was about a factor of two (Table 3).

Small-scale variability, the range between replicate determinations on a single station, was always well less than a factor of 1.5 (Table 2 and Hayward, 1978). Diel variations were investigated on CLIMAX II comparing casts taken three times a day (at about 0600, 1600, and 2200 local time) at each of ten stations (Table 2). Over eight
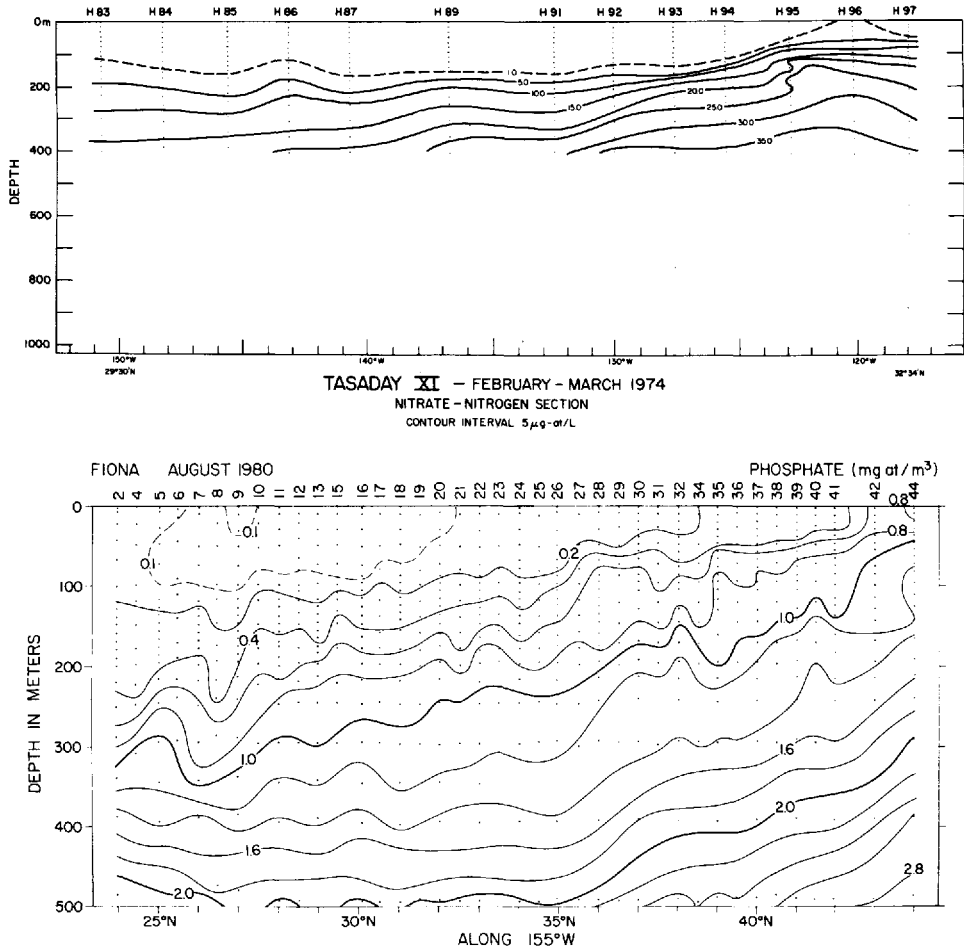
Figure 3. (a) Winter E-W vertical section of NO_3 from the CLIMAX area to San Diego. (b) Summer N-S vertical section of PO_4 from 24N to 44N along 155W.

complete 24-h stations, there were no significant differences between collection times (Friedman two way ANOVA $p > .20$). We have observed this same result with less extensive sampling schemes on other cruises (unpublished data). Within-station variability appears to be due to small-scale spatial heterogeneity rather than temporal cycles.

On the mesoscale, there were significant differences between stations on each of several cruises. The differences in mean values between stations were usually less than a factor of 2 (Hayward, 1978). Between-station differences could be detected only by sampling with very closely spaced replicates at a station. No between-station differences could be detected on Climax II, where within-station replicates were separated

Table 2. CLIMAX II. Diel changes in integrated chlorophyll. There were no significant differences between times or stations (Friedman two way ANOVA by ranks, $p > .2$).

	Approx. local time		
Sta	0600	1600	2200
1	9.44	16.21	
2	7.93	10.35	14.58
3	9.52	9.25	7.41
4	9.39	15.34	14.52
5	15.82	15.41	19.20
6	11.76	11.63	17.27
7	16.20	11.26	
8	18.48	10.46	12.28
9	7.43	13.07	14.75
10	8.76	17.37	18.82
$\overline{X}$	11.47	13.04	14.85
s	3.93	2.85	3.83
$s/\overline{X}$	.34	.22	.26
OVERALL $\overline{X}$	13.00		
s	3.68		
$s/\overline{X}$	.28		

Table 3. Cruise means of integrated water column chlorophyll. *N*—number of casts or cruises, *H/L*—ratio of highest to lowest value, *S*—standard deviation, *CV*—coefficient of variation.

| Cruise	Date	$\overline{X}$	N	Range	H/L	S	CV
Summers							
CLIMAX I	Sept. 1968	11.57	9	9.85–13.84	1.4	1.51	0.13
CLIMAX II	Aug. 1969	13.00	28	7.41–19.20	2.6	3.68	0.28
ARIES IX	Oct. 1971	11.69	7	8.29–15.82	1.9	3.26	0.28
CATO I	June 1972	13.76	6	10.82–17.45	1.6	3.39	0.25
C'BOG	Aug. 1972	11.84	10	8.26–17.69	2.1	3.12	0.26
TASADAY I	June 1973	15.00	6	13.46–16.37	1.2	1.21	0.08
TASADAY II	July 1973	13.85	8	10.44–18.27	1.8	2.44	0.18
CLIMAX VII	Aug. 1973	14.04	14	9.49–18.59	2.0	2.50	0.18
DRAMAMINE II	May 1974	21.57	7	19.06–25.23	1.3	2.25	0.10
AG76-1	Aug. 1976	18.82	11	16.94–22.41	1.3	1.89	0.10
AG76-3	Sept. 1976	15.75	25	11.81–18.15	1.5	1.72	0.11
INDOPAC XV	June 1977	15.11	18	11.21–19.49	1.7	2.65	0.18
FIONA	Aug. 1980	23.17	14	14.65–33.35	2.3	4.28	0.18
Summer	cruise means	15.32	13	11.57–23.17	2.0	3.70	0.24
Winters							
FCRG 71-2	Nov. 1971	11.48	5	9.98–14.09	1.4	1.56	0.14
SOUTHTOW XIII	Feb. 1973	19.14	14	12.92–23.32	1.8	3.29	0.17
TASADAY XI	Mar. 1974	13.66	11	10.51–18.16	1.7	2.52	0.18
Winter	cruise means	14.76	3	11.48–19.14	1.7	3.95	0.27
Overall	cruise means	15.22	16	11.57–23.17	2.0	3.62	0.24
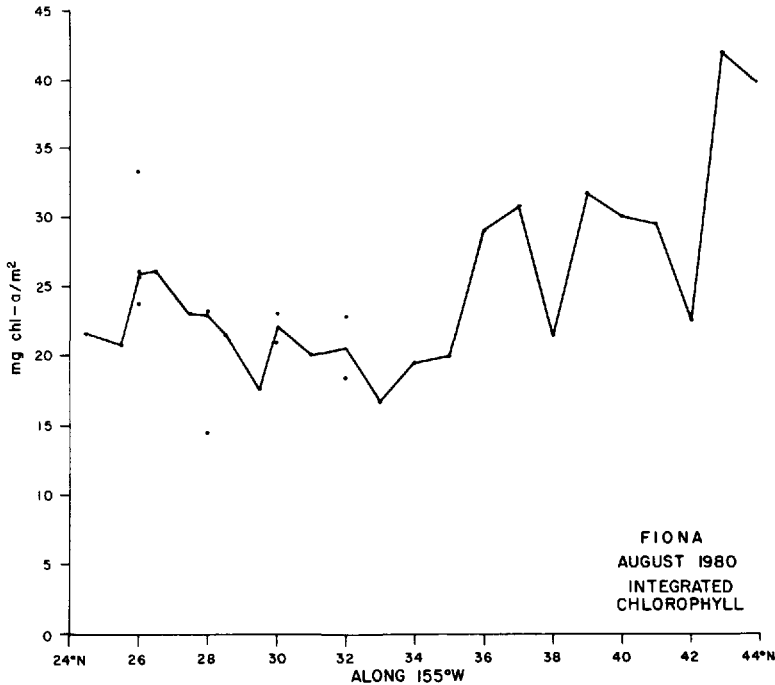
Figure 4. FIONA—latitudinal gradient in integrated chlorophyll. Each dot represents a cast. The line connects median values.

by several hours. It appears that within-station variability although small, is sufficient to mask mesoscale patterns.

Large-scale variability of vertically integrated chlorophyll was only slightly greater in magnitude than mesoscale variability. The range over all cruise means was 11.57 to 23.17 mg/m^3, with a C.V. of 0.24. There was no evidence of seasonal cycles (Table 3). A previous report of a seasonal difference in chlorophyll (McGowan and Williams, 1973) was based upon single summer and winter cruises separated by 18 months, and the observed change may have been due to interannual rather than seasonal differences. Large-scale spatial patterns in total chlorophyll were observed within the central gyre, although the magnitude of the spatial gradient was again less than a factor of 2. In 1980 (FIONA), there was a significant south-to-north decrease across the gyre from a maximum at 26N to a minimum at 33N (Kendall correlation, $p < .02$; Fig. 4). The value of integrated chlorophyll at the CLIMAX area, near 28N, (23 mg chl-a/m^2) was about 50% greater than the long-term average (15 mg chl-a/m^2; Table 3). Higher chlorophyll concentrations were found north of 36N in the Transition Zone and Subarctic environments.

Primary production. Vertically integrated primary production is somewhat more variable than chlorophyll on all scales. This is due, in part, to inherently greater

Table 4. Cruise means of integrated primary production. *N*—number of casts or cruises, *H/L*—ratio of highest to lowest value, *S*—standard deviation, *CV*—coefficient of variation, *T*—incubation time, hours:minutes.

Cruise	Date	$\overline{X}$	N	Range	H/L	S	CV	T
Summers								
CLIMAX I	Sept. 1968	102.09	7	78.9–123.0	1.6	14.2	0.14	5:30
CLIMAX II	Aug. 1969	165.99	10	88.4–262.4	3.0	60.9	0.37	5:58
ARIES IX	Sept. 1971	57.93	5	27.7– 89.8	3.3	22.5	0.38	5:06
CATO I	June 1972	89.81	6	67.5–125.6	1.9	23.8	0.26	5:58
CLIMAX VII	Aug. 1973	52.91	3	26.2– 77.7	3.0	25.8	0.49	6:01
DRAMAMINE II	May 1974	107.60	3	77.7–160.2	2.1	45.7	0.42	6:00
INDOPAC XV	June 1977	106.71	5	82.5–138.5	1.7	22.6	0.21	8:16
FIONA	Aug. 1980	169.67	18	49.3–269.8	5.5	64.5	0.38	7:32
Summer cruise means		106.59	8	52.9–169.7	3.2	43.2	0.41	
Winters								
SOUTHTOW XIII	Feb. 1973	56.92	6	33.4– 94.1	2.8	21.9	0.38	6:11
TASADAY XI	Feb. 1974	110.23	4	89.4–123.6	1.4	16.1	0.15	6:23
Winter cruise means		83.58	2	56.9–110.2	1.9			
Overall cruise means		101.99	10	52.9–169.7	3.2	41.2	0.40	

$\overline{X}$ is the per-cruise mean total uptake per experiment (mg C/m²/expt.)

variability in the technique. It may also be that true primary production is more variable than phytoplankton standing stock because production is a rate.

Small-scale variability, estimated as the range of measurements over two days at a station, was generally less than a factor of 1.2. However, this was significantly greater than the variability in the technique, estimated from the replicate casts on the same day (Hayward and Venrick, 1982).

In 1980, the only cruise for which replicate casts at the same station were made, between-station or mesoscale variability was significantly greater than small-scale variability. Between-station differences were about a factor of two to three (Table 4).

Large-scale variability was the same order of magnitude as the mesoscale variability, with a C.V. of 0.40, ranging over factors of three to four. There was no evidence of a seasonal cycle in primary production. Summer means ranged from 53 to 170 mg C/m³/experiment, a factor of 3.2 over eight cruises. The two winter cruises ranged from 57 to 110 mg C/m²/experiment. The 1980 transect through the gyre suggested a south-to-north decrease in primary production (Fig. 5), similar to that of chlorophyll. This decrease, however, was not significantly greater than the mesoscale variability (Kendall correlation, $p > .2$). Production at 28N was higher than the long-term mean by a factor of about 1.7.

Macrozooplankton biomass. There was also relatively low heterogeneity in macrozooplankton biomass on all scales. The meter net and the plankton trawl showed similar patterns. The range of values within a cruise was typically about half to double the
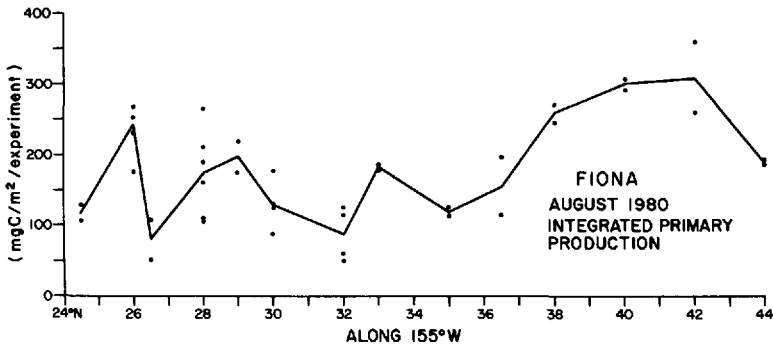
Journal of Marine Research

Figure 5. FIONA—latitudinal gradient in integrated primary production. Each dot represents a cast. The line connects median values.

cruise mean, and the range of mean values between cruises was less than a factor of three (Tables 5 and 6).

Small-scale heterogeneity in sequential meter net tows at a station was very low. Sets of three replicate tows at a station usually differed by well less than a factor of two (Fig. 6). There was significant diel variability, presumably due to vertical migration. When averaged over a cruise, night-time biomasses exceeded daytime biomasses by a factor ranging from 1.2 to 1.8 ($\overline{X} = 1.51$, Table 5). Day and night samples were considered separately for the following comparisons.

Mesoscale variability was little greater than within-station variability. The range of

Table 5. Day-Night ratio of macrozooplankton biomass. Day samples were taken near noon and night samples near midnight. N/D—night to day ratio.

		DAY		NIGHT		
Cruise	Date	$\overline{X}$	N	$\overline{X}$	N	N/D
Plankton trawl						
Summers						
CLIMAX II	Aug. 1969	28.41	7	33.54	7	1.18
ARIES IX	Sept. 1971	15.20	3	22.20	3	1.46
CATO I	June 1972	9.90	2	16.17	3	1.63
TASADAY I	June 1973	12.21	6	19.57	6	1.60
Cruise means		16.43	4	22.78	4	
Winters						
SOUTHTOW XIII	Feb. 1973	10.76	6	19.30	6	1.79
TASADAY XI	Feb. 1974	8.70	4	14.88	4	1.71
Cruise means		9.79	2	17.09	2	
Meter Net						
AG76-3	Sept. 1976	56.23	7	64.75	23	1.15
MARIANA II	Aug. 1978	47.23	12	73.50	10	1.56

Table 6. Cruise means of macrozooplankton biomass for night samples. *N*—number of samples or cruises, *H/L*—ratio of highest to lowest value, *S*—standard deviation, *CV*—coefficient of variation.

Cruise	Date	$\overline{X}$	*N*	Range	*H/L*	*S*	*CV*
AG76-1	Aug. 1976	68.44	19	46–129	2.8	23	0.33
AG76-3	Sept. 1976	64.75	23	49–81	1.7	9	0.14
INDOPAC XV	June 1977	92.96	27	56–135	2.4	22	0.24
MARIANA II	Aug. 1978	73.50	10	61–88	1.4	11	0.16
FIONA**	Aug. 1980	82.25	18	56–149	2.7	24	0.29
Cruise means		76.38	5	65–93	1.4	12	0.15

*Night samples only.
**CLIMAX area stations only (26–30N).

values between stations within a cruise was typically less than a factor of three, with a C.V. of less than 0.35 (Table 6).

Large-scale temporal heterogeneity was estimated from the differences between cruises. Biomass estimates between cruises range over a factor of 3 for the plankton trawl samples and 1.4 for the meter net samples (Table 5). Based upon the four summer and two winter plankton trawl cruises, there was no evidence of a seasonal
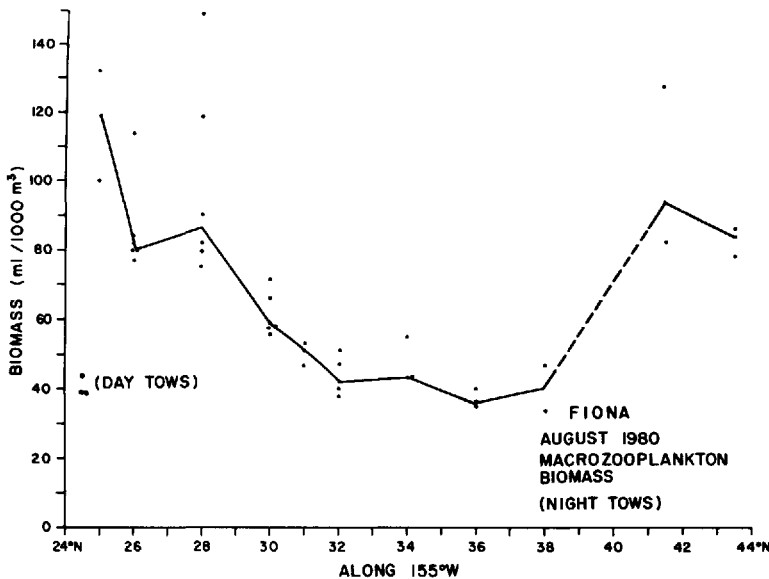

Figure 6. FIONA—latitudinal gradient in macrozooplankton biomass. Each dot represents a sample and the line connects median values. The dashed portion of the line represents an area where the interleaving station (at 39.5N) was dominated by salps and the biomass is not comparable to that of the other stations.

cycle. Large-scale variability in space could be examined only with the data from the 1980 transect, where there was a significant south-to-north decrease in biomass of about a factor of three (Kendall correlation $p < .01$). Macrozooplankton biomass increased north of 36N in the Transition Zone and Subarctic environments (Fig. 6). At 28N, macrozooplankton biomass was similar to the long-term mean. The variability in biomass over large spatial scales appeared to be greater than the interannual variability at the CLIMAX area. However, there were fewer years included in the interannual comparisons of macrozooplankton biomass than there were for chlorophyll or primary production and temporal heterogeneity over long periods may have been underestimated.

4. Discussion

There was low heterogeneity of vertically integrated chlorophyll, primary production and macrozooplankton biomass on all scales in the central North Pacific. Diel changes were evident only in macrozooplankton biomass, apparently due to vertical migration. No seasonal cycles were detected. Unlike most other oceanic ecosystems, mesoscale heterogeneity was little greater than that on smaller scales for each property except primary production. Large-scale spatial variability at 28N was roughly the same in magnitude as interannual variability. The 1980 transect suggested a south-to-north decrease in the magnitudes of the biological properties investigated which was not observed on earlier transects along the same meridian (McGowan and Williams, 1973; Venrick et al., 1973). However, chlorophyll and primary production were elevated with respect to the long-term mean at the CLIMAX area. Thus, this trend may be due to anomalous conditions near 28N. At present, we have no explanation for this.

Variability in nutrients, chlorophyll, and primary production has also been described from a 14-month time series near Hawaii (Bienfang and Szyper, 1981). They found no seasonal changes in nutricline depth and no diel or seasonal changes in chlorophyll. They did, however, observe larger fluctuations in primary production (more than a factor of 20 between cruises).

Heterogeneity in chlorophyll, primary production and macrozooplankton biomass is one index of the biological response of the system to its physical structure. Low variability is coincident with relatively stable physical structure in the upper layers and it suggests that the overall level of physical forcing is low. The absence of seasonal cycles at the CLIMAX area appears to be due to the lack of winter mixing sufficiently intense to alter the shape of the nutricline or increase upward transport of new nutrients (Fig. 1 and McGowan and Hayward, 1978). Low mesoscale variability appears to be due to the rareness of major physical disturbances on mesoscales, and lack of advection of large patches of water with anomalous characteristics from outside the system.

Although low in magnitude, there were detectable spatial gradients in production and carrying capacity (phytoplankton and zooplankton biomass) in the central North Pacific. These were probably caused by variations in nutrient flux to the euphotic zone which, in turn, may be related to changes in the physical structure of the water column (McGowan and Hayward, 1978; Hayward and McGowan, 1981). The 1980 transect (FIONA) crossed a mesoscale feature at 26.5N which appeared to be an eddy. This was characterized by a depression of isolines of temperature, salinity, and nutrients (Fig. 3b) and by a decrease in the rate of primary production (Fig. 5). The physical processes which caused the spatial gradient and the effects of the eddy will be discussed elsewhere.

Primary production was more variable on mesoscales when compared to smaller scales than was chlorophyll or macrozooplankton biomass. This suggests that the environmental factors affecting primary production fluctuate on different spatial and temporal scales than those affecting standing stock. Production may respond more rapidly to transient environmental changes because it is a physiological response, and the time lags required for population changes are not necessary. The greater variability in productivity suggests that relatively more measurements will be needed to describe large-scale patterns of production than will be needed for chlorophyll or macrozooplankton biomass.

Comparisons with other oceanic ecosystems show that the central North Pacific is qualitatively different with respect to both the overall magnitude of heterogeneity and the relative heterogeneity of different scales. These differences can be expected to affect ecosystem structure.

The Sargasso Sea, an analogous environment in the Atlantic Ocean, might be assumed to be very similar to the central North Pacific. However, at least the western part of the Sargasso Sea appears to be much more heterogeneous than the central North Pacific. Direct comparisons are difficult because of differences in the techniques and sampling schemes used in the two areas. Based upon, usually, single measurements made at two-week intervals near Bermuda, spring increases of as much as 5–10 times have been reported for chlorophyll (Menzel and Ryther, 1960; Deevey, 1971), primary production (Menzel and Ryther, 1960), and macrozooplankton biomass (Menzel and Ryther, 1961; Deevey, 1971). The magnitude of the spring bloom also differed between years. It is unclear to what extent these observations may have been influenced by Gulf Stream rings (Wiebe *et al.*, 1976; Ortner *et al.*, 1978; The Ring Group, 1981). We are not aware of any data sets with which to compare large-scale spatial patchiness in the Sargasso Sea with the central North Pacific.

The California Current ecosystem is much more heterogeneous than the central North Pacific. During 1969, integrated water column chlorophyll, averaged over large areas, showed a seasonal change of a factor of 3–5, as well as strong N-S and onshore-offshore gradients (Owen, 1974). Over meso- and large-scale spatial intervals, integrated chlorophyll frequently varied by as much as a factor of 20. Primary

production showed meso- and large-scale spatial changes of at least a factor of 10 (Owen, 1974; Owen and Sanchez, 1974; Hayward and Venrick, 1982). Seasonal and interannual variability in primary production, averaged over the southern California bight was at least a factor of 2-3 (Smith and Eppley, 1982). Macrozooplankton biomass also varied spatially by a factor of 20 or more over meso- and large-scales (Smith, 1974), although, when very large-scale spatial averages are computed, the amplitude of the seasonal cycle was a factor of 2–3, with somewhat larger interannual variability (Bernal, 1980).

Seasonal cycles and spatial patchiness are also intense in the Subarctic Pacific, where advection from outside the system may be less significant than in the California Current. Seasonal changes in primary production of about a factor of 3 have been observed (Larrance, 1971). There is a spring bloom of at least a factor of 10 in average macrozooplankton biomass, and there is considerable interannual variability in the timing and magnitude of the bloom (LeBrasseur, 1965). Closely spaced (less than 20 km) measurements of macrozooplankton biomass frequently differ by a factor of 10 or more, and large-scale spatial patchiness is even greater.

Patterns of heterogeneity are important aspects of the biological structure of these ecosystems. The low overall heterogeneity in the central North Pacific, especially on mesoscales, suggests that environmental disturbances do not have a major impact here upon macrozooplankton and nekton populations. This is because mesoscale patchiness (a scale roughly related to the ambit of an individual over its lifetime) is low in magnitude, and parcels of water on this scale are not substantially different from each other. An individual macrozooplankter in the central gyre normally would be exposed to as much heterogeneity, as least in these four properties, in a few days as it would in its entire lifetime. Indeed, the amount of environmental heterogeneity encountered by an individual is almost as much as is encountered by the whole population in the eastern part of the North Pacific central gyre. Individuals must cope with small-scale patchiness, but most of the population is exposed to relatively similar environmental conditions on time and space scales greater than a few days. Thus, if these four properties are good indices of environmental conditions, most of the population should experience a similar fate. The data shown here were not sampled on appropriate scales to say whether this is also the case for phytoplankton and microzooplankton which have much smaller generation times and ambits.

Other studies in the central North Pacific have shown low variability in chlorophyll and primary production (Venrick, 1979), biomass of microplankton (Beers *et al.*, 1982) and mesopelagic fish (Barnett, 1975), and in the species structure of phytoplankton (Venrick, 1982), dinoflagellates (Weiler, 1980), copepods (McGowan and Walker, 1979, 1983), larval fish (Loeb, 1979), chaetognaths (Lyons, 1976), and mesopelagic fish (Barnett, 1975). Low variability in species structure is not necessarily a consequence of low environmental variability, but a stable environment may help to create conditions where strong regulation of species structure is possible (Hayward and McGowan, 1979; McGowan and Walker, 1983).

Differences between ecosystems in the ways in which the heterogeneity in these properties is apportioned among different scales may be as important an aspect of their structure as differences between the absolute values of the properties. Zooplankton populations in the central North Pacific are rarely exposed to fluctuations in the given properties of more than a factor of 2–3 on any spatial or temporal scale. These changes probably fall within the range of individual adaptation, hence the success or failure of the population seems likely to depend upon how well individuals are adapted to the average environment. In contrast to this, individuals in other, more heterogeneous pelagic ecosystems may live in mesoscale patches in which values of these properties may vary by factors of 20 or more. There is great heterogeneity on scales that are similar to, or larger than, the ambit of an individual macrozooplankter over its lifetime. Significant fractions of these populations may complete their life cycles in qualitatively very different environments, and thus may experience different fates than other fractions of the population in different patches. The consequences of this in terms of long-term changes in population size depend both upon the quality of adaptation of the individuals to the average environment and upon variations in the intensity of mesoscale patchiness.

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