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# Spatial patterns of grazing-related parameters in California coastal surface waters, July 1979

by James L. Cox[1], Loren R. Haury[2] and James J. Simpson[2]

## ABSTRACT

A surface survey using underway continuous mapping of temperature, chlorophyll, zooplankton (>153 $\mu$m) wet weight density, and activity of the zooplankton digestive enzyme laminarinase was undertaken for a 20-day period during active upwelling in the California coastal region between Pt. Arena and Pt. Conception, California, U.S.A., during July, 1979. The resulting data set was used in an analysis of spatial aspects of grazing activity in surface waters using the laminarinase activity of zooplankton samples and two independent computational means to estimate grazing rates.

Both computational means for estimating grazing rate showed strong correlations with grazing activity and indicate that laminarinase activities reflect grazing activity with a time lag on the order of two days. In all regions zooplankton abundance was highest in regions of high chlorophyll concentration, but this relationship was most pronounced where zonal upwelling produced alongshore bands of high grazer and phytoplankton abundance. In such areas, a significant negative correlation between grazer abundance and laminarinase activities was noted. This correlation was not observed at Pt. Conception, where zonal patterns were interrupted by offshore extensions in surface temperature and chlorophyll distributions, resulting in offshore patches of high chlorophyll.

Correspondence of high chlorophyll and high zooplankton biomass in zonal features was interpreted as a behavioral response by grazers to the upwelling circulation regime which optimizes residence time in the phytoplankton-dense inshore region. Laminarinase negative correlations can be interpreted as an approach to grazing equilibrium which is more nearly achieved where conditions permit such prolonged residence time. Complex circulation in areas where zonal upwelling is interrupted by unique topographical features such as at Pt. Conception, may counteract behavioral localization by grazers, and reduce their potential to persist in regions of high phytoplankton standing crop.

## 1. Introduction

Spatial distributions of properties (e.g., temperature and chlorophyll) in coastal upwelling areas have been used as the principal means of determining interactions

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between physical circulation and biological production in these systems. A major shortcoming of this approach has been the difficulty in assessing the impact of grazing by zooplankton on phytoplankton distributions, a component which has been shown theoretically to be a factor of overwhelming importance (Walsh, 1976). This paper presents the results of measurements of the spatial distributions of temperature, phytoplankton, zooplankton, and a new enzymatic measure of zooplankton grazing activity at various locations in the California coastal upwelling zone. Statistical analyses and distributional maps of the observed parameters are used to examine the potential of this enzymatic technique to reveal spatial differences in grazing, and to determine the influence of physical structure on biological variables of the system.

Certain general features of the mesoscale spatial patterns of zooplankton distribution associated with coastal upwelling are now evident from recent studies. Zooplankton biomass maxima are almost always observed at a distance from the coastline which is determined by the magnitude of upwelling intensity and offshore transport (Andrews and Hutchings, 1980; Smith *et al.*, 1981). This spatial abundance peak is often expressed as a band (or bands) roughly parallel to the coast, although under conditions of especially intense upwelling, discrete mesoscale patches may be transported farther offshore (Andrews and Hutchings, 1980).

Zooplankton biomass maxima usually overlap chlorophyll maxima, but with a slight seaward displacement (Peterson *et al.*, 1979; Andrews and Hutchings, 1980; Walsh *et al.*, 1980). These zooplankton maxima appear to result primarily from physical transport and behavioral aggregation within the upwelling zone, and not from *in situ* growth (Peterson *et al.*, 1979; Andrews and Hutchings, 1980).

Such mesoscale patterns are important structural features of coastal upwelling systems, and undoubtedly can be used in a general way to determine the influence of grazing on the distributions of other properties. Where zooplankton biomass is high, we may reasonably expect potentially intense grazing. However, there are two factors which complicate this interpretation. First, zooplankton-phytoplankton interactions are strongly influenced by patchiness on spatial scales much smaller than the mesoscale. Second, grazing intensity is not necessarily proportional to zooplankton biomass. Because both of these factors are important to the design of our study, we will briefly discuss each.

Within small-scale patches of abundant herbivores, phytoplankton density can be greatly reduced by grazing, and conversely, low grazer abundance may lead to higher phytoplankton density (Mackas and Boyd, 1979). This leads to a negative correlation between phytoplankton and zooplankton. However, data sets consisting of "point" observations in mesoscale surveys (transect series of fixed stations) usually produce positive correlations between zooplankton and phytoplankton (e.g., Peterson *et al.*, 1979; Andrews and Hutchings, 1980). This discrepancy illustrates

the importance of sampling approach. Clearly, a small set of "point" observations may obscure important aspects of mesoscale patterns, since the mean state prevailing in different mesoscale subregions may be inadequately represented. In our study, we have attempted to overcome this problem by continuous underway pump sampling of surface chlorophyll and zooplankton during mesoscale grid mapping. This approach has the advantage of providing a spatially-averaged estimate of biomass, and permits a much higher density of sampling locations along transect lines. As detailed a sampling in the vertical is not practical on this scale. However, an unambiguous interpretation of surface samples requires some vertical information. Our sampling strategy provided the necessary vertical data.

Our sample set provides detailed information on spatial differences in phytoplankton and zooplankton biomass in several regions. Translating this information into estimates of grazing intensity is difficult for a variety of reasons. At-sea grazing experiments produce highly variable results and may be difficult to interpret (Gamble, 1978; Dagg and Grill, 1980); they are subject to substantial experimental errors (Rigler, 1971; Roman and Rublee, 1980), and are clearly inappropriate for detailed spatial studies. In a general sense, it can be assumed that grazing will be proportional to zooplankton biomass and prevailing phytoplankton concentration. However, the validity of this concept is subject to some question in a patchy environment (Mullin and Brooks, 1976), because of uncertainties regarding the persistence of patchiness patterns (Haury *et al.*, 1978). These uncertainties are primarily due to the difficulty in obtaining a "pure time series" on patches because of water movements and dispersion relative to the point of observation (Steele, 1978).

Temporal information, however, can be obtained by measurements of digestive enzyme activities which reflect the grazing history of zooplankton samples. The digestive enzyme *laminarinase*, assays of which are used in this paper, appears to reflect the grazing history of zooplankton on a time scale of about one to two days (Cox, 1981; Cox and Willason, 1981). Laminarinase activity is induced by the presence of its substrate in the gut of grazers and depends on the time averaged concentration of phytoplankton food and its rate of ingestion.

We have used a combination of laminarinase measurement and various computational techniques involving temperature, zooplankton and phytoplankton measurements to estimate grazing. Our results, although they apply to surface waters only, provide a picture of major horizontal spatial variations in grazing activity which should add to understanding of its role in determining important biological features of coastal upwelling systems.

## 2. Methods

During July 1979, the R. V. *New Horizon* made transect grids in the Pt. Conception region and between Pt. Reyes and Pt. Arena as part of the California Coastal

Fronts Program. Samples were also collected during the two transits between the regions. Contiguous, successive zooplankton samples were collected from a portion of the flow of a continuously operated ship's seawater pump (flow $> 300\ l \cdot min^{-1}$) with an intake (20 cm diameter) at about 3 m depth on the hull centerline aft of amidship. The flow rate should have been sufficient to overcome zooplankton avoidance effects (Miller and Judkins, 1981). The sampling stream was directed into a small net (153 $\mu$m mesh) designed to be rapidly rinsed and emptied so that there would be a minimum of delay between successive sample collections. Contents of the net were rinsed down the cod end funnel and collected on a sieve of the same mesh, blotted, wrapped in Parafilm and frozen at $-20°C$.

To determine the volume of water filtered by the flow sampler, measurements were made at least every three hours of the time required for the hose to fill a large vessel of known volume. Total volume filtered for each sample was then determined from the duration of each collection and the prevailing estimated flow rate. During the cruise, flow rates varied from 6.5 to 22.4 liters per minute, but the majority of samples ($> 90\%$) were collected at a rate of 10-15 liters per minute. Variations in flow rate at a constant setting never exceeded 2.5% with successive samples. Larger variations were due to deliberate adjustments of the flow controller. Filtration times were kept close to 20 minutes, with few exceptions. Delay time between successive samples on a transect ranged from one to five minutes. Total volume filtered ranged from 97 to 519 liters, with the majority of values from 200 to 300 liters.

Flow sample collection began with the Pt. Conception grid, continued up the California coast until the Pt. Arena region was reached, where another grid pattern was covered. Collection continued on the return route, and a smaller grid (Pt. Conception, Leg 2) was done in the Pt. Conception region. A total of 321 samples were obtained.

The spatial locations of the zooplankton samples were determined by time indexing the sample intervals with the cruise track, which was obtained from satellite and Loran C fixes made at hourly intervals or less. The positions corresponding to the time midpoints of the filtrations are shown in Figures 1, 3 and 4 for the Pt. Conception, Leg 1; Pt. Conception, Leg 2; and Pt. Arena-Pt. Reyes regions, respectively. The alongshore sampling between the Pt. Conception and the Pt. Arena-Pt. Reyes regions is shown in Figure 5. The mean distance represented by the sampling interval was 5.49 km ($\pm$ 2.21 S.D.).

Because a centrifugal pump was used for collecting the samples, the potential existed for damage to filtered material. Occasionally, fresh samples were observed microscopically for evidence of pump damage. Copepods, chaetognaths, *Ceratium*, and numerous other taxa were consistently observed alive or with little or no evidence of fragmentation. Gelatinous forms were sometimes collected alive, but many could have been destroyed since fragments would be difficult to distinguish or would be lost through the meshes of the net. Some samples contained undamaged larval

and juvenile stages of euphausiids, but adults were damaged by the pumping system, as evidenced by the presence of disconnected eyes and other body parts.

To supplement the pumped collections from the Pt. Conception region, zooplankton samples were taken every 15 km along the cruise track with a 0.5 m diam, 202 $\mu$m mesh net towed at 75 cm sec$^{-1}$ between the surface and 2 m depth. Volumes filtered ranged from 13 m$^3$ in rich coastal waters to 349 m$^3$ in the relatively oligotrophic offshore waters; mean volumes filtered by the 68 tows was 117 m$^3$ (Std dev 63 m$^3$). The map of zooplankton displacement volume (m$l$ m$^{-3}$) obtained with the net agreed well qualitatively with that of zooplankton wet weight (g m$^{-3}$) derived from the pump samples, although the pump estimates of absolute biomass were about three times higher than the net estimates. This difference was probably due to the difference in mesh sizes and the shallower sampling depth of the net. As would be expected, the net captured more of the larger, mobile plankton (e.g., euphausiids). However, the relative proportions of species of the smaller grazers (e.g., copepods) were similar in both types of samples.

*a. Sample processing.* Frozen samples were kept on dry ice during weighing and splitting procedures. Wet weights were determined to ± 0.01 mg on each frozen sample. Weight aliquots (representing approximately 1/3 of the total sample) were taken from each sample and preserved in buffered formalin (10%). Taxonomic evaluation of these samples will be reported elsewhere and is referred to only anecdotally in this paper.

After weighing, the material was placed in 20 m$l$ glass containers and kept frozen at −20°C until homogenation. To each vial, 10.0 m$l$ of 0.25, succinate buffer, pH 5.08 (made isotonic with seawater using NaCl) was added. The contents were homogenized using a Polytron homogenizer, which uses a combination of ultrasonic disruption and high speed blade maceration. The resulting homogenates were immediately refrozen until analysis.

*b. Sample analysis.* Frozen homogenates were thawed, mixed thoroughly, and subsampled for various analyses. An aliquot of 250 $\mu l$ was taken and mixed with 10.0 m$l$ of 90% acetone and left to extract at 2°C in the dark for 24 hours. The chlorophyll-*a* and phaeopigment content of this extract was determined by the fluorometric technique (Strickland and Parsons, 1968), using a Turner Designs fluorometer calibrated with a pure extract of chlorophyll-*a* (Sigma). From these values, phytoplankton wet weight was calculated on the basis of an assumed carbon to chlorophyll-*a* ratio for phytoplankton in upwelling regions (surface) of 45 (Lorenzen, 1966), and an assumed carbon to wet weight ratio of 0.10 (Strickland, 1960). These values were used to estimate the percentage of the total wet weight of the sample due to phytoplankton. If this value exceeded 1%, it was subtracted from the total wet weight. Of the 321 samples, 147 contained greater than 1% phytoplankton and only five exceeded 10%. The corrected sample wet weight is thus the wet weight

of the zooplankton fraction and is called here $gWW$ (gm). Zooplankton wet weight per unit volume of water filtered, or $gWW$ m$^{-3}$, is called $WW$.

From the thawed homogenate, 100 $\mu l$ were removed for analysis of laminarinase activity. The aliquot for laminarinase activity was dispensed into a microcentrifuge tube, mixed with 500 $\mu l$ of substrate (3 mg ml$^{-1}$ of 95% pure laminarin from Spectrum Chem. Co.). The substrate solution was made up in the same isotonic buffer solution used for homogenation. The mixture was maintained for 50 minutes at 37°C, the temperature for optimal enzyme rate (Cox, unpublished data). A log-linear plot of enzyme rate vs. temperature from 8° to 37°C ($N = 9$) gave a correlation coefficient ($r$) of 1.00 ($Q_{10} = 1.72$), indicating a purely thermochemical effect of higher incubation temperature. Assays were therefore run at 37°C because the higher rates observed at this temperature afford better precision, and because 37°C is an accepted standard in enzymology. The reaction was stopped by addition of 500 $\mu l$ of distilled water combined with ice-bath chilling at 2°C, then centrifuged for five minutes at 12,000 G, after which 500 $\mu l$ of supernatant were analyzed for glucose using the Glucostat method (Sigma).

Laminarinase activities are reported in two ways. First, enzyme activity per unit wet weight of zooplankton biomass was expressed as the catalysis rate at an estimated Vmax at the measurement temperature of 37°C (Cox, 1981), referred to hereafter as $LA$ ($\mu g$ glucose $gWW^{-1}$ min$^{-1}$). Second, laminarinase activity at 37°C and Vmax per unit volume of seawater (m$^3$), which is an index of volumetric grazing activity, was computed by multiplying each $LA$ value by the corresponding zooplankton wet weight per m$^3$ ($WW$) value for that sample. This parameter is hereafter termed $TLA$ ($\mu g$ glucose min$^{-1}$ m$^{-3}$).

Temperature and *in vivo* chlorophyll-*a* fluorescence (Turner Designs, Model 10) were determined from the same pump stream and recorded at 16-second intervals. Chlorophyll-*a* fluorescence was calibrated with discrete half-hourly or hourly 140 ml samples taken from the same pump stream for *in vitro* determinations. *In vivo* fluorescence was adjusted to chlorophyll-*a* (mg m$^{-3}$) by a running average method using the discrete measurements.

Vertical sections of extracted chlorophyll from water bottle casts on the line transects were made to determine the relationship between surface chlorophyll distributions (corrected *in vivo* fluorescence) and the vertical distributions. Two of these sections are presented in the results.

The temperature and chlorophyll-*a* values from the surface observations were broken into intervals coinciding with the zooplankton samples and an average calculated for each interval. The complete data set thus consists of a temperature, chlorophyll-*a*, zooplankton wet weight density ($WW$), laminarinase activity per unit zooplankton wet weight ($LA$), and laminarinase activity m$^{-3}$ ($TLA$) for all samples. All variables except temperature were normalized by simple logarithmic transformation prior to parametric statistical testing.

The data were analyzed in two ways. First, untransformed data were used in the construction of contour maps of properties to reveal their coarse to mesoscale features. Second, log transformed data were sorted by geographical region and by 0.5°C temperature intervals within regions (for reasons explained in the next section). These two data sets then were used as the basis for inter-regional comparisons. Relationships between log-transformed variables within regions also were examined. The sorting of data by 0.5°C temperature intervals within regions groups data from different locations within each region. Because the temperature of the water from which a sample was collected was a good indicator of the biological characteristics of that sample (e.g., the magnitude of *TLA* or *WW* and the species composition of the zooplankton), the separate locations within regions appeared to be biologically homogeneous. We therefore have used the means (and their standard deviations) of the variables grouped by temperature in these statistical tests.

## 3. Results

*a. Surface mapping.* Temperature, chlorophyll-*a*, zooplankton wet weight density (*WW*), and volume specific laminarinase activity (*TLA*) are plotted as contour maps in Figures 1, 3 and 4. The central region was not mapped since there were no transects normal to the shore. The two transects along the central coast (Fig. 5) appear to run mainly in a high chlorophyll-*a*, low temperature band parallel to the coast. These data are plotted in Figure 5 as individual points along the axis of the transects.

Shipboard observations of wind speed and direction, combined with land-based measurements from the Santa Barbara airport, were used to document general wind conditions before and during transects. During Leg 1 at Pt. Conception, winds consistently exceeded 5.2 m sec$^{-1}$ and typically ranged from 10.4-15.6 m sec$^{-1}$ over the survey period, with a direction ranging from 310°-340°. In the northern regions, speeds were considerably lower (4.2-8.3 m sec$^{-1}$) with variable headings (350°-160°). Prior to Leg 2 at Pt. Conception, winds were diminished ($< 2.6$ m sec$^{-1}$), although during the last few hours of the Leg 2 survey, speeds increased to 10.4-15.6 m sec$^{-1}$ with an average heading of 300°.

The plots for Pt. Conception, Leg 1 (Fig. 1a, b) show a band of high chlorophyll-*a* roughly parallel to the shore. This band has good spatial concordance with the 13-14°C temperature interval. The feature also shows undulations which mark the apparent location of offshore extensions of the main upwelling band. At the end of these extensions, detached, roughly circular regions of high chlorophyll concentration ("blobs") are found. These appear to be progressively more displaced in a southwesterly direction at lower latitudes, and all are centered at a temperature of approximately 14.7°C. They are connected to the main high chlorophyll-*a* zone by bands of southwesterly-directed chlorophyll-*a* concentrations of intermediate value.
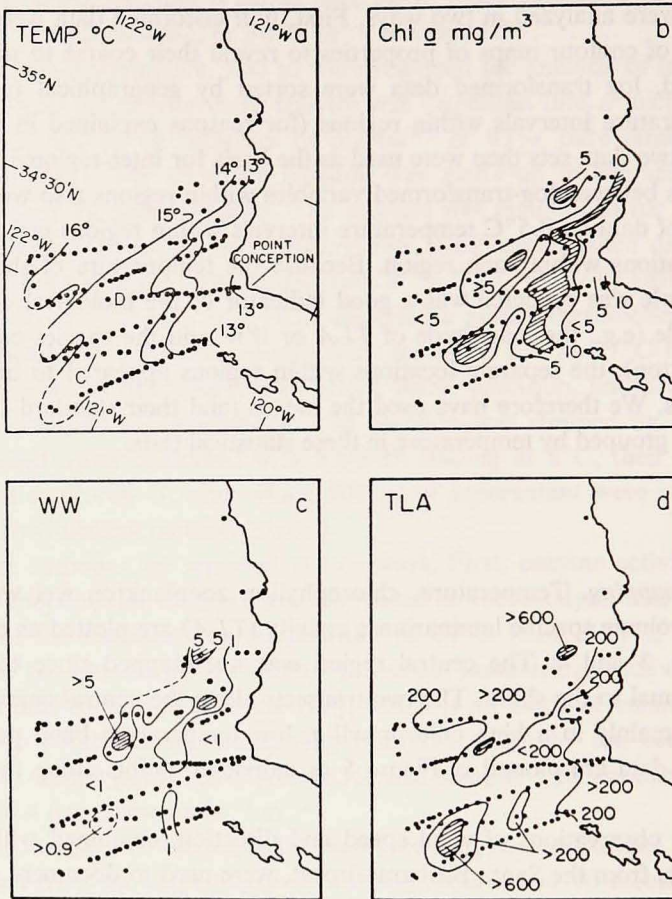
Figure 1. Contoured data for surface properties, Pt. Conception region, Leg 1. Survey was completed during 9-15 July 1979. Contours were constructed (as in Figs. 3 and 4 also) by linear interpolation between several pairs of adjacent points. In some cases, contours are drawn to meet subjective criteria of smoothness and continuity, especially at the edges of the sampling point coverage (dashed lines). Contour intervals have been deliberately made broad for ease of interpretation and suppression of fine-scale features caused by biological and sampling variability. Dots indicate the midpoint of linear transect segments which correspond to the mean values of continuously measured variables during the transect segment; zooplankton were collected continuously during the same period. Letters C and D designate the transects from which the vertcial sections of chlorophyll-*a* shown in Figure 2 come.

Some evidence of high inshore chlorophyll-*a* is shown directly off Pt. Conception. Figure 2 shows two vertical sections of chlorophyll taken in the Pt. Conception region (lines C and D, Fig. 1a). These sections, presented along with traces of relative fluorescence from surface pumping, show that the surface properties reflect depth distributions of chlorophyll within this region.
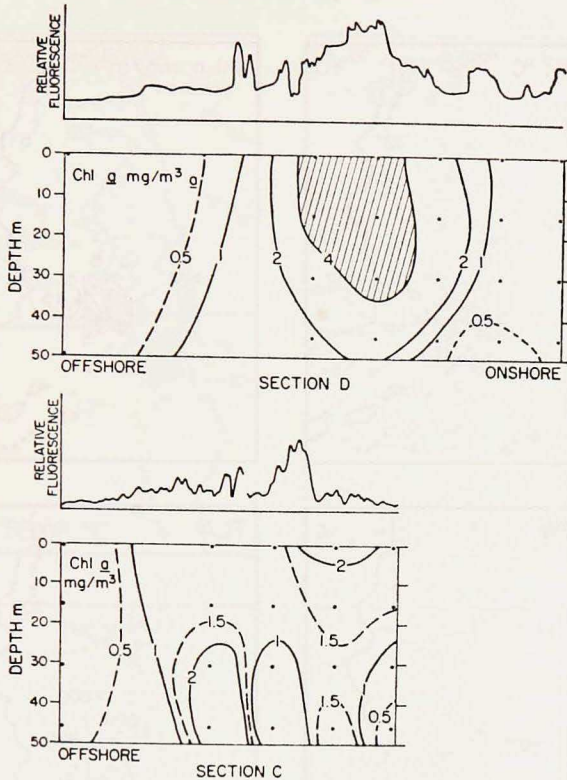
Figure 2. Vertical sections of chlorophyll-*a* along two transect lines of the Pt. Conception, Leg 1 survey. These transect lines (C and D) are indicated in Figure 1a. Corresponding traces of chlorophyll-*a in vivo* fluorescence are shown along with the vertical sections; these represent the signal from which surface chlorophyll data were derived.

High zooplankton wet weight density (*WW*) occurs in an alongshore band (Fig. 1c), displaced slightly more offshore than the chlorophyll-*a* band. These densities, however, are less continuous than the chlorophyll densities, and decline somewhat at lower latitudes. Offshore "blobs" of high *WW* decrease in density at lower latitudes, and are displaced to the northwest of the chlorophyll-*a* "blobs."

Laminarinase activity (*TLA*) (Fig. 1d) is generally higher in both the inshore and offshore regions surrounding the main high chlorophyll-*a* band. *TLA* shows higher values in the northwestern stations near the axis of offshore extensions. In the region of the offshore "blobs," *TLA* activity is highest where high *WW* overlaps high chlorophyll-*a* density.

Data for Pt. Conception, Leg 2 (Fig. 3) are much less extensive, but certain features are evident. Isotherms show a projection of cold water which is spatially coincident with the second offshore extension feature mapped during Leg 1, except
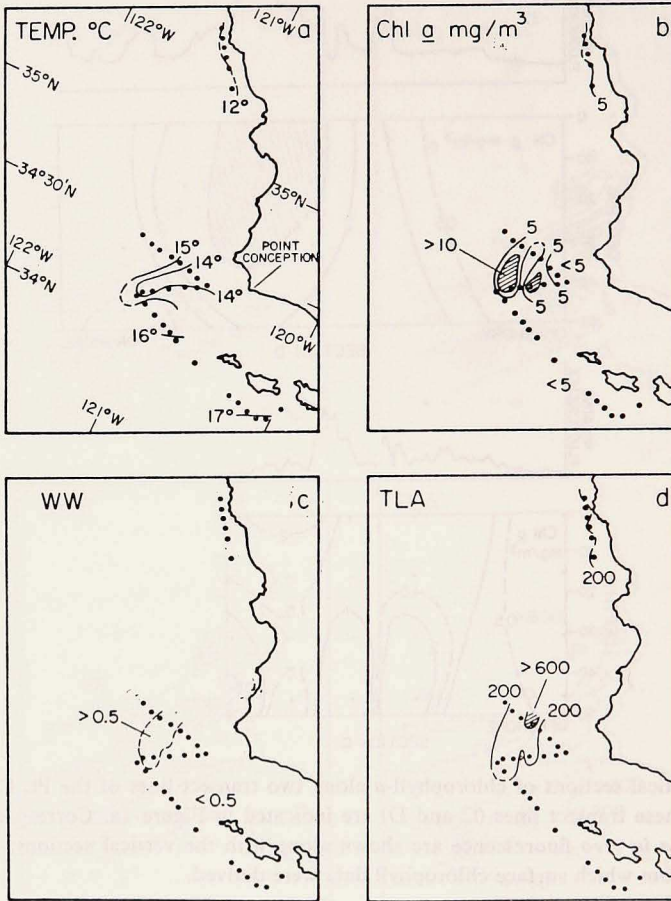
Figure 3. Contoured data for surface properties, Pt. Conception region, Leg 2. Survey was completed during 22-23 July 1979.

that the water is much warmer than in Leg 1, and the 14° and 15° isotherms are much closer to shore. This may be a result of weak or no upwelling caused either by the reduced winds experienced before and during the Leg 2 survey or by changes in wind direction unfavorable to upwelling. Two high chlorophyll-*a* features (Fig. 3b) are present. The outermost, centered at 14.7°C, is like the offshore "blobs" of Leg 1. Insufficient data are available to document the occurrence of the main band of high chlorophyll-*a* off Pt. Conception, but such a feature seems to be represented in the small series of stations closer to shore in the northern sector. Zooplankton densities (*WW*) are generally lower than during Leg 1, but are nonetheless consistent with the chlorophyll-*a* contours. *TLA* is somewhat higher north of the maximum chlorophyll-*a* densities. This distribution is similar to the Leg 1 data.
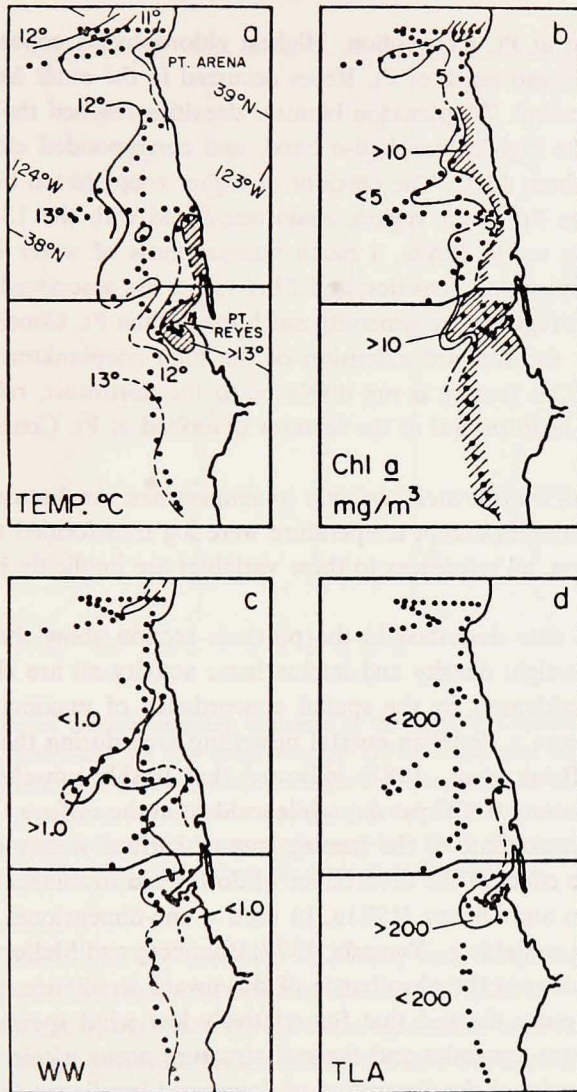
Figure 4. Contoured data for surface properties, Pt. Arena and Pt. Reyes. Surveys were completed during 21–22 July. Horizontal line through the middle of the figure divides the two sections. See text for explanation of dividing line.

Contour plots in the Pt. Arena and Pt. Reyes region (Fig. 4) are limited in their offshore scale, but show no evidence of offshore extensions such as those observed at Pt. Conception. Between Pt. Arena and Pt. Reyes, chlorophyll-*a* concentrations were high in an irregular band which is seemingly unrelated to coastal contours. This is to be expected because the bathymetry and coastline in this region are much

more regular than at Pt. Conception. Highest chlorophyll-*a* concentrations to the south of Pt. Arena and north of Pt. Reyes occurred in the outer half of the 11° to 12°C isotherm interval. Zooplankton biomass densities reached their highest values just seaward of the high chlorophyll-*a* band, and corresponded closely to a sharp thermal front at about 13°C. The corridor of higher zooplankton biomass extended southward into the Pt. Reyes region, again associated with the 13° isotherm. Immediately adjacent to Pt. Reyes, a much warmer mass of water is evident. High chlorophyll-*a*, zooplankton densities, and *TLA* values are associated with this water. *TLA* values in the region were generally much lower than Pt. Conception, and were only enhanced in the seaward extension of the high zooplankton biomass of Pt. Reyes (Fig. 4d). This feature is not displaced to the northwest, relative to chlorophyll-*a* and *WW*, as in several of the features described at Pt. Conception, Leg. 1.

*b. Relationships of transformed variables to temperature.* As discussed in the Methods section, all variables except temperature were log transformed to normalize the data. In this section, all references to these variables are implicitly in $\log_{10}$ form except where noted.

The contoured data described in the previous section show that chlorophyll-*a*, zooplankton wet weight density and laminarinase activity all are closely related to temperature, as evidenced by the spatial concordance of maxima with particular isotherms. Data from a Peruvian coastal upwelling area during the southern hemisphere summer (Brink *et al.*, 1981) indicated that freshly upwelled water in this region warmed at about 0.4°C per day while resident at the surface.

An independent estimate of the heating rate of surface waters can be obtained by considering the effect of the absorbance of downward irradiance on upper ocean structure. Simpson and Dickey (1981a, b) used a one-dimensional second moment turbulence closure model (e.g., Yamada, 1977; Blumberg and Mellor, 1980) to model the relationship between the absorbance of downward irradiance and upper ocean structure. Their results showed that for relatively low wind speeds ($\leq 10$ m s$^{-1}$) significantly different dynamics and thermal structure occur within the mixed layer when a realistic model of the absorption of downward irradiance (e.g., Paulson and Simpson, 1977) is used instead of the commonly used single exponential parameterization of downward irradiance (e.g., Denman, 1973). Recently, Dickey and Simpson (1982) simulated the diurnal response of the upper ocean with this model. Conditions for these simulations included (1) summer and winter thermal forcing typical of mid-latitudes, (2) constant and time-varying wind stresses, and (3) oceanic and coastal water type. The predicted diurnal variability in sea surface temperature was greatest in summer under low wind speed conditions. Most of the wind speeds measured during this study were between 4 and 8 m s$^{-1}$. Type III water (Jerlov, 1968) is typical of biologically productive coastal regions. For this water type and wind speeds within the observed range, the simulations predict a mean rate of heating
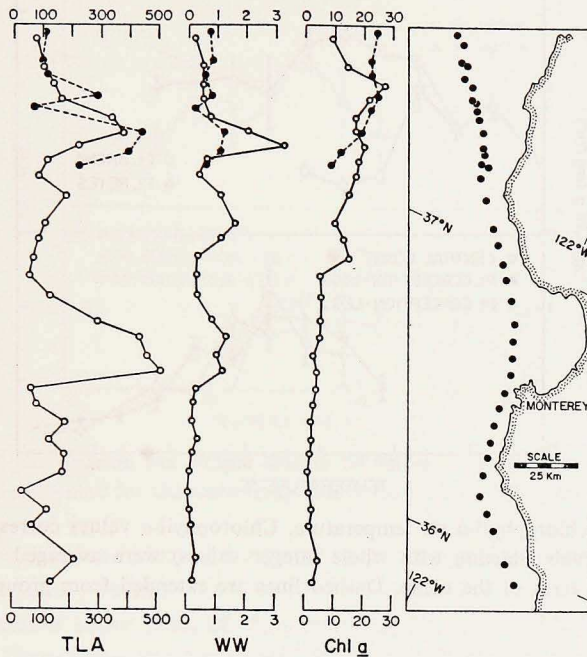
Figure 5. Locations of surface mapping transects in the Central California coastal region. In these transects, midpoints for the south-to-north (17-18 July) pass and north-to-south (22 July) pass fall along almost identical lines. Values for chlorophyll-a, zooplankton wet weight (*WW*), and *TLA* appear to the left and correspond to the sampling midpoint locations plotted on the chart. The solid lines with open circles are data from the transect to the south; the dashed lines connecting filled circles from the transect to the north.

between 0.4 to 0.6°C per day (see Fig. 2, Dickey and Simpson, 1982). This is in good agreement with the results reported by Brink *et al.* (1981).

Initially, one might be surprised by the close agreement between these two warming rates, given the geographical separation of the two experimental sites. However, an examination of the net surface heat flux for the two experiments supports this agreement. The net heat flux at the air-sea interface can be written as

$$Q_T = (1 - \alpha) Q_S - Q_{BN} - Q_L - Q_{SE}$$

where $Q_T$ is the total heat flux into the ocean, $Q_S$ is the incident solar flux, $\alpha$ is the albedo of the sea surface, $Q_{BN}$ is the net long-wave flux, and $Q_L$ and $Q_{SE}$ are the latent and sensible heat fluxes from the sea surface to the atmosphere. Mean climatological values of the total daily incident solar flux reaching the sea surface at 15S lat. (Peru experiment) for the period February-April are approximately 14.6% less than similar values for the Pt. Conception region for the period June-August (List, 1951). An estimate of the net long-wave flux was made from the Stefan-
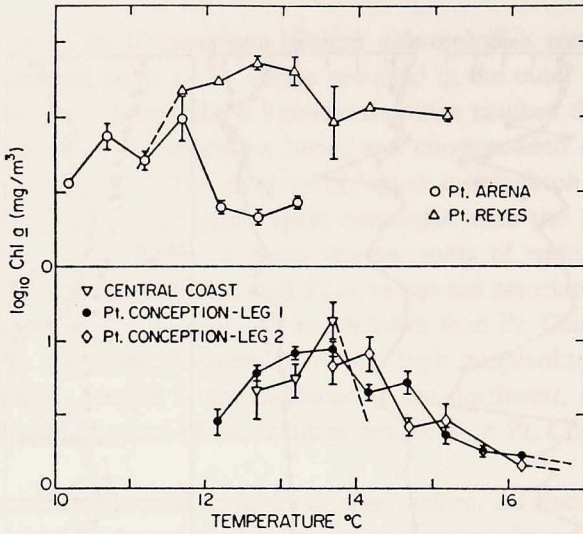
Figure 6. Plots of chlorophyll-*a* vs. temperature. Chlorophyll-*a* values corresponding to 0.5°C temperature intervals (starting with whole integer values) were averaged. Vertical brackets indicate standard error of the mean. Dashed lines are extended from grouped data to single data sets.

Boltzmann law. For this calculation a mean surface temperature of 17°C was assumed for the Peru region (Stuart *et al.*, 1976) and a mean temperature of 14°C was used for our study area. Under these assumptions, the net long-wave flux off Peru is approximately 4% greater than that off the California coast. The latent heat flux scales directly with the mean wind speed. This term is expected to be a small component of $Q_T$, given the observed wind speeds. Generally, the sensible heat flux is negligible over the open ocean (Friehe and Schmitt, 1976; Simpson and Paulson, 1979). Hence, the net total heat flux into the ocean off California during our observations is approximately 20% higher than the total heat flux off Peru during the observational period reported by Brink *et al.* (1981). The difference between our warming rate of 0.5°C per day and the warming rate of 0.4°C per day reported by Brink *et al.* (1981) is consistent with the above estimated difference in the total heat flux. A more detailed discussion of the surface thermal boundary condition over the ocean is given by Simpson and Paulson (1979).

We have no data to indicate the time interval represented by a 0.5°C warming of surface waters, or even if warming has a linear relationship with time. However, we will assume a warming rate of 0.5°C per day because it is consistent with both the observations of Brink *et al.* (1981) and the theoretical studies of Simpson and Dickey (1981a, b) and of Dickey and Simpson (1982). With this assumption, transformed values of chlorophyll-*a*, *WW*, and *TLA* were grouped by 0.5°C temperature intervals for each of the regions studied. This rate of heating (0.5°C per day)
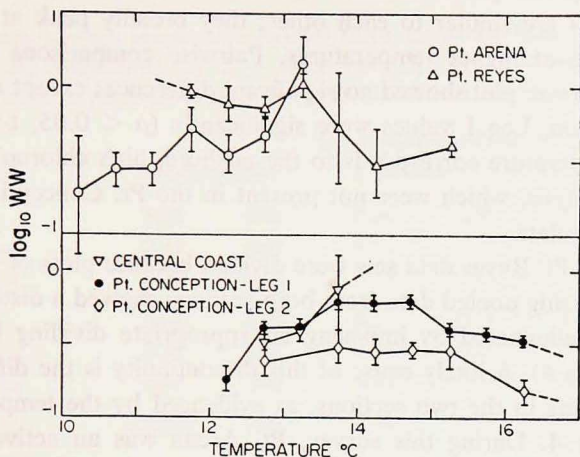
Figure 7. Plots of zooplankton wet weight density (*WW*) vs. temperature. Averages and standard errors were computed for the same temperature intervals as in Figure 6.

should serve as a relative index of temporal sequences which occurred within each region during the survey period.

Figures 6, 7 and 8 show plots of chlorophyll-*a*, *WW*, and *TLA* vs. temperature for each region. Data from Pt. Arena and Pt. Reyes showed patterns distinctly different from those in the Pt. Conception and in the Central Coast data, and hence
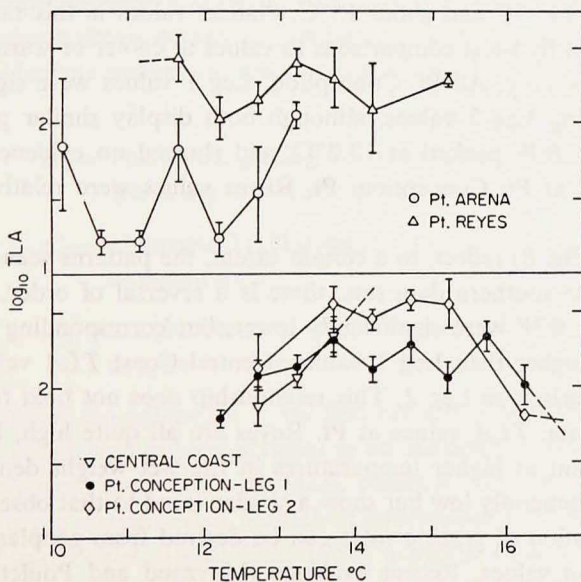


Figure 8. Plots of *TLA* ($\mu$g glucose/min m$^3$) vs. temperature, all regions. Averages and standard errors were computed for the same temperature as in Figure 6.

are plotted in separate panels in these figures. Chlorophyll-*a* values from the latter data sets (Fig. 6) are similar to each other; they broadly peak at 13°-14°C, then gradually decline at higher temperatures. Pairwise comparisons of chlorophyll-*a* values from the lower plot showed no significant differences except at 14.7°C, where the Pt. Conception, Leg 1 values were significantly ($p < 0.05$, t-test) higher than Leg 2. This temperature corresponds to the offshore, high chlorophyll-*a* "blobs" in the mapping analysis, which were not present in the Pt. Conception, Leg 2, or in the Central Coast data.

Pt. Arena and Pt. Reyes data sets were divided because plots of various variables vs. temperature using pooled data from both sections showed a distinct discontinuity which could be eliminated by imposing an appropriate dividing line between the two sections (Fig. 4). A likely cause of this discontinuity is the different dynamical processes occurring in the two sections, as evidenced by the temperature structure shown in Figure 4. During this survey, Pt. Arena was an active upwelling area while Pt. Reyes was not. In addition, major topographic differences between these two sections may contribute to the discontinuity. Chlorophyll-*a* patterns in these two northern sections were distinctly different from each other (Fig. 6). Pt. Reyes peaked broadly at 12.7°C, and was generally very high relative to all other areas. Pt. Arena chlorophyll-*a* peaked at 11.7°C, and declined sharply at higher temperatures. Both these patterns showed significant differences from the southern patterns as determined by pairwise t-test comparisons at overlapping temperatures.

Zooplankton wet weight densities (*WW*) showed similar patterns in the southern data sets (Fig. 7), reaching maximum values at 13.7°C, and exhibiting a broad plateau between 13.7°C and about 15°C. Plateau values in this range were all significantly different by t-test comparisons to values at cooler or warmer temperatures within the same survey. All Pt. Conception, Leg 1 values were significantly higher than corresponding Leg 2 values, although both display similar patterns. The Pt. Arena values for *WW* peaked at 13.2°C, and showed no evidence of the plateau pattern observed at Pt. Conception. Pt. Reyes values were relatively constant up to 13.2°C.

*TLA* values (Fig. 8) reflect, to a certain extent, the patterns seen in *WW* (Fig. 7). In the case of the southern data sets, there is a reversal of order. Pt. Conception, Leg 2 values for *WW* were significantly lower, but corresponding *TLA* values are all significantly higher than Leg 1 values. Central Coast *TLA* values are also depressed in comparison to Leg 2. This relationship does not hold for the Pt. Arena and Pt. Reyes data. *TLA* values at Pt. Reyes are all quite high, but do not show the decline evident at higher temperatures in the wet weight densities. Pt. Arena *TLA* values are generally low but show a similar trend to that observed in *WW*.

An approximation of grazing rates can be derived from zooplankton wet weight and chlorophyll-*a* values. Recent evidence (Mayzaud and Poulet, 1978) suggests that grazing rate per unit of zooplankton biomass is a linear function of phytoplank-

Table 1. Correlations between temperature-interval mean values for $TLA_T$, $Z_T$ and $C_T$ for different values of the temperature lag, $T$. A temperature lag of 0.5°C corresponds to a time lag of 1 day. Number in parentheses refer to number of means used in statistical estimate.

|  | Both regions | | Correlation coefficients<br>Southern | | Northern | |
|---|---|---|---|---|---|---|
| Correlation | | | | | | |
| $TLA_T$ vs. $Z_T$ | 0.58 | (40) | 0.84 | (25) | 0.48* | (15) |
| $TLA_T$ vs. $Z_{T-0.5}$ | 0.58 | (34) | 0.72 | (22) | 0.75 | (12) |
| $TLA_T$ vs. $Z_{T-1}$ | 0.48 | (30) | 0.53 | (19) | 0.68 | (11) |
| $TLA_T$ vs. $C_T$ | 0.46 | (40) | 0.57 | (25) | 0.52 | (15) |
| $TLA_T$ vs. $C_{T-0.5}$ | 0.48 | (34) | 0.70 | (22) | 0.43* | (12) |
| $TLA_T$ vs. $C_{T-1}$ | 0.67 | (30) | 0.82 | (19) | 0.82 | (11) |
| $Z_T$ vs. $C_T$ | −0.03* | (40) | 0.59 | (25) | 0.27* | (15) |
| $TLA_T$ vs. $Z_T\,C_T$ | 0.59 | (40) | 0.79 | (25) | 0.63 | (15) |
| $TLA_T$ vs. $Z_{T-0.5}\,C_{T-0.5}$ | 0.42 | (34) | 0.78 | (22) | 0.63 | (12) |
| $TLA_T$ vs. $Z_{T-1}\,C_{T-1}$ | 0.68 | (30) | 0.89 | (19) | 0.86 | (11) |

\* Correlation coefficients which are nonsignificant at 95% level.

ton density. In dimensional terms, this function can be expressed:

$$mg(\text{chl-}a) \cdot (g(gWW))^{-1} \cdot (\sec(\text{time}))^{-1} = s \cdot mg(\text{chl-}a) \cdot m^{-3} \qquad (1)$$

where $s$ (units of $g^{-1}\ m^3\ sec^{-1}$) is the slope of the line passing through the origin. Grazing rate per unit volume of seawater then becomes a function of the product of the index of phytoplankton density (chl-$a$(mg m$^{-3}$)) and zooplankton wet weight density ($WW$). Absolute volumetric grazing rate, referred to hereafter as $G$, can be expressed as:

$$G_T = s\,Z_T C_T \qquad \begin{aligned} &G_T = \text{volumetric grazing rate at mean temperature } T \\ &\quad (\text{chl-}a \text{ mg m}^{-3} \text{ time}^{-1}) \end{aligned} \qquad (2)$$

$$C_T = \text{chlorophyll (chl-}a \text{ mg m}^{-3}) \text{ at mean}$$
$$\text{temperature } T.$$

$$Z_T = \text{zooplankton wet weight density, } WW \text{ (g m}^{-3})$$
$$\text{at mean temperature } T.$$

Since we didn't know the values for $s$, we first examined the relationship of $Z_T C_T$ to a relative $G_T$, assuming $s$ to be equivalent to an unknown constant for all regions.

Values of $Z_T C_T$ were compared with $TLA_T$ values to see if approximated grazing rates were reflected in enzyme rates. Published information (Mayzaud and Conover, 1976; Mayzaud and Poulet, 1978; Cox, 1981) suggests $TLA$ should reflect *prior* grazing activity, so "temperature lag" correlations were also examined. The correlation coefficients computed from the "temperature mean" data (Table 1) show that the highest correlations are obtained in comparisons of $TLA_T$ with $Z_{T-1}\ C_{T-1}$. If
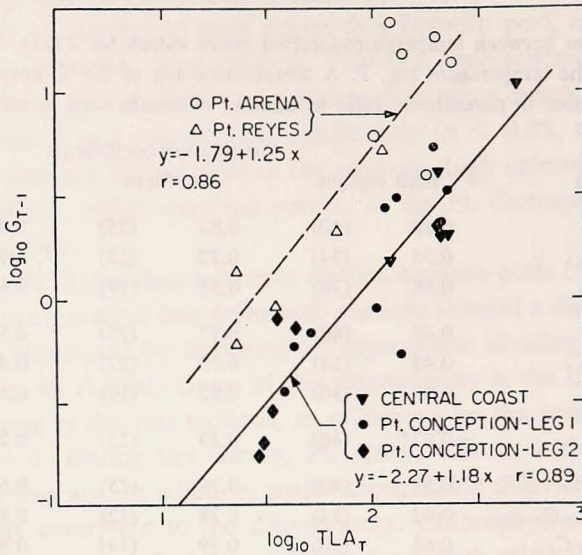
Figure 9. Regressions of $G_{T-1}$, defined as $\log_{10}$ [chl-$a$, mg m$^{-3}$]$_{T-1}$ [WW zooplankton, g m$^{-3}$]$_{T-1}$ against $\log_{10}$ $TLA_T$. Values for the two northern sections appeared to represent a distinctly different relationship when compared to the three more southerly surveys, and thus were regressed separately.

we accept the approximate temporal equivalency of 0.5°C/day, this means that $TLA$ values best represent grazing activity from about two days prior to the time of sample collection. This time lag corresponds well with laboratory experimental data on the time for induction of laminarinase activity (Cox, 1981; Cox and Willason, 1981).

The correlation coefficients indicate some differences in the northern and southern data sets. As might be expected, $TLA_T$ and $Z_T$ have a high correlation, since $Z_T$ is a component in the calculation of $TLA_T$. This is only true, however, for the southern data. Northern data show a nonsignificant correlation, indicating that $LA$ is a more important component in the determination of $TLA$ values in that region. Correlations between $TLA_T$ and $C_{T-1}$ indicate that, for each region, $C_{T-1}$ is the most important component in determining the relationship between $TLA_T$ and $Z_{T-1}$ $C_{T-1}$. Lower correlation coefficients are obtained in each case for pooled data, indicating that the relationships are different by region, as shown in the regression plot (Fig. 9), a result which might be expected from the very different patterns shown in these regions. Confidence intervals for the slopes and intercepts appear in Table 2.

Although highest values of the correlation coefficient are indicated for a $T$-1 lag, conclusions regarding the lag in laminarinase parameters compared to grazing estimates should be interpreted with caution. The correlation coefficients for $T$-0.5 and

Table 2. Regression statistics and comparisons for $G_{T-1}$ vs. $TLA_T$.

| Area | y-intercept (±S.E.) | $p^a$ | slope (±S.E.) | $p^a$ |
|------|------|------|------|------|
| Pt. Arena and Pt. Reyes | −1.79 (±0.42) | | 1.25 (±0.25) | |
| | | <0.01 | | >0.15 |
| Pt. Conception (Leg 1&2) and Central Coast | −2.27 (±0.34) | | 1.18 (±0.15) | |

a. $H_o$: $x_1 = x_2$, t-test.

no lag are also high so that, while the basic conclusion that enzyme parameters are related to grazing rate may be valid, the lag period itself is an issue which will require further study. Also, our initial assumption that $s$ is constant is almost certainly a source of error with regard to these comparisons.

The correlation between $TLA_T$ and $Z_T C_T$ values documents the relationship of grazing activity to laminarinase measurements, but without appropriate values for $s$, $G_T$ cannot be expressed in absolute terms. To obtain approximate absolute values of $G_T$, calculations were performed to obtain another, independent estimate of absolute grazing rate. In upwelling areas, such as off Peru and southern California, rates of phytoplankton doubling from 1.0 to 2.0 $d^{-1}$ have been observed (Walsh, 1976; Walsh *et al.*, 1980; Eppley *et al.*, 1977). Assuming a doubling rate of 1.5 as a constant condition throughout our survey, we calculated potential rates of chlorophyll-*a* increase for successive values of $T$ for each mean value of chlorophyll-*a* shown in Figure 6, according to the following relationship:

$$CE_T = C_{T-0.5} + 1.5 C_{T-0.5} \qquad CE_T = \text{expected chlorophyll-}a \text{ (mg m}^{-3}) \qquad (3)$$
$$\text{at temperature } T \text{ if no grazing}$$
$$\text{removal occurred}$$

$$C_{T-0.5} = \text{Chlorophyll-}a \text{ (mg m}^{-3}) \text{ at } T\text{-}0.5°C.$$

Grazing rate per unit volume of seawater, designated $G'_T$, was calculated according to:

$$G'_T = CE_T - C_T . \qquad (4)$$

$G'_T$ and $Z_T C_T$ showed a highly significant correlation ($r = 0.92$), and the regression relationship was $G'_T = 3.37 + 1.69 (Z_T C_T)$. It should be noted that these two variables might be expected to show high correlation, since $C_T$ is a component of $G'_T$. However, all correlations of $C_T$ with $CE_T - C_T$ by individual area or by all areas combined were not different from zero at the 95% confidence level; the quantity $CE_T - C_T$ therefore is statistically independent of $C_T$.

The value for the slope of the regression relationship is equivalent to the slope, $s$ (Eqs. (1) and (2)). Addition of the Pt. Reyes data to the pooled data biases the
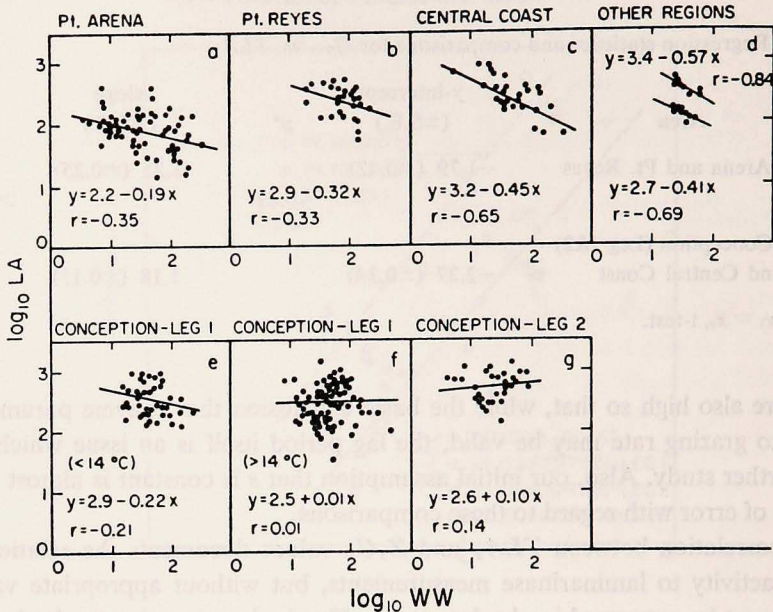
Figure 10. Regressions of $\log_{10} LA$, against $\log_{10} WW$ for various surveys. Data in plot "d" were taken from Cox (1981) and are used for comparison.

slope estimate considerably. With the Pt. Reyes data deleted, the regression relationship becomes $G_T' = 0.53 + 3.53 (Z_T C_T)$ $(r = 0.89)$, indicating that the higher $C_T$ values of the Pt. Reyes data set may have caused saturation of the grazing function. Both slope estimates correspond well with estimates of $s$, using natural particulate matter, derivable from literature sources (e.g., $s = 2$ to 4, from Adams and Steele, 1966).

*c. LA and zooplankton biomass density.* $LA$, or laminarinase activity per unit of sample weight ($\mu$g glucose g$^{-1} \cdot$ min$^{-1}$) in a previous study showed an inverse relationship with zooplankton wet weight density, $WW$ (Cox, 1981). This relationship is also observed in plots of log transformed $LA$ vs. log transformed $WW$ (Fig. 10), in all regions except Pt. Conception, Leg 1 and 2, where regressions showed no significant negative correlation (F test, $< 0.05$). Pooled Pt. Conception, Leg 1 data (all temperatures) yielded a slope which was not significantly different from zero. The data was divided at 14°C, to see if values from lower temperatures would yield the negative correlation seen in more northerly, and generally cooler data subsets. This was found to be the case (Fig. 10e and f), although the correlation coefficient is considerably lower than in the more northerly data sets. Pt. Conception, Leg 2 data (Fig. 10g) cover the same temperature range as the warmer ($> 14$°C) data set from Leg 1 (Fig. 10f), and slopes of both regressions are not significantly different from zero.

## 4. Discussion

The contoured data showed that offshore extensions of upwelling are observable at Pt. Conception. Headlands and nearshore topographic features can fix their position of departure (Arthur, 1965; Peffley and O'Brien, 1976; O'Brien et al., 1977) and wind may affect their offshore extent and degree of development. Pt. Conception bathymetry and coastline may enhance the formation of offshore extensions.

The processes which regulate phytoplankton production in the extensions are likely to be the same as in the mainstream of zonal upwelling along the coast. This appears to be true for the central coast data and the southern region, where chlorophyll-a vs. temperature patterns overlap (Fig. 6). Qualitative differences, however, are evident in the comparison of the northern and southern data, where development of a chlorophyll-a peak occurs at a cooler temperature but at approximately the same distance from shore. This is undoubtedly a reflection of a general latitudinal gradient in surface temperature along the coast. In the north, chlorophyll-a peaks sharply at the thermal front region except for the Pt. Reyes data which show high inshore chlorophyll-a concentrations as well.

Peaks of zooplankton concentration, in the case of zonal upwelling bands, are located just seaward of the high chlorophyll-a band. Peak abundances are apparently due to behavioral aggregation, a phenomenon we will refer to as "localization." Localization has been interpreted as a result of vertical migratory responses within the upwelling circulation regime (Peterson et al., 1979). The potential benefit of localization suggests that it may be an important survival feature for grazers in eastern boundary currents. Localization continuously re-establishes contact between zooplankton which ride the current equatorward and phytoplankton populations which are dispersing seaward from the upwelling core.

When such a system is not disturbed by the formation of offshore extensions, the result may be a prolonged co-occurrence of grazing zooplankters with their phytoplankton food supply. Co-existence of zooplankton and phytoplankton in the same water mass for a period of several days is a necessary but not sufficient condition for an approach to equilibrium between grazing rate per unit volume and phytoplankton production rate per unit volume. Near equilibrium, assuming a constant rate for phytoplankton doubling, $G$ (volumetric grazing rate) should be relatively constant, regardless of zooplankton density. A constant value of $G$ should be reflected in relatively constant values of $TLA$, and consequently, an inverse relationship between $LA$ and zooplankton wet weight density.

Inverse relationships of $LA$ and $WW$ of zooplankton are evident in all of the regions studied, except for the Pt. Conception region (Fig. 10). Because $TLA$ is the product of $WW$ and $LA$, equilibrium conditions would predict:

$$LA \cdot WW = k \qquad\qquad (5)$$
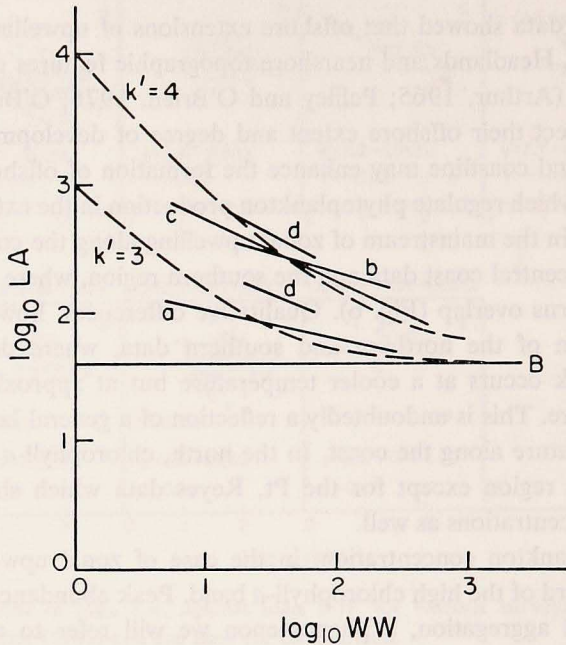
or, $\log (LA) + \log (WW) = \log k$ .

Figure 11. Regression lines from Figure 10 superimposed on theoretical $\log_{10} LA$ vs. $\log_{10} WW$ function. See text for computation of theoretical functions. Regression lines are labelled according to letter key shown in Figure 10; theoretical functions are shown as dashed lines, which approach lower limit "B" asymptotically.

Such a relationship would yield a slope of $-1$ on a log-log plot; observed slopes are much less. We interpret the observed slopes as resulting from a minimum, non-zero value of $LA$ which is observable at zero grazing. Data from laboratory studies of *Calanus pacificus* show that starvation reduces $LA$ to a level significantly higher than zero (Cox and Willason, 1981). During starvation, $LA$ levels out and remains roughly constant at about 40 $\mu$g glucose $gWW^{-1}$ min$^{-1}$. Accepting this value as the constant $B$, the equilibrium relationship of the equation can be rewritten:

$$\log (LA-B) + \log (WW) = \log k = k' \qquad (6)$$

which reduces to a nonlinear set of functions for different values of $k'$ (Fig. 11). Linear regression functions from Figure 10 are superimposed showing that they are approximately tangential to this set of curves. The two data sets from Cox (1981) were taken from geographically limited areas (Fig. 10d) and thus show very tight data fits. The clear inverse relationship shown indicates that equilibrium conditions were prevailing. Of the regional data sets, the central coast (Fig. 10c) shows the best fit to the expected function.

Equilibrium conditions between phytoplankton production and zooplankton graz-

ing rates must persist for at least two days for zooplankton ingestion rates to be reflected in values of $LA$. Since the inverse relationship of $LA$ and $WW$ is *not* detectable in the Pt. Conception data, it can be concluded that either co-occurrence of less than two days under equilibrium conditions is prevalent, or that equilibrium is not achieved.

Localization behavior tends to prolong co-occurrence between phytoplankton and zooplankton in zonal upwelling regions, such as in the Pt. Reyes-Pt. Arena area. Here equilibrium conditions appear to be achieved. However, the formation of upwelling extensions, such as at Pt. Conception, appears to interfere with this behavior and prevents achievement of equilibrium. A possible interpretation of localization suggests that zooplankton migrate up into the spreading layer and stay there until a critical temperature, indicative of post-bloom conditions, occurs. At that temperature, they migrate down and ride shoreward currents back to the general vicinity of the upwelling core. Such a sequence of events should be less effective within an upwelling extension, because of the complexity of water circulation in such a structure.

Both zooplankton wet weight densities ($WW$) and $TLA$ are displaced to the north and northwest of the extensions and their terminal chlorophyll "blobs." This could be due to circulation patterns resulting from translocation of these features. Such wake effects have been documented for cold core rings in the Sargasso Sea (Wiebe and Boyd, 1978). Interestingly, $TLA$ is highest where high $WW$ overlaps high chlorophyll-*a* densities (Fig. 1).

Surface observations, as these examples demonstrate, can reveal important mesoscale and larger features in regions where surface distributions reflect the prevailing physical dynamics. Zooplankton populations, however, show significant vertical structure, much of which is related to population maintenance within the coastal circulation regime (Peterson *et al.*, 1979). Biomass and laminarinase activity patterns of unsorted plankton samples from the surface, such as presented here, provide only a small part of the features important to the dynamics of the zooplankton populations.

Species differences between the southern region and the Pt. Arena-Pt. Reyes area are important for interpreting the data sets. These regions appear to be fundamentally different grazing regimes. The northern regions, which show chlorophyll and $WW$ maxima at lower temperatures (Figs. 6 and 7) and a significantly different relationship between $TLA_T$ and $G_{T-1}$ (Fig. 9), have reduced numbers of *Calanus pacificus*, while *Acartia* is the dominant species. In contrast, the southern region is overwhelmingly dominated by *C. pacificus* and early developmental stages of euphausiids. Such differences may be responsible for different localization patterns in the various regions.

Species differences between regions in other grazing organisms not known to have laminarinase, or in predators, could also have an important impact on the

observed systems. Larvaceans were the numerically dominant plankton in the near-shore areas of both regions; doliolids were more abundant in the southern region. Among predators, chaetognaths, medusae and siphonophores were more abundant (relative to grazer abundance) off Pt. Conception.

## 5. Summary and conclusions

Analysis of 20 days of continuous underway data consisting of temperature, chlorophyll-*a*, zooplankton wet weight densities, laminarinase activity per unit zooplankton wet weight, and laminarinase activity per unit volume of seawater, taken as part of the California Coastal Fronts Program during July 1979, yields the following results:

1) Enzyme activities of laminarinase in zooplankton samples reflect grazing intensity with a time lag of approximately two days.

2) Zooplankton grazers of different regions along the California coast show fundamental differences in aggregation and digestive enzyme activity in response to high concentrations of chlorophyll-*a*. These differences may be related to the temperature at which highest chlorophyll concentrations are achieved in these different coastal upwelling regions.

3) The formation of upwelling extensions at headlands such as Pt. Conception tends to disturb mechanisms which promote co-occurrence of high zooplankton and phytoplankton densities. These mechanisms are effective in zonal upwelling, and may result in continuous co-occurrence of zooplankton and phytoplankton within the same water mass for a period exceeding two days. The ordered coherence of this spatial pattern is apparently disrupted by formation of the southwesterly-directed extensions.

4) Extension formation may act to disperse zooplankton away from the zonal upwelling axis; this may result in the formation of offshore high chlorophyll regions which are less effectively grazed than phytoplankton in the main axis of zonal upwelling.

5) Approach to equilibrium conditions in upwelling regions between zooplankton grazing rates and phytoplankton production is a function both of zooplankton localization behavior and of the circulation patterns associated with upwelling. A complex interplay between these two factors determines whether or not equilibrium is ever approached.

6) The degree of spatial coherence between phytoplankton and zooplankton populations in a given upwelling area appears to provide an independent indicator of the level of complexity of the prevailing physical dynamics in that area.

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