

LONGSHORE VARIATION IN THE DISTRIBUTION OF PLANKTON IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

The similarity of plankton samples, in terms of abundances and faunal composition, was studied as a function of distance from 100 m to 10 km by sampling with pumps from two ships simultaneously. The biomass of phytoplankton and abundances of several (but not all) zooplankters become more dissimilar the greater the separation between samples. The faunal composition changed with distance during the day but not at night.

INTRODUCTION

Knowledge of the spatial scales on which the abundance or composition of plankton changes significantly has practical importance in planning the spacing of biological oceanographic sampling stations in order to characterize a region or to detect the effects of a natural or anthropogenic perturbation (e.g. Weibe et al. 1973). It has conceptual importance in view of the intimate relation between patches or layers of abundant food and the survival and growth of zooplankton and larval fish (e.g. Mullin and Brooks 1972; Lasker 1975). In coastal waters, onshore-offshore gradients in biomass and species composition have often been observed (e.g. Eppley et al. 1977); less well known is the nature of longshore changes.

Platt et al. (1970) found that the variability in biomass of coastal phytoplankton increased as the area within which samples were taken increased to 2.6 km², and then became constant up to 10.4 km². Our original intent, stimulated by these results, was to determine whether a particularly important scale of spatial variation could be detected by departures from a simple, linear correlation between the degree of dissimilarity of two samples and their separation. Computer simulations later indicated, however, that even if patches of uniform size (but of various concentrations) had been superimposed on a "background" of uniform, low concentration, we would have been unable to distinguish the size of these patches with our sampling program.

METHODS

In March 1976, we took simultaneous samples of plankton from two ships (the R/V *David Starr Jordan* and the R/V *Townsend Cromwell*). Each pair of stations consisted of samples taken every 5 m from the surface to 35 m while the ships were separated by a known distance. This distance was varied such that spatial separations

from 100 m to 10 km in longshore direction were achieved between stations both day and night. The depth of the bottom exceeded 50 m throughout the study, and the separations were chosen haphazardly over the 8 days of the cruise. From 17 through 18 March, the *Jordan* followed a cruciform drogue set at 17 m; from 19 through 25 March, the *Jordan* was at a geographically fixed station off Del Mar, California. On 24 March, sets of consecutive samples of zooplankton were taken from two fixed depths, and the records of a nearby current meter were used to determine the spacing between these samples.

Water from each depth was drawn by a diaphragm pump through a 7.5-cm diameter, plastic hose at 150 liters/minute and was collected in two 200-liter plastic tubs. After the temperature had been measured, one 50-ml aliquot was filtered through a Whatman® GF/C glass fiber filter (1-2 μm retention, the catch hereafter called "total"), and another through a Gelman® polycarbonate filter of 5 μm retention (the catch hereafter called ">5 μm"). Powdered MgCO₃ was added to both filters, which were then stored in 90% aqueous acetone in a refrigerator for at least 24 hours. After centrifugation, the extracted chlorophyll and phaeophytin in the supernatant were determined by fluorometry (cf. Mullin and Brooks 1976). Approximately 350 liters of water collected from each depth was drained from the tubs through a flow meter into a 73 μm-meshed net, and the catch was preserved in ~5% Formalin-seawater for subsequent counting.

Hypotheses concerning vertical versus horizontal variation were tested by comparing the range of conditions to be found over all depths at any station to the range at any depth over all stations and dates.

As an index of the dissimilarity between any two simultaneous measurements at a particular depth, the absolute value of their difference divided by their sum was used. This index can range from 0 for identical data to .+1 where one of the pair is zero; although the index is slightly nonlinear, it is relatively independent of the magnitude of the measurements. It is a poor index if many pairs include one zero, but this was the case only once in the data we used. The relation between this index of dissimilarity and the horizontal distance between measurements was then examined through linear regression. Note that in this analysis, the pairs of measurements of a property from each depth are treated as replicates for one scale of separation, i.e. the particular depth from which a pair was

taken is unimportant. The implicit assumption is that variation is on a similar scale at all depths sampled.

The percent similarity index (cf. Miller 1970) was also used to compare the relative proportions of different kinds of zooplankton in pairs of samples; this index is a measure of relative composition and is insensitive to absolute differences in abundance between the samples.

The samples of zooplankton were randomized and counted without knowledge of the identity of the sample. The categories of zooplankton counted, and thus contributing to the percent similarity index, were twelve developmental stages of the copepod, *Calanus pacificus*; adult *Corycaeus anglicus* (copepod); total *Evadne* (cladoceran); total *Sagitta* (chætogonath); and total larvaceans. For calculating the index of dissimilarity as a function of distance, we used as one category the sum of *Calanus* naupliar stages, and the *Evadne*, *Corycaeus*, *Sagitta*, and larvacean categories. These categories were chosen to avoid many zeros and ranged typically from a few tens to several hundreds (*Calanus*, *Corycaeus*, chætogonaths) or thousands (*Evadne*, larvaceans) of individuals per m³. In samples separated by 0.1 km and ~9 km, the copepodid stages of *Acartia tonsa* were also counted.

RESULTS

The data are suitable for examining the nature of the relation between large and small phytoplankton. The simplest hypothesis is that $>5 \mu\text{m}$ chlorophyll is a constant fraction of total chlorophyll; an alternative hypothesis (e.g. Malone 1971) is that large cells are particularly important when the total crop is large. In the latter case, a regression of $\log(>5 \mu\text{m}$ chlorophyll) on $\log(\text{total chlorophyll})$ should have a slope of >1.0 . When all data ($n = 231$) are pooled, the calculated slope is 1.02, but the 95% confidence limits include 1.0. Hence, the simplest interpretation is that $>5 \mu\text{m}$ chlorophyll is a fixed proportion of total chlorophyll, independent of crop size (in this case 47%).

Figure 1 shows the vertical distribution of temperature for each pair of stations, arranged according to increasing separation of the pair. The associated dates show the haphazard timing of pairs during the 8 days of the study. The haphazard arrangement reduces the likelihood that a unidirectional, temporal change in the area would appear to be a simple function of separation. In an ideal study, all samples would be synoptic.

Profiles of temperature varied somewhat between stations but were sufficiently similar that median range of temperature at each depth was less than the median range over 35 m at each station ($p = 0.013$ for one-tailed, rank sum test on ranges). This means, unsurprisingly, that the vertical variation in temperature exceeded that horizontally and temporally.

The same tendency was true for chlorophyll; the hori-

zontal and temporal variation (as measured by the range) at a depth was less than the variation in the upper 35 m of the typical station. However, the difference was not statistically significant ($p = 0.08$ for one-tailed rank sum test on ranges). Thus, a population of zooplankton distributed vertically throughout the upper 35 m would typically experience at least as wide a range of conditions at a single station as would a population confined to a single depth throughout the study.

Similarity in temperature is one indication of physical similarity between stations. The indices of dissimilarity for temperatures measured 0.1 km apart were no less than

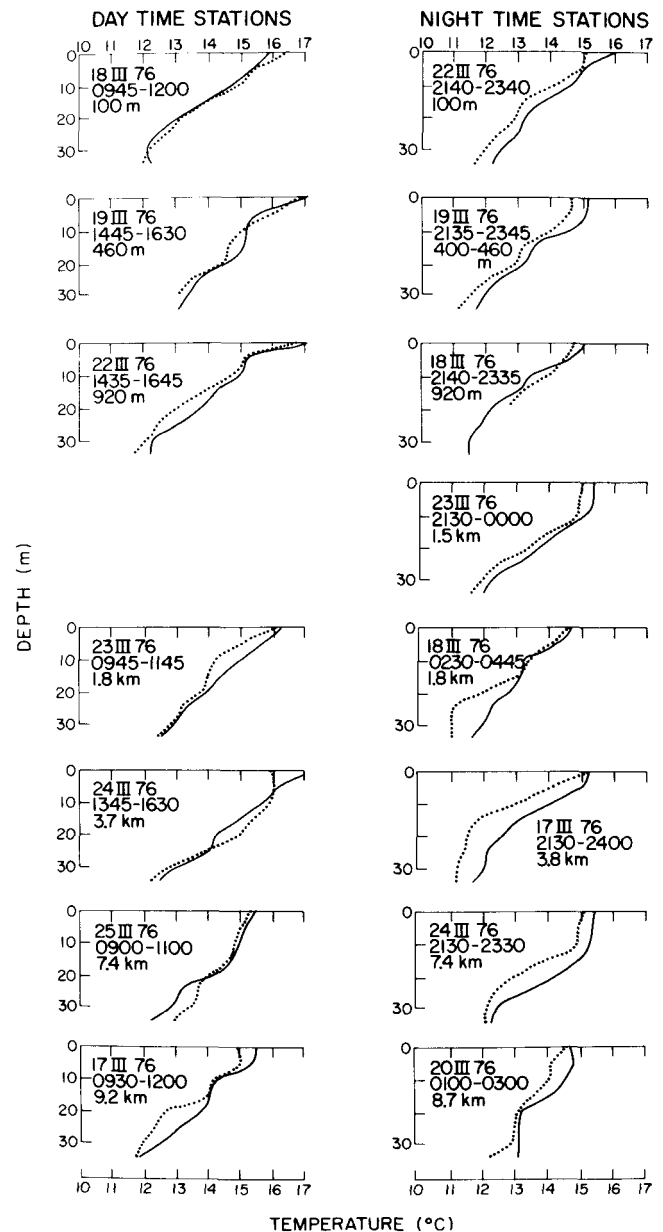


Figure 1. Profiles of temperature measured simultaneously on the R/V David Starr Jordan (solid line) and R/V Townsend Cromwell (dotted line) separated by different distances.

the indices for measurements 8.7 and 9.2 km apart ($p = 0.34$ for one-tailed, rank sum test). Further, there was no significant correlation between index and distance in the complete set of data ($r = 0.1$ for $n = 115$, $p > 0.1$ of no correlation). The stations farthest apart were thus as similar, in terms of temperature, as the stations nearest to each other.

This was not the case for either total or $>5 \mu\text{m}$ chlorophyll; the concentrations measured 0.1 km apart were less different than those measured 8.7 and 9.2 km apart, and there was a significant, positive correlation between index of dissimilarity and spatial separation ($p < 0.05$ for all 4 tests). Thus, concentrations of chlorophyll at a given depth at stations far apart were generally more dissimilar than those at stations close together (Figure 2). This trend obviously has an upper limit at some distance, since concentrations never become infinitely large or small. Relations other than a linear one between distance and dissimilarity in chlorophyll were tested; in some cases these accounted for more variability than did the linear relation, but the improvement was not statistically significant by F test.

The abundances of *Corycaeus* and the larvaceans did not become more variable with distance (i.e. no significant correlation between dissimilarity and separation), but the variability in *Calanus* nauplii, *Evadne*, and *Sagitta* increased ($p < 0.05$ of no correlation for $n = 97$). As noted above, this trend must have an upper limit at some greater distance. The relations for *Calanus* and *Evadne* are shown in Figure 3.

This result would be obtained if *Corycaeus* and the larvaceans were much less variable at all distances sampled than were the other three categories. However, the indices of dissimilarity refute this explanation; these indices for the larvaceans at 0.1 and 1.0 km separation are less than the comparable indices for *Calanus*, *Evadne*, and *Sagitta*, but the indices for *Corycaeus* are greater.

It therefore seems that the predominant scales of variability fall into three groups: 1) The larvaceans were relatively homogeneous in distribution at all scales sampled; 2) *Calanus*, *Evadne*, and *Sagitta* became more variable with increasing distance; and 3) *Corycaeus* was relatively variable even in closely spaced samples. There is no obvious, biological reason for this; the two carnivores (*Sagitta*, *Corycaeus*), the two most narrowly defined categories (*Calanus*, *Corycaeus*), the two most abundant categories (*Evadne*, larvaceans), and the two categories with the most consistent gradient in abundance with depth (*Evadne* and larvaceans, both of which were usually much more abundant in the upper 10 m than at 30-35 m) all split into different groups.

The percent similarity index, which is based on the relative abundances of the 16 counted categories (i.e. each developmental stage of *Calanus* treated as a dis-

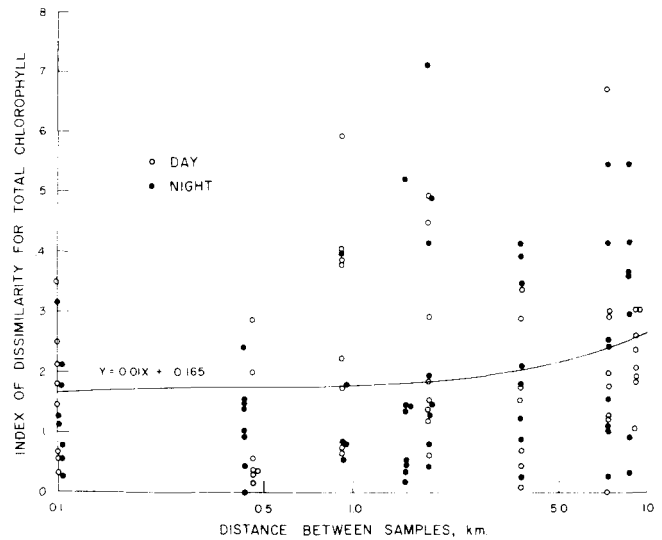


Figure 2. Index of dissimilarity ($|A-B| / (A+B)$) as a function of distance. The linear relation appears curved on the semi-logarithmic plot.

tinct entity) decreased from 82% for the nearest samples to 68% for the farthest (Figure 3). Even at almost 10 km, however, some samples were very similar (index $> 85\%$).

It is not surprising that samples taken far apart are less similar in composition than those taken close together. When day and night are treated separately, however, an interesting aspect emerges. The samples taken at night show no decrease in percent similarity with increasing separation ($p > 0.1$ of no correlation), while samples taken during the day are increasingly similar as they are closer together ($p < 0.01$ of no correlation). For the daytime samples alone, the linear regression equation is $Y = -1.97X + 82.7$, where X is separation in km and Y is percent similarity index. The slopes of the linear regressions for daytime and nighttime data are significantly different. Recalculation of percent similarity indices to include available data on *Acartia* copepodites indicates that the pattern is maintained in spite of this addition.

This finding is interestingly, though probably coincidentally, like that of Miller (1970), who studied change in percent similarity index over time while following a "migrating" drogue. Miller's results indicated that the decrease in similarity with time at 100 m occurred primarily during the daylight hours; the temporal decay in similarity appeared to be suspended at night.

DISCUSSION

We do not know how general these results will prove to be, in terms of applicability to other seasons or other coasts. Based on our results, simultaneous samples from specific depths within one or two kilometers of each other in a longshore direction are likely to be as similar as samples spaced more closely; at greater separation, samples are increasingly likely to be dissimilar in abundance

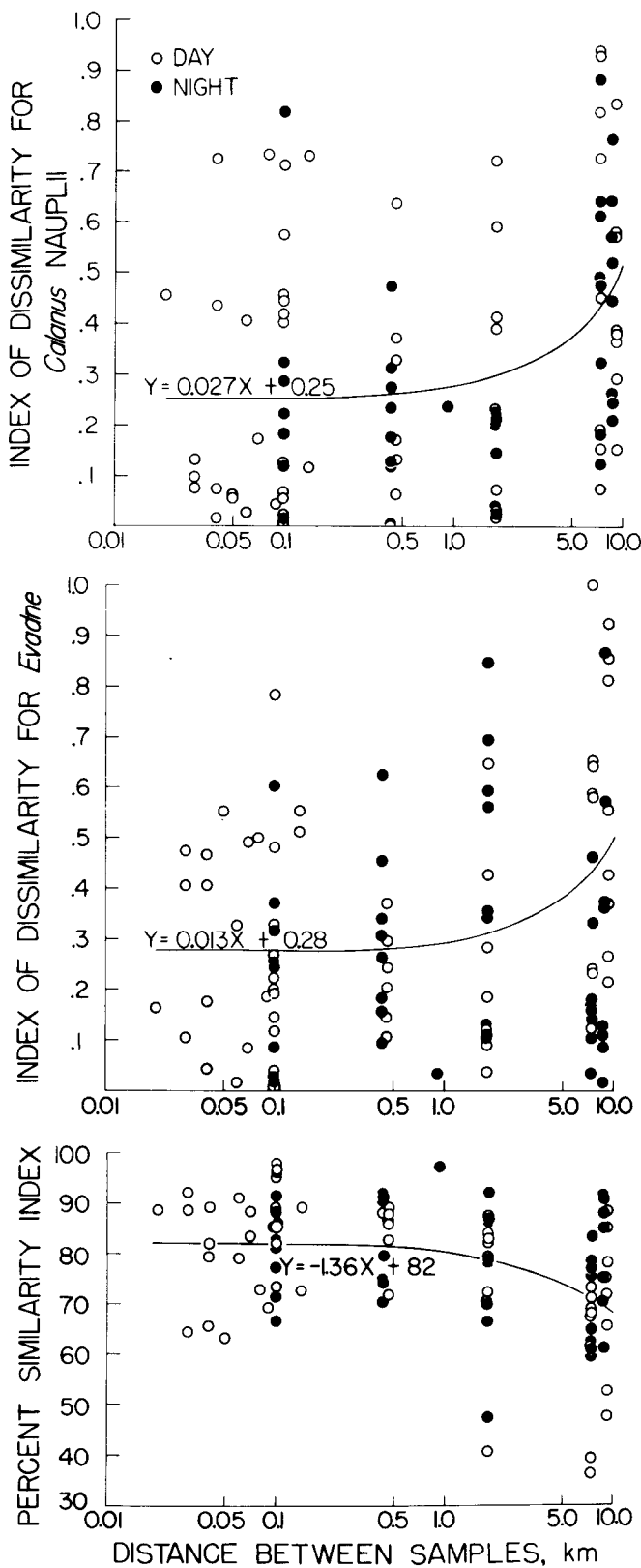


Figure 3. Upper—Index of dissimilarity for *Calanus* nauplii as a function of distance; Middle—Index of dissimilarity for *Evadne* as a function of distance; Lower—Percent similarity of zooplankton as a function of distance. In all, the linear relation appears curved on the semi-logarithmic plot.

of some species and in relative composition. Location of “replicate” or “control” stations for plankton sampling should be adjusted accordingly, depending upon the degree of similarity that the investigator requires (or the dissimilarity that is to be detected) and the inevitable limitations of time and funding.

The finding that the faunal composition of widely spaced samples is more similar at night than by day, if it proves to be general, raises the possibility that an anthropogenic change in composition might be more easily detected at night, since the unperturbed composition would be similar over a large area.

The biological causes of this finding are not clear. Migration into the surface layers of abundant, homogeneously distributed forms that therefore dominate the percent similarity index at night could give this result, but except for the rare copepodite stage V and adult *Calanus*, which were most abundant at night, the categories we counted were similar in abundance night and day. This also suggests that predation on the zooplankton was not markedly higher at night than by day.

The result could also be obtained if the zooplankters dispersed horizontally and vertically during the night and were more aggregated by day; were this the case, the variance in abundance of each category should be significantly greater by day than at night. This was true ($p < 0.05$ by F test) for some categories, notably *Sagitta* and the youngest naupliar *Calanus*, but not true for larvaceans and the early copepodite stages of *Calanus*. The most abundant category (*Evadne*) was more variable during the day, but the significance was questionable ($p \sim 0.05$). *Corycaeus* was significantly more variable at night. The overall evidence is therefore equivocal.

Another explanation—one which seems less biologically plausible than those already examined—is that although the zooplankters are equally patchy day and night, patches of all categories tend to overlap much more at night than by day. Thus, the relative composition of samples taken at night tends toward constancy because the abundances of categories vary together horizontally. One can imagine several hydrodynamic or biological causes of such covariance; it is less easy to explain why this agreement should break down each day. Tending to refute this hypothesis (in addition to its implausibility) is the finding of Smith et al. (1976) that longshore patches of nearshore zooplankton off Oregon during the daytime tended to be multispecies entities.

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