

DIEL CHANGES IN THE VERTICAL DISTRIBUTION OF BIOMASS AND SPECIES IN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

Displacement volumes were measured, and selected species of zooplankton were counted from sets of vertically stratified samples taken in the Southern California Bight in April 1965 to provide information on vertical distribution and changes in distribution caused by diel migration and bottom topography. Day/night differences were found in total biomass in the upper 225 m, and there was a diel redistribution of selected species and biomass within the water column. Depending on the size fraction sampled, from $\frac{1}{3}$ to $\frac{2}{3}$ of the nighttime biomass in the upper 56 m of water was redistributed below this depth during the day. For most copepods considered, this change was caused by diel vertical migration, but larger zooplankters could either have been descending below 225 m or avoiding capture in the surface layers more successfully during the day than at night.

RESUMEN

Se han obtenido muestras de plancton a varios niveles de profundidad en el seno del Sur de California, durante Abril de 1965, con objeto de obtener información sobre la distribución batimétrica y variaciones en la distribución en relación con la luz y la topografía del fondo. Se midieron los volúmenes de plancton por el método de desplazamiento, y se contaron las especies seleccionadas de estas muestras. Diferencias nocturnas y diurnas han sido observadas en la biomasa, para los estratos de 225 m. a 0 m. de profundidad, y las especies seleccionadas así como la biomasa, presentaron una redistribución diaria en esa columna de agua. De acuerdo con la magnitud de la fracción de la muestra utilizada ($\frac{1}{3}$ hasta $\frac{2}{3}$ del total), la biomasa nocturna en el estrato de 0-56 m. de profundidad, aparecía distribuida durante el día por debajo de aquel nivel. En la mayor parte de los copépodos analizados, este cambio era debido a la migración vertical; pero los zoopláncteres de mayor talla podían descender por debajo de los 225 m. de profundidad o evitar ser capturados por la red en dichos estratos, efecto que conseguirían con mayor éxito durante el día que de noche.

INTRODUCTION

Very little information is available on the vertical distribution of zooplankton within the Southern California Bight. In April 1965 a set of vertically stratified samples was taken with two different mesh sizes at locations within the bight. We analyzed samples from 28 of these stations where a vertical series was complete for differences in the vertical distribution of biomass and species with time of day, and in the areal distribution of biomass with respect to bottom topography. The basins may provide refuge for a significant biomass of mesopelagic animals that migrate into the upper 200 m at night.

MATERIAL AND METHODS

Samples from Expedition X were obtained from the Scripps Institution of Oceanography Invertebrate Collection. The cruise was conducted off the southern California coast in April 1965 (Figure 1). Series of vertically stratified samples were collected using the Brown-McGowan opening-closing nets (bongo nets) (McGowan and Brown 1966). The two nets on each

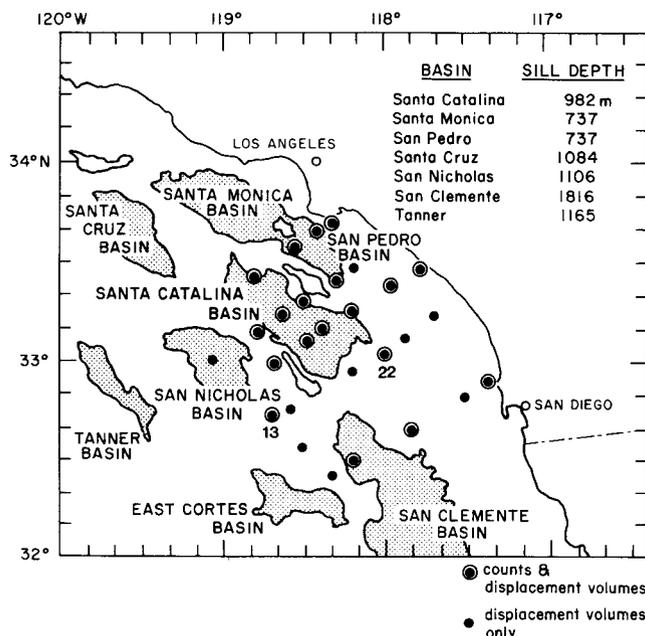


Figure 1. Station locations of samples from Expedition X showing basin topography at sill depth.

frame were of different mesh sizes, 333 μm and 505 μm .

Four bongo frames were placed equidistant on the wire, and a depth recorder on the bottom frame was used to trace the course of the tow. The maximum wire paid out during a tow was 400 m. According to the expedition leader, Edward Brinton, (pers. comm.) a messenger was sent to open the nets when 300 meters of wire was out. Another 100 m of wire was lowered, and then raised. The nets were set to close after a predetermined volume of water was filtered (440.5 m^3 per net). The winch speed was adjusted so that the nets made an oblique tow within a stratum before they closed. It is not certain that the nets fished each depth uniformly within the desired stratum only, but every effort was made to achieve this. Adding together the catches of the four frames is thus an integration to 225 m.

The maximum depth of each tow was determined from depth recorder traces, and a mean maximum depth for all tows was calculated. We calculated the depths of the shallower frames on the assumption that the frames were equidistant on the wire and the wire angle was kept constant. The mean strata fished were 0–56 m, 56–113 m, 113–169 m, and 169–225 m. At several stations this vertical series was complete for one of the sizes of nets but not the other.

Displacement volumes were measured on all samples from stations shown in Figure 1. Because the mesh size on the two nets on each frame differed, two size fractions of samples were represented, and are considered separately. Displacement volumes were measured by pouring the sample into a graduated cylinder, noting the volumes, removing the animals by pouring the sample through 333- μm mesh netting into a second graduated cylinder, waiting up to 5 minutes until the dripping ceased, and then noting the volume of liquid in the second cylinder. The difference between the first measurement and the second is the displacement volume of the organisms (Ahlstrom and Thraillkill 1963). We removed larger gelatinous organisms and small fish before measuring.

The following organisms were enumerated in the 333- μm samples at stations shown in Figure 1: female *Calanus pacificus*, male *C. pacificus*, *C. pacificus* copepodite stages III–V (counted separately), female *Eucalanus bungii*, male *E. bungii*, *E. bungii* copepodites (lumped), female *Pleuromamma borealis*, male *P. borealis* and copepodites (lumped), and sexually mature (greater than 11 mm) *Euphausia pacifica* males and females. These animals were selected because of their abundance in all samples. *E. pacifica* is the only one that could migrate below 500 meters into the basins during the day. Samples were split with a

Folsom plankton splitter. From 1/32 to 1/4 of each sample was counted for the above organisms.

RESULTS

The ratio of the displacement volumes from samples taken with nets of two different meshes (333 μm and 505 μm) was calculated for each depth and—because a balanced set of data existed—a one-way analysis of variance was performed to see if that ratio differed with depth. The mean ratio varied from 2.2 at the surface to 1.3 in the deepest strata. The ANOVA was weakly significant ($.05 < P < .10$). Figure 2 shows the mean displacement volumes of the different size fractions in separate strata. There is an enhancement of smaller organisms near the surface day and night in the 333- μm fraction.

A variation of the Rank Sum test was used to test for differences in the biomass, integrated to 225 m from each kind of net, between samples taken over the basins and those taken away from basins. (Basins and stations are shown in Figure 1.) The test gives equal weight to day and night, combining them to increase sample numbers and look for overall effects of the basins. The test was not significant for either the 333- μm or the 505- μm samples, thus suggesting no effect of seabottom topography on biomass in the overlying water column above 225 m at these deepwater locations. However, considering only night samples, for which the effect of the basins is hypothesized, there was significantly more material caught over the basins in the 505- μm samples when compared with nonbasin locations (Rank Sum $p = .05$). The 333- μm samples showed no difference in location. These results may

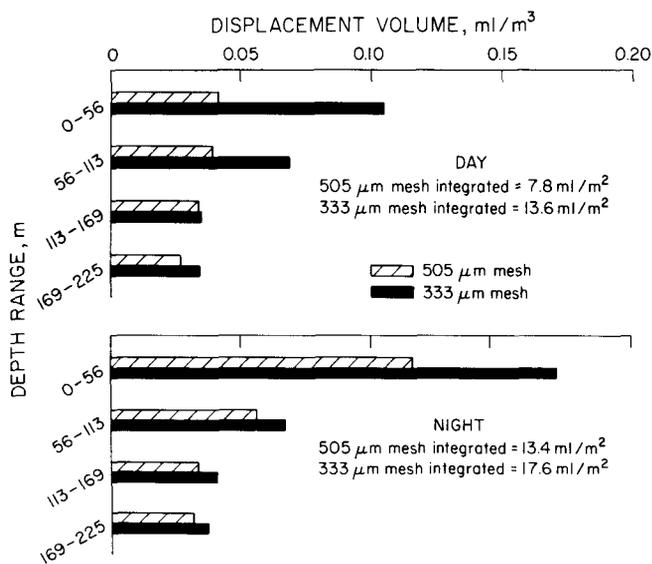


Figure 2. Day and night vertical distribution of mean displacement volumes from nets of two different mesh sizes.

TABLE 1
 Radio (Night:Day) of Displacement Volumes

	505 μm	333 μm	
0-56	2.9	1.6	333 μm n = 8 day
56-113	1.4	1.0	n = 11 night
113-169	1.0	1.2	505 μm n = 9 day
169-225	1.2	1.1	n = 10 night
Integrated	1.7	1.3	

Volumes are for those stations at which all strata were sampled by one (but not necessarily both) of the meshes of net.

be complicated by onshore/offshore differences in abundance independent of "enrichment" by basins. Further tests of this hypothesis should be based on stations equidistant from shore over and away from basins.

Rank Sum tests comparing day samples to night samples showed a significant difference in the integrated catch for the 505- μm samples ($P < .01$), with more material being caught at night (Figure 2, Table 1). This difference in the 505- μm samples suggests either that there are large animals migrating from below 225 m into the upper water column at night, or that avoidance of the nets by large animals is reduced at night. We roughly estimated the fraction of that increase in biomass at night caused by *E. pacifica*, since the migration of this species was determined by microscopic analysis of the samples (see below). Although the lengths of euphausiids were not recorded, a minimum and maximum estimate is possible. The weight of individual euphausiids was obtained from Miller (1966). Weibe et al. (1975) estimated that wet weight is 0.73 g/ml of displacement volume. We used that estimate to determine that 11-mm and 20-mm *E. pacifica* were from 14–67% of the mean displacement volume in the night 0–56-m stratum, and none during the day (Figure 3). Other kinds of euphausiids were present in the samples, so it seems that a major portion of the night enhancement of total biomass comes from euphausiids.

Because the 333- μm samples include, of course, the 505- μm fraction, it might be expected that the 333- μm samples also should show a significant difference between day and night, but the test was not significant. A comparison of the 333–550- μm fraction of animals in the upper 56 m of water, obtained by subtracting the displacement volume of the 505- μm -mesh catch from that of the paired 333- μm -mesh catch, showed no change in this biomass associated with time of day. Thus we detected little or no movement of organisms of this size into the upper 225 m at night. This 333–505- μm fraction constituted from 32–61% of the total biomass caught with the 333- μm net in the 0–56-m stratum, but was less in deeper water (from 1–25%). The nocturnal enhancement in the 505- μm

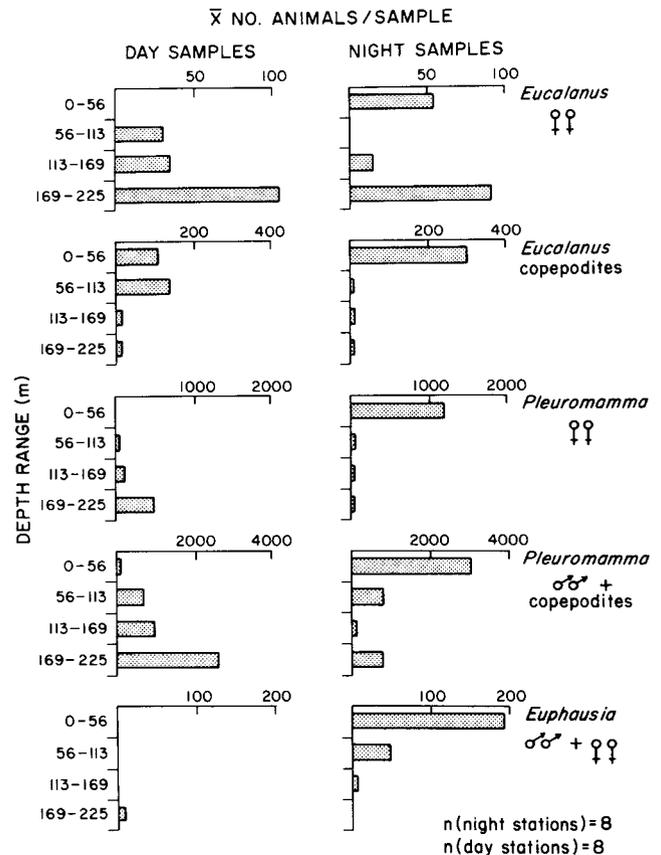


Figure 3. Day and night vertical distribution of selected species.

fraction apparently is obscured by nondiel variation in the larger biomass of the more conservative 333- μm fraction, and so the integrated 333- μm catches show no day/night differences. However, when the upper stratum is considered alone (Table 1), there is significantly more material caught by the 333- μm net at night than by day (Rank Sum $P < .01$). Figure 2 and Table 1 indicate that most of the difference in integrated 505- μm night catch also occurs in the upper strata.

A comparison of total counts of all animals identified (Figure 4), integrated to 225 m, shows no difference between day and night (Rank Sum Test). Tests of individual kinds of animals day vs night showed no difference in numbers in the water column except for *Euphausia pacifica*. Either euphausiids migrated at night from below 225 m into the sampled water column, or they were less able to avoid the nets at night; there is no way to distinguish which. Brinton (1967) presents inconclusive evidence for the diel changes in avoidance capability of *E. pacifica*, but also shows it to be a strong migrator. Pieper (1979), using acoustics, showed an upper daytime depth of *E. pacifica* to be between 130 and 280 m in the San Pedro and Santa Catalina basins off southern California. Thus the low

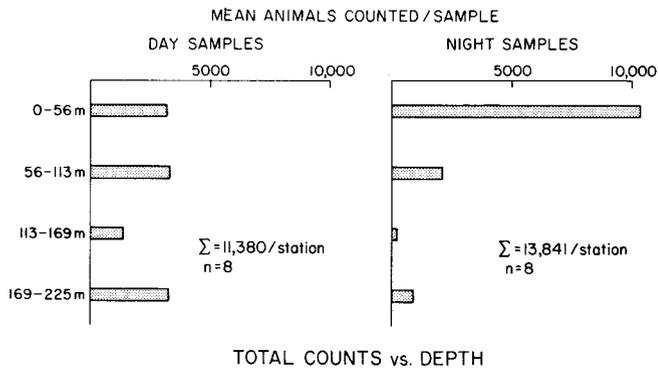


Figure 4. Day and night vertical distribution of total animals counted.

number of this species caught in the surface during the day may not be the result of avoidance.

Within the water column sampled, however, there was a change in the distribution of animals day and night. Most groups counted were concentrated nearer the surface at night (Figures 3-5). Only for *Calanus* CIII and IV were there no differences in the day vs night distribution. If these stages make diel migrations, they might be doing so within the 56-m surface stratum, and the migration could not be detected by the sampling regime. *Calanus* adults and CV, however, performed a detectable migration within the upper 169 m (Figure 5), as did all other groups of animals counted (Figure 3). *Pleuromamma*, *Eucalanus*, and *Euphausia* migrated to the upper 56 m at night from at or below 169 m. There appeared to be a group of *Eucalanus* females that remained below 169 m and did not come to the surface at night.

Figure 6 shows the density (σ_t) distribution at two stations on the sampling grid, and the horizontal lines indicate the strata sampled by the bongo nets. These stations are shown in Figure 1. There was a gradient extending from about 30 m to 100 m, above and below which the density is fairly uniform. Animals migrating into the surface strata thus swam through a pronounced density gradient into the mixed layer.

DISCUSSION

Banse (1964), in a review of the literature on vertical distribution, finds that at least half of the night population of animals fished by 0.3-mm nets in the surface layers remains in the upper layers during the day. Our results also show that a large fraction of the biomass remains in the surface during the day, since the night:day ratio of the 333- μm catches in the upper 56 m is only 1.6 (Table 1). Comparison of the biomasses of the 333-505- μm fraction showed no difference in day vs night, suggesting populations of smaller animals always resident in the surface. Although it is impossible to detect the effect of reduced avoidance of

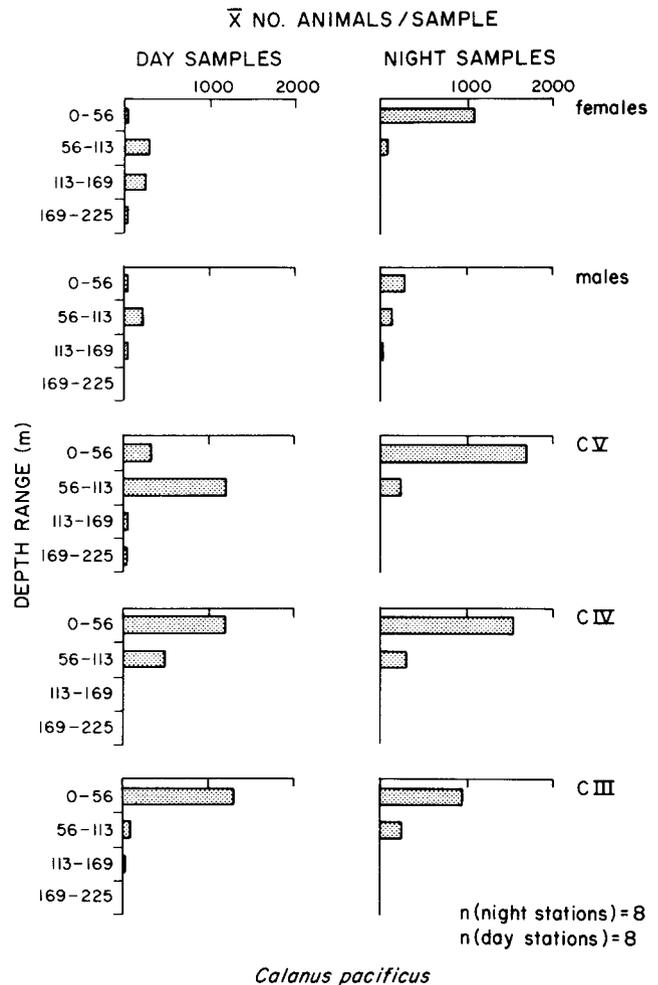


Figure 5. Day and night vertical distribution of developmental stages of *Calanus pacificus*.

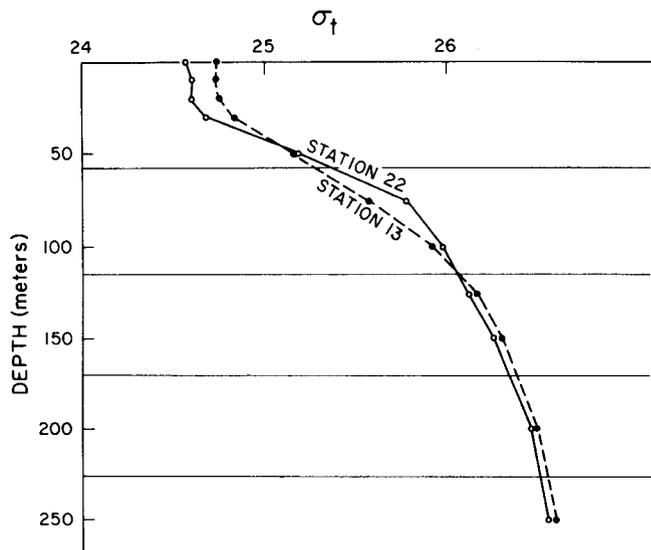


Figure 6. Vertical distribution of σ_t at two selected stations.

nets by rare, larger animals at night, the fact that there was no significant difference in the biomass of this 333- μm fraction day vs night, and that the integrated counts of all species (except *Euphausia*) showed no diel difference, indicates that most animals were being sampled uniformly day and night, and that changes in their apparent distribution according to time of day were not artifacts of differential efficiency of capture.

To assess the transport of material into deeper water, it is necessary to know the diel changes of animals within the water column. Animals remaining in the surface contribute to the organic matter in deeper water only through a rain of fecal material, exoskeletons, and corpses falling from the surface. Actively migrating animals, however, represent a behavioral transport of materials to depth, and estimates of that transport from this study indicate that about $\frac{1}{3}$ of the nighttime 333- μm catch at the surface, and $\frac{2}{3}$ of the nighttime 505- μm catch at the surface are redistributed deeper during the day, mainly in the form of euphausiids. Vinogradov (1968) concludes that this behavioral transport is the more important route of material from surface to deep water. Kuenzler (1967) calculates that transport of a heavy metal downward by migrating zooplankton may be equal to or greater than transport by vertical eddy diffusion. Animals eating at the surface and migrating deep during the day can hasten the transport of organic matter through excreting, defecating, and moulting at depth. However, Fowler (1982), in a review of biological transport processes, suggests that the more important route for vertical flux of pollutants downward is from biogenic debris in the form of fecal pellets.

The results also suggest that the fraction of the biomass in the form of smaller organisms is greater at the surface than at depth. This is likely because herbivores, which tend to be smaller, remain near the surface within the euphotic zone where the phytoplankton is.

Huntley and Brooks (1982) demonstrated an ontogenetic development of vertical migration in *Calanus pacificus* reared in a large tank. The present data shows further evidence of this phenomenon. There was no detectable diel vertical migration of *Calanus* CIII and CIV in the data, but CV and adults showed clearly different day and night depths (Figure 5). *Eucalanus* females also migrate from deeper depths than do *Eucalanus* copepodites (Figure 3). It is likely that the ontogenetic development of diel vertical migration is fairly widespread among many kinds of organisms, with the smaller juvenile stages undergoing smaller migrations within the surface waters, and the amplitude increasing as they get older (Gardiner 1933). Thus the smaller plankton of the surface

contains juvenile forms of many organisms that will later be part of the migrating plankton.

In this study the population of migrating *Calanus* seemed to be contained within the upper 169 m. Esterly (1911) found *Calanus* off San Diego migrating from depths of 365–457 m. Since the sampling on Expedition X did not go any deeper than 225 m, we cannot say for certain that there were no deeper *Calanus*, but there may be seasonal effects on diel vertical migration (Koslow and Ota 1981). Esterly's study was done in June and July, whereas Expedition X was undertaken in April. All of the other organisms counted were contained in the deepest strata sampled in this study, indicating that the deepest part of their range may be below 225 m. But except for *Euphausia* the total numbers contained in the 225-m water column did not change from day to night, indicating that animals deeper than 225 m were not migrating to the surface at night. Longhurst et al. (1966), from a vertical profile in May, showed that *Eucalanus* and *Pleuromamma* occur deeper than 225 m in the Southern California Bight, while the bulk of the *Calanus* population is contained in the upper 250 m. *Euphausia pacifica* occurs to 600 m (Brinton 1967). Thus our samples may not bracket the entire population of *Pleuromamma*, *Eucalanus*, and *Euphausia* in the water column.

It was unlikely that there would be any demonstrable effect of bottom topography on biomass in the overlying 225 m, yet the night 505- μm tows caught a greater biomass over the basins than away from the basins. This may be a statistical artifact, or it may mean that the basins concentrate larger organisms. More intensive sampling throughout the water column, and identification of the specific organisms responsible for the increase in biomass are necessary to investigate this effect. Clearly, the biggest differences were in the changes in the day/night distributions of biomass and species, changes showing a crowding of larger organisms toward the surface at night, and a diel redistribution of species within the water column.

ACKNOWLEDGMENTS

We wish to thank Edward Brinton, who undertook Expedition X and provided data associated with it; George Snyder of the SIO Invertebrate Collection; Mary Anne Ogle for typing the manuscript; and Jeffrey Napp, John R. Beers, and two anonymous reviewers for critically reading the manuscript.

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