INVESTIGACION COOPERATIVA DE LA ANCHOVETA Y SU ECOSISTEMA -ICANE- ENTRE PERU Y CANADA
CALLAO 1981 PERU

SHORT TERM VARIATION IN THE VERTICAL DISTRIBUTION OF COPEPODS OFF THE COAST OF NORTHERN PERU*

by

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ABSTRACT

Vertical profiles of chlorophyll a, oxygen, density and copepods were collected during November 1977 near 9°S off Peru. The majority of three groups of copepod, the Oncaeidae, the Oithonidae and small calanoids, remained above the depth (~30m) where concentrations of oxygen became less than 0.5 ml.1^{-1} both day and night. Centers of population of all three groups were in or below the pycnocline at all times. In daytime all three groups accumulated at depth, while at night all three groups showed some dispersion throughout the upper 30m with statistically significant separation in the layers of Oncaeidae and small calanoids. Small calanoids were always higher in the water column than the Oncaeidae at night. The rather small, daily vertical excursions by the Oncaeidae and small calanoids exposed them to mean onshore, poleward flow by day and mean offshore, equatorward flow at night.

RESUMEN

En perfiles verticales frente al Perú cerca de 9°S se colectó datos de clorofila a, oxígeno, densidad y copépodos en noviembre de 1977. La mayor parte de los tres grupos de copépodos, Oncaeidae, Oithonidae y pequeños calánidos, se mantuvieron por encima de la profundidad a la cual la concentración de oxígeno es menor que 0.5 ml por litro (alrededor de 30 m) tanto en el día como en la noche. Los centros de población de los tres grupos se situaron siempre sobre o por debajo de la picnoclina. Durante el día los tres grupos se acumularon en la profundidad mientras que en la noche se dispersaron un tanto en los 30 m superiores manteniendo una separación estadísticamente significativa entre Oncaeidae y los pequeños calánidos, ocupando estos últimos una capa superior. Las reducidas excursiones verticales diarias de Oncaeidae y de los pequeños calanoides exponen a ambos al flujo promedio hacia la costa y el polo durante el día y hacia afuera y el ecuador durante la noche.

INTRODUCTION

The association of vertical structure, layering, in the distribution of zooplankton with variables in the water column that might cause or strongly influence that structure has been described in several areas of the world's oceans. The variables most frequently observed to correlate with layering of zooplankton are density (Banse, 1964; Longhurst, 1976; Boyd, 1973; Zalkina, 1977), oxygen (Longhurst, 1967; Antezena-Jerez, 1978), and potential food (Anderson, Frost and Peterson, 1972; Vinogradov, 1972; Hobson and Lorenzen, 1972; Mullin and Brooks, 1972). These variables are usually not independent of one another which complicates any analysis of vertical profiles for meaningful, possibly causative, relationships. Never-

theless, experiments continue because in the organization of marine ecosystems, space is a resource that could be partitioned by swimming metazoans. The trophic structure of a marine system could vary considerably as a function of the living space occupied by an organism or group of organisms and temporal patterns in the ways that space is used.

Off Peru feeding patterns of the herbivorous copepod **Calanus chilensis** were modified according to food availability. In areas of high concentrations of food, **C. chilensis** fed evenly day and night, a pattern it shared with the omnivorous **Centropages brachiatus**. When food became scarce, **C, chilensis** fed primarily in daytime and ranged to deeper depths while **C. brachiatus** fed primarily at night (Boyd, Smith and Cowles, 1980). Thus when food

was relatively scarce, these two species partitioned their time of feeding, and C. chilensis broadened its living space in the vertical.

In the preeent study we sampled zooplankton in the upper 35m of the water column at 5m intervals with the ship anchored for 42 hours (9° 20' S, 78° 15' W; Figure 1) and with the ship

Figure 1. Map of the Peruvian coast showing locations of anchor study (●) and drogue study (●).
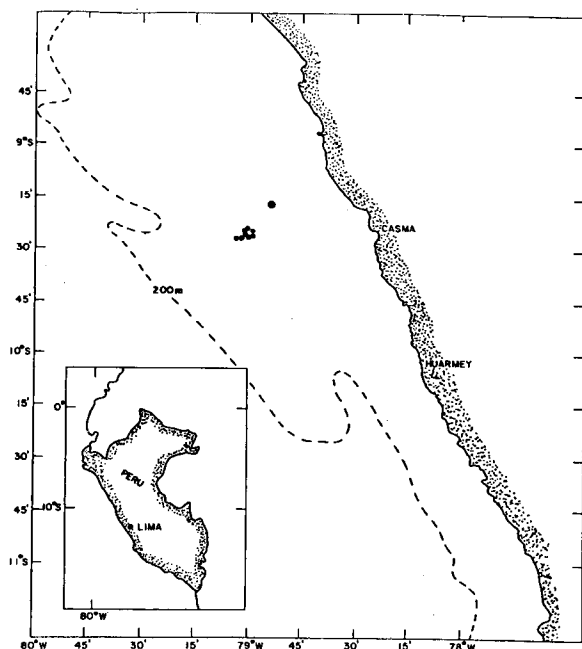
following a drogue set at 10m for 32 hours near 9° 28' S, 78° 58' W. This study was conducted in November, 1977, from C. S. S. Baffin as part of the Canada-Peru study of the ecosystem of the Peruvian anchovy (I.C.A.N.E.; Doe, 1978). We shall describe vertical distributions of organisms, chlorophyll a, and oxygen and examine the data from the anchor station for evidence of vertical structure in the distribution of organisms and the influence of the pycnocline on vertical structure.

METHODS

Zooplankton were sampled each 5 meters of the upper 35 meters by a reciprocating pump attached to a 3.2 centimeter internal diameter hose. Water was discharged from the hose on deck through a plankton net of 158 μm aperture mesh. Each depth was sampled for 5 minutes and flow rate of the pumping system, which averaged 80 liters per minute, was measured by allowing the outflow to fill a large container of known volume. Collections were preserved in 5°/o neutral formalin. All organisms in each sample were identified to genus or group and counted. The configuration of the pump and hose were such that the copepods were generally in poor condition, precluding any reliable identification of stages of the life cycle. We have chosen three categories for analysis: species

of **Oncaea**, species of **Oithona**, and small calanoids. These categories contain both adults and late copepodids, with the calanoid category being **Paracalanus parvus** largely.

The water column was sampled each four hours for vertical profiles of salinity, temperature, oxygen, chlorophyll a, nutrients and zooplankton. Temperature and salinity observations were made using a Guildline 8705 digital conductivity, temperature and depth probe (CTD) with a 500 decibar pressure sensor. Water samples for dissolved oxygen, nutrients and chlorophyll a were obtained from a hydrocast after each CTD cast. Dissolved oxygen was determined by the Winkler method (**Strickland and Parsons**, 1968) with an uncertainty of 0.2 ml. l^{-1} at oxygen concentrations below 0.5 ml.l^{-1}. Chlorophyll a was measured fluorometrically as described in **Lorenzen** (1966). Wind speed and direction data were recorded daily by ship's officers. Further details and data can be found in **Doe** (1978).

RESULTS

Hydrographic and nutrient data suggest that both the anchor study and the drogue study were not within zones of active upwelling. Mean sea-surface temperatures were 18.0 ± 0.2°C during the anchor study and 17.6 ± 0.4°C during the drogue study while average surface nitrate concentrations were 1.47 μg-atoms l^{-1} and 0.35 μg-atoms l^{-1} respectively. Winds paralleled the coast just before and during both studies with speeds averaging 13 ± 5 knots in the anchor study and 11 ± 4 knots in the drogue study.

During the anchor study, oxygen concen-

Figure 2. Vertical distributions of oxygen and chlorophyll a in the upper 40m during the anchor and drogue studies.
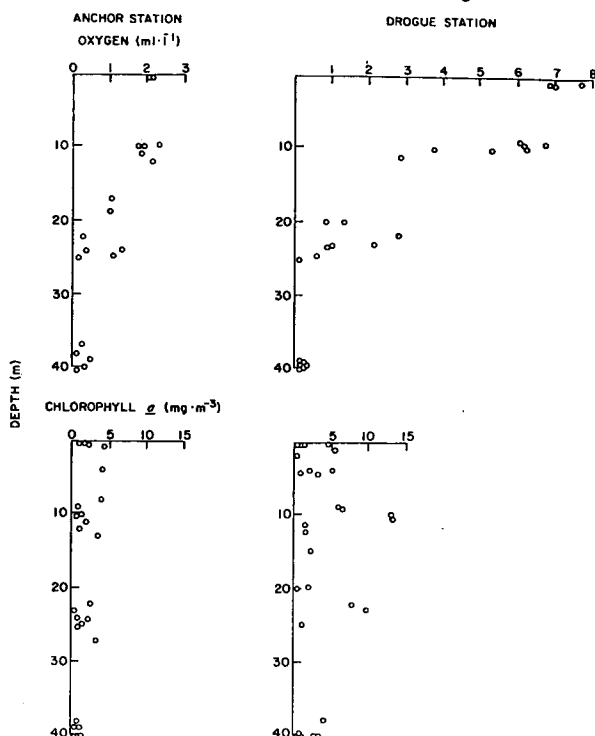
trations were less than 2.5 ml 1^{-1} at the surface and generally less than 0.3 ml 1^{-1} below 30m (Figure 2). Chlorophyll a was less than 5.0 mg m^{-3} and without structure in the upper 40m (Figure 2). The abundance of copepods in general was sharply reduced above 10m and below 30m at all sampling times (Figure 3), the lower boundary corresponding with the depth where concentrations of oxygen became less than 0.3 ml 1^{-1}. At night the depth of maximum abundance of total organisms was at 20m with species of **Oncaea** and small calanoids composing that layer (Figure 3). In daytime, the

Figure 3. Profiles of abundance of species of **Oncaea** and **Oithona** and small calanoids collected during the anchor study. In the upper panel, ● represents total organisms, o represents species of **Oithona** and △ represents species of **Oncaea**. The bottom panel shows distributions of small calanoids, and time is local satandard time.
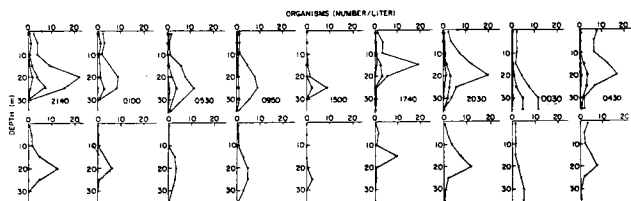
composition of the layer of maximum abundance was the same, but it occurred at 25m (Figure 3). Throughout the anchor study species of **Oithona** were less abundant than the **Oncaea** spp. or calanoids and more evenly distributed throughout the upper 35m (Figure 3). Bimodality in the profiles of small calanoids and species of **Oncaea** at night suggests vertical migration (Pearre, 1979). Since there was no vertical structure in chlorophyll a, the layers observed in the copepods do not correlate with layers of phytoplankton.

During the drogue study, higher and more variable surface concentrations of oxygen were observed (Figure 2), but below 30m, concentrations were less than 0.3 ml 1^{-1}. Vertical distribution of chlorophyll a had subsurface maxima exceeding 10 mg m^{-3} in several samples (Figure 2). The depth of maximum concentration of chlorophyll a varied from 10 to 25m. The depth of maximum total number of copepods was 15m day and night, with small calanoids dominant numerically (Figure 4). When a subsurface maximum in chlorophyll a was observed, peaks in abundance of copepods were observed just beneath it generally.

We converted the absolute numbers of each profile of copepods to relative abundance (percent) in 35m in order to smooth effects of horizontal patchiness and examine the vertical distributions of the copepods throughout each timeseries with respect to centers of populations and dispersal, concentrations of oxygen, and movement of the pycnocline (sigma-t = 25.35 to 25.75). In the anchor study, the effect of the concentration of oxygen less than 0.5 ml 1^{-1} on distributions is clear. For the most part the lower contour enclosing the 10% level of total numbers of each group of

Figure 4. Profiles of abundance of species of **Oncaea** and **Oithona** and small calanoids collected during the drogue study. Symbols are the same as in Figure 3 and time is local time.
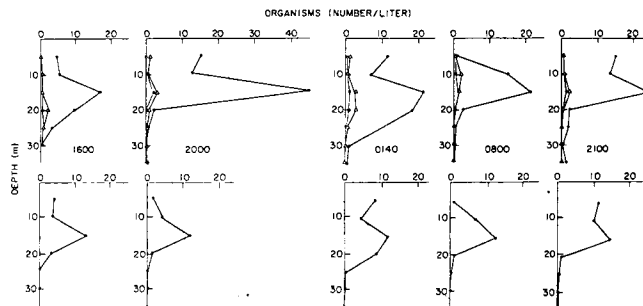
copepod is above the depth where oxygen becomes less than 0.5 ml 1^{-1} (Figure 5). During daytime, the population center relative abundance $> 30\%$ of species of **Oithona** covered approximately five meters and varied in depth from 15 to 25m (Figure 5), while the population center of species of **Oncaea**, which also spanned approximately 5m, was at depths of 15 to 30m (Figure 5). The day-

Figure 5. Relative abundance of three groups of copepod collected during the anchor study. The abscissa is depth in meters. A △ represents the depth at which σ_t was 25.35, and an X represents the depth at which σ_t was 25.75.
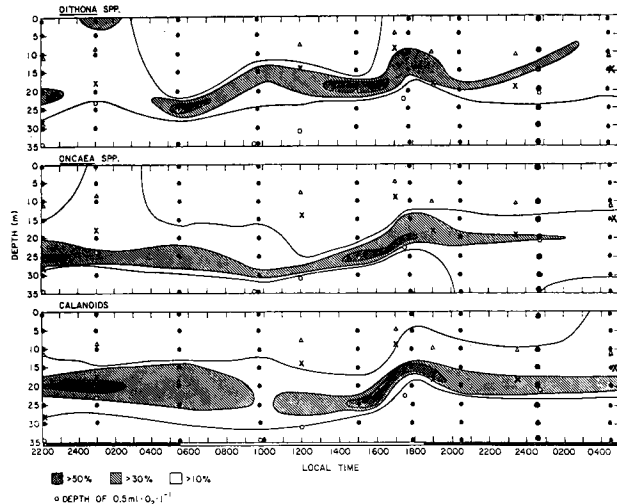
time population center of small calanoids spanned 5 to 10m and was at depths of 15 to 27m. At night, population centers similar to those observed in daytime tended to be maintained but dispersion through the water column occurred, presumably for feeding, and was evident in the wider depth range enclosed by the 10% contours (Figure 5). The species of **Oithona** show the greatest night-time dispersion while the small calanoids show the least (Figure 5).

During the drogue study, the greatest depth of the 10% relative abundance contour was well above the depth where concentrations of oxygen were less than 0.5 ml 1^{-1} (Figure 6). The population centers (relative abundance $> 30\%$) of all three groups spanned 5 to 10m day or night and

occurred at depths ranging from 5 to 25m (Figure 6). Night-time dispersion occurred in all three groups, most noticeably in the small calanoids and species of **Oncaea** (Figure 6). The dispersion at night seen in Figures 5 and 6 indicates migration by some individuals in the populations during both the

Figure 6. Relative abundance of three groups of copepod collected during the drogue study. The abscissa is depth in meters. Symbols are the same as in Figure 5.
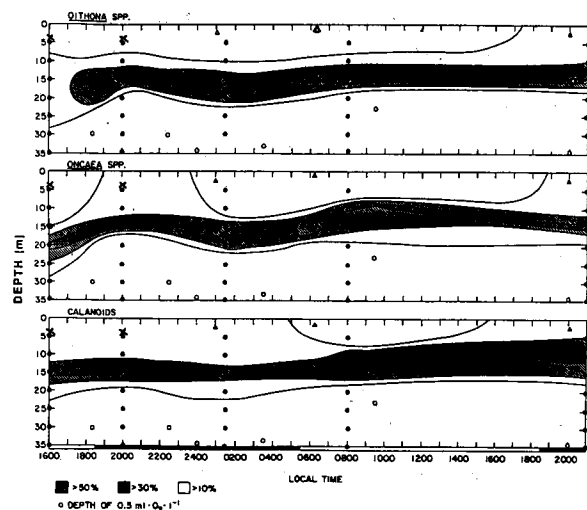
anchor and drogue studies and confirms the suggestion of vertical migration observed as bimodalities in the vertical profiles (Figures 3 and 4).

The overall pattern in both the anchor and drogue studies has four noteworthy components. Most of the population of all three groups remained above the depth where oxygen concentrations were less than 0.5 ml 1^{-1} day and night. Population centers of all three groups were in or below the pycnocline day and night. In daytime, all three groups accumulated at depth. At night all three groups showed some dispersion throughout the upper 30m.

The anchor station, because of its more complete coverage of distributions of copepods and water column structure over time and because the sampling platform was fixed, is useful for looking at relationships between density structure and vertical distribution of copepods. The depths of maximum abundance of the three groups of copepod from Figure 3 has been replotted along with depths of sigma-t equalling 25.35, 25.55 and 25.75 (Figure 7). A sigma-t of 25.75 was generally the botton of the pycnocline while 25.35 was the top. The maximum abundance of the small calanoids and species of **Oncaea** were below the bottom of the pycnocline, with one exception, while the species of **Oithona**, if they had a clear depth of maximum abundance (Figure 3), realized it without any relationship to the pycnocline (Figure 7). Thus, while the oxygen minimum layer establishes a lower boundary for the distribution of these copepods, the botton of the pycnocline seems to establish an upper boundary for small calanoids and species of **Oncaea** (Figure 7).

Inspection of Figure 5 shows that near sunset the population centers of all three groups of copepod move toward the surface, suggesting cohesive diurnal vertical migrations (**Pearre**, 1979). However, density profiles show that a different water mass in which the botton of the pycnocline was nearrer the surface was sampled at that time (Figure 7). The vertical distribution of the copepods with respect to the pycnocline was similar to thar observed at other times in the series (Figure 7), suggesting that observed vertical excursions in the centers of population were not the result of cohesive vertical migration but rather a result of the shoaling of the pycnocline from some physical process which carried the copepods with it. If density data had not been available, vertical migration would have been described for the copepods quite incorrectly.

In Figure 7 the depth of maximum abundance of species of **Oncaea** is generally deeper than the depth of maximum abundance of small calanoids, while the depth of maximum abundance of **Oithona**

Figure 7. Depths of three σ_t surfaces (25.35, 25.55 and 25.75) and depths of maximum abundance of three groups of copepod during the anchor study.
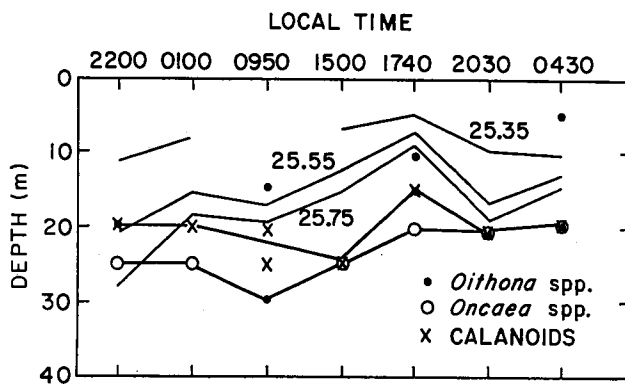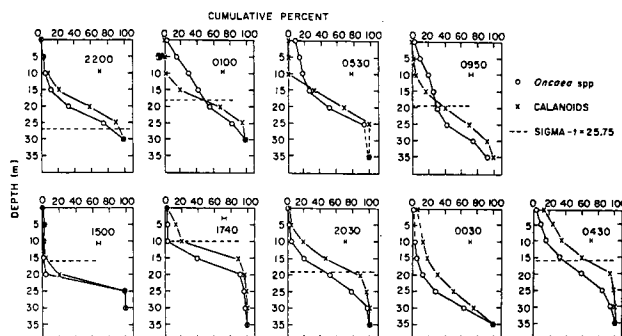
Figure 8. Cumulative frequencies in the vertical distributions of species of **Oncaea** and small calanoids collected during the anchor study. Dashed line is depth of σ_t equalling 25.75. Time is local time. The 95°/o confidence interval is shown beneath local time.

is variable. We used the Kolmogorov-Smirnov test (**Tate and Clelland,** 1957) modified for discrete samples (**Conover,** 1972), and not as used by **Shulenberger** 1957) modified for discrete samples (**Conover,** 1972), and not as used by **Shulenberger**

(1978), to test whether such layering in the vertical distributions of small calanoids and species of **Oncaea** was significant (Figure 8). In all profiles sampled at night, small calanoids were significantly (P ≤ .05) higher in the water column than were species of **Oncaea** below the pycnocline (sigma-t = 25.75; Figure 8). In daytime below the pycnocline, there was no significant difference in depth frequently (Figure 8). Above the pycnocline at night there were significant differences between the two groups in depth, but no consistent pattern was apparent. Early in the series species of **Oncaea** were significantly higher in the water column than were calanoids; late in the series calanoids were higher than species of **Oncaea** (Figure 8). At all times except the first profile, more than 50% of both groups of copepods were located at or below the bottom of the pycnocline (Figure 8).

We pooled all data above and below the depth of sigma-t = 25.75 by day and by night in order to generalize the patterns. At night above the depth of sigma-t = 25.75, small calanoids were significantly higher in the water column than were species of **Oncaea** except at 1 and 5m (Figure 9). At night below the pycnocline, small calanoids were significantly higher in the water column at all depths than were species of **Oncaea** (Figure 9). In daytime above sigma-t equalling 25.75, species of **Oncaea** were significantly higher in the water column than

Figure 9. Cumulative frequencies in the vertical distributions of species of **Oncaea** (O) and small calanoids (X) for pooled data collected during the anchor study. The 95% confidence interval is shown in the upper right-hand corner of each graph.

were small calanoids (Figure 9), while below sigma-t = 25.75 small calanoids were significantly higher than **Oncaea** at depths of 10 to 20m but not significantly different at depths greater than 20m (Figure 9). In general, at night small calanoids were significantly higher in the water column than were species of **Oncaea**, while in the daytime there were no significant differences below 20m, where the bulk of both groups occurred (Figure 5). Thus, in the anchor study the daytime accumulation of species of **Oncaea** and small calanoids at depth seen in Figure 5 can be confirmed statistically, while dispersion of these groups at night has the feature of statistically significant layering.

The Kolmogorov-Smirnov test applied to the vertical distributions of species of **Oithona** at the anchor station showed that at night **Oithona** was generally significantly higher in the water than small calanoids, while in the day **Oithona** was either higher or not significantly different from the other two groups. The general overall pattern at night was that species of **Oithona** were highest in the water column, small calanoids were below them, and species of **Oncaea** were deepest in the water column. In the day, statistical separation of layers was not as pronounced (Figure 9) because of the tendency of all three groups to accumulate just above the oxycline (Figure 5).

When the Kolmogorov-Smirnov test was applied to the results from the drogue study, small calanoids were significantly higher in the water column than species of **Oncaea** except at 0800 hr. and 2000 hr when the vertical distributions were not significantly different. Species of **Oithona** had no consistent vertical distribution with respect to the other two groups during the drogue study.

DISCUSSION

For the most part 35m covered the depth range inhabited by species of **Oncaea** and **Oithona** and the small calanoids since abundances had decreased to nearly zero at 35m (Figures 3 and 4). The oxygen depletion in subsurface waters off Peru establishes a very distinct lower boundary for the disitribution of many organisms in the water column and causes most zooplankton to inhabit a relatively thin surface layer. Restriction to the upper 35m maintains zooplankton within currents which may be quite variable in this complex upwelling system (**Brink, Halpern, Huyer and Smith**, 1980) and have strong influence on the distribution of zooplankton in the X and Y dimensions (**Smith, et al.**, this volume). The major features of the mean circulation at 15°S off Peru also occur at 10°S (**Brink, et al.**, 1980), suggesting that offshore and equatorward flow was restricted to the upper 20 to 25m during our study with onshore and poleward flow beneath. Considering the data from the anchor station (Figure 8) in view of the mean circulation, at night an average of 78% of the small calanoids and 49% of the species of **Oncaea** were found in the layer
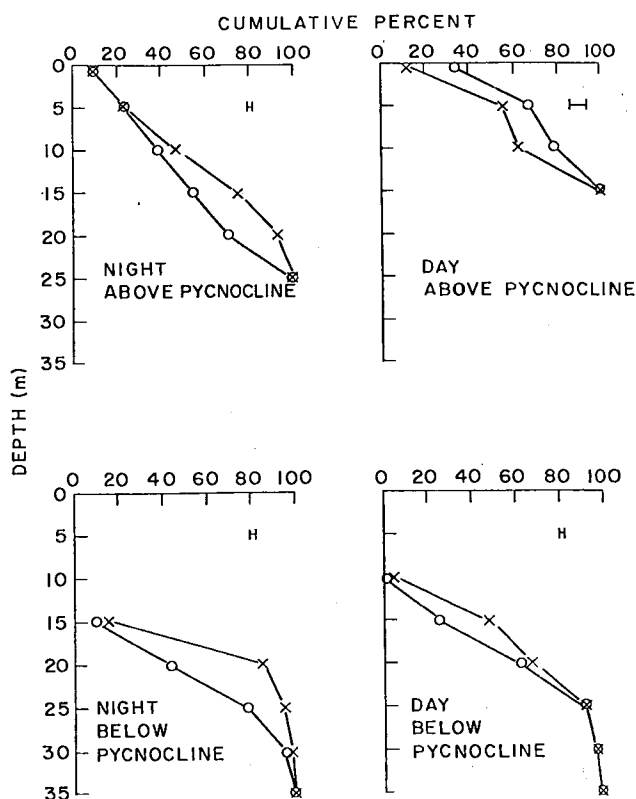
having offshore, equatorward flow. In the day, an average of 70o/o of the small calanoids and 82o/o of species of **Oncaea** were in the layer of onshore, poleward flow. Most of the **Oithona** at the anchor station were in the layer of offshore, equatorward flow both day and night. Thus, the rather small vertical excursions of species of **Oncaea** and the small calanoids were sufficient to expose them on a daily basis to a mean circulation tending to maintain them in one place. The response of the surface layer to wind, however, is strong and rapid (within one day) and introduces considerable day-to-day variability into the mean circulation (**Brink, et al.**, 1980). The behavior of at least two major groups in the zooplankton off Peru is "tuned" to the mean upwelling circulation.

Studies of patchiness in the distribution of zooplankton are frequently conducted by collecting data at a fixed, shallow depth from relatively long transects. These studies have shown that abundance of zooplankton varies six-fold over 80 to 100 kilometers in the North Sea (**Mackas and Boyd**, 1979) and off Georges Bank (**Denman and Mackas**, 1978) with maximum abundances of 60 per liter at the surface in the North Sea and 30 per liter off Georges Bank. Physical processes which lift or mix subsurface zooplankton into the layer being sampled can create patches of 100 meters in length in Massasschusetts Bay (**Haury, McGowan, and Wiebe,** 1978). The restriction of most zooplankton to the upper 35m off Peru and the abundance (up to 20 organisms per liter) and vertical structure of those organisms (for example, Figure 3) suggests that any patchiness observed at the surface should be correlated unambiguously with either the upwelling circulation or coastally trapped waves (**Smith,** 1978) which dominate the physical processes off Peru (**Brinck, et al.**, 1980). The strong and shallow vertical gradients in zooplankton combined with physical processes should dominate any patchiness at the surface in this area. Cross-shelf gradients in numbers of zooplankton off Peru at 15oS are on the order of 1 to 10 organisms per liter over 30 kilometers (**Smith, et al.**, this volume) while the vertical gradients observed in this study were

1 to 20 organisms per liter over 30 meters.

Previous studies of vertical distribution of Cyclopoida in the equatorial Pacific Ocean have shown that several of the species of **Oncaea** and **Oithona** likely to be in our samples have centers of population (25 – 75o/o) extending to 150m (**Zalkina**, 1970), emphasizing the reduction in living space experienced by the Cyclopoida collected off Peru. In contrast with our results, the Oithonidae tended to occur deeper in the water column (75 – 150m) than the Ocaeidae (25 – 125m) with the vertical distributions of the two groups separate by night and overlapping by day (**Zalkina**, 1970). The compression of most of the zooplankton into a surface layer of 35m suggests that competitive interactions among zooplankters might be intensified off Peru. The significant and small scale layering of the three groups of zooplankton in this study might be a response to competition. The layering is such that small calanoids, presumed to be grazers, are frequently at the bottom of the pycnocline, and when a subsurface maximum in chlorophyll a occurs, they are just beneath it. The Oncaeidae whose feeding habits are not well known but may be carnivores are found consistently beneath the small calanoids. The vertical structure observed in this study may be an important factor in the transfer of organic material within the upwelling sistem. At the moment, the trophic significance of these small, but numerically dominant (**Dagg, et al.**, 1979), copepods is unexplored.

ACKNOWLEDGMENTS

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