

Distribution of *Euphausia mucronata* at the upwelling area of Peninsula Mejillones, northern Chile: the influence of the oxygen minimum layer*

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SUMMARY: Analysis of zooplankton samples from 53 stations obtained around Peninsula Mejillones (Northern Chile), from two strata: 0-50 m and 150-200 m, during active upwelling in December 1996, allowed the study of horizontal and vertical distribution of *Euphausia mucronata*, endemic "Krill" of the Humboldt Current. Information from CTDO and a fluorometer was used to analyze the influence of oceanographic variables on distribution of *E. mucronata*. *E. mucronata* was found distributed all around the Peninsula, although with greater aggregations in the southern area, especially in the deeper layer. Stepwise multiple regression showed that none of the variables (temperature, salinity and chlorophyll) was significantly correlated to numerical abundance of the species. However there was a significant effect of depth of the oxygen minimum layer (OML), defined as 0.5 ml O₂ l⁻¹, on integrated abundance of the species, such that individuals are more likely to be found in areas where the OML is deeper. A vertical distribution parameter suggested a diurnal migrational pattern. This parameter was also correlated with distance to shoreline. The OML rises abruptly in nearshore areas because of active upwelling, but there are still nearshore zones where the OML remains deep. Therefore *E. mucronata* appears to aggregate around the upwelling lenses and filaments, where phytoplankton is more concentrated, but at the same time avoiding places where the OML is too shallow.

Key words: Euphausiids, upwelling, vertical-migration, oxygen.

INTRODUCTION

Eastern boundary currents (EBC) are worldwide recognized because they give rise to highly productive ecosystems. One of the most productive, although poorly known EBC systems, is the Humboldt Current. This sustains the large fisheries of Peru and Chile and may play an important role in carbon cycling and the global climate.

The large marine ecosystem of the Humboldt Current is characterized by its wind-driven upwelling,

which fertilizes the euphotic layer, inducing high primary production rates in coastal waters in northern Chile (Rodríguez *et al.*, 1991; Marin *et al.*, 1993), and hence supporting a nearly continuous production of zooplankton herbivores year round in these areas (Escribano and Rodríguez, 1994).

At northern Chile, a major upwelling point is located off Península de Mejillones (23°S). This area seems subject to intermittent upwelling throughout the year (Rodríguez *et al.*, 1991; Navea and Miranda, 1980). The zooplankton appear dominated by two abundant species, the copepod *Calanus chilensis* and the euphausiid *Euphausia*

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mucronata. The former has received some attention in the last few years, on aspects of life cycle and population dynamics (e.g. Escribano and Rodriguez, 1994, 1995; Escribano *et al.*, 1997). *E. mucronata*, however, an endemic and very abundant “krill” of the Humboldt Current (Antezana, 1978) has not yet been studied. Its relatively large size, its abundance and wide distribution suggest that this species may comprise a great proportion of the zooplankton biomass, playing a major role in channeling primary production to higher trophic levels.

Another particular feature of the upwelling area of northern Chile is that the subsurface undercurrent, typically containing low oxygen waters, tends to rise nearshore, entering into the upper euphotic layer, and thus creating an oxygen minimum layer (OML). This OML, which is located about 200 m depth offshore and near 30-50 m nearshore (Morales *et al.*, 1996a), may greatly influence zooplankton distribution and perhaps give rise to special adaptations to life under low oxygen levels. For instance, vertical distribution of anchovy larvae *Engraulis ringens*, one of the most important small pelagic fish for Peru and Chile, appears well restricted to upper 50 m waters, or at oxygen levels greater than 0.75 m l^{-1} (Morales *et al.*, 1996b). Moreover it is known that low oxygen ($< 0.7 \text{ m l}^{-1}$) may decrease survival of copepods and affect their vertical distribution (Roman *et al.*, 1993). In the eastern tropical Pacific vertical distribution of euphausiids also appears to be limited by the OML (Sameoto *et al.*, 1987).

Low oxygen in the upper 50 m of coastal waters may impose very narrow limits for vertical distribution of zooplankton. However, in most marine systems, zooplankton typically performs diel vertical migration (Zaret and Suffern, 1976) and euphausiids are recognized as very active migrators (Ohman, 1990). Thus the organisms ought to either restrict their vertical migration or develop some special adaptations to enter the OML. In the former case, individuals are probably more exposed to visual predators and likely to be subject to strong offshore advection during upwelling. Typical circulation patterns during coastal upwelling imply an upper Ekman layer advected offshore (e.g. Wroblewski, 1982; Peterson *et al.*, 1979). Being advected from upwelling centers, where food is more likely to be available, does not seem advantageous. Adaptations to low oxygen, on the other hand, may imply metabolic adjustment or changes in behavioral patterns.

Distribution of *E. mucronata*, was found to be associated with the OML (Antezana, 1978) in the

Humboldt Current, and thus suggesting the ability of this krill to cope with low oxygen. Such possibility, however has not been studied in nearshore areas, where upwelling circulation and a very shallow OML may impose special constraints. In this work we analyze the spatial distribution of *E. mucronata*, as related to oceanographic conditions during upwelling in nearshore waters, and examine interactions between horizontal and vertical distribution, given the presence of a very shallow OML reported for this area.

MATERIAL AND METHODS

During December 1996 a 3-4 days cruise was carried out off Península de Mejillones, covering 53 sampling stations from nearshore to about 24 km offshore (Fig. 1). At each station CTD profiles were obtained from 200 m to surface, or from near the bottom to surface in shallower locations, using a SeaBird SBE-19 and an Ocean Sensor OS200 CTD's. One CTD was equipped with a YSI recently calibrated Beckman oxygen sensor and the other with a Westar Fluorometer.

Zooplankton was sampled using a General Oceanics Hensen-Net with 0.5 m opening diameter, 2.5 m of length and with $200 \mu\text{m}$ mesh net. The net was equipped with a mechanical double trigger allowing an opening-closing system at desired

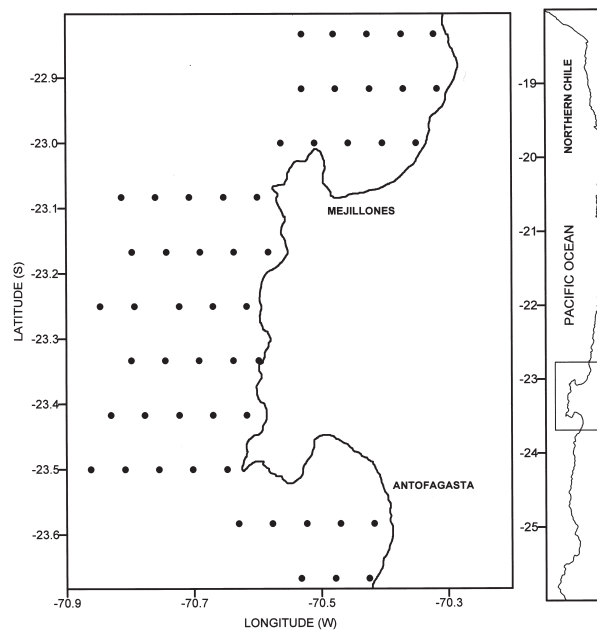


FIG. 1. – Peninsula Mejillones (Northern Chile) indicating the sampling stations to capture *Euphausia mucronata*. The northern is Bay of Mejillones while the southern is Bay of Antofagasta.

depths. Samples were obtained through vertical tows from two strata: 0-50 m and 50-200 m. For this, the net was slowly lowered and then vertically towed at speeds of about 1 m s⁻¹. In its mouth the net was equipped with a previously calibrated digital General Oceanics flowmeter.

No water samples were taken during the cruise, but a few days before, the CTD's and their sensors had been calibrated through *in situ* measurements. Temperature was calibrated using reversing thermometers at five depths, salinity was measured with an Autolab salinometer. Oxygen measurements were made from water samples from five depths: 0, 5, 10, 20, 80 m from three different locations at the northern side of the Peninsula (Fig. 1). Oxygen concentration was measured using the standard Winkler method (Strickland and Parsons, 1972). From the same depths, but on different days, 36 samples for Chlorophyll were taken using 5 l Niskin bottles. Chlorophyll-*a* concentration was measured after filtration of 500 ml of seawater using GF Whatman filters. Extraction of pigments was made at low temperature and darkness for 24 h. Extracts were then measured in a spectrophotometer following Strickland and Parsons (1972). Fluorescence measurements were thus plotted against Chlorophyll-*a* concentration. A linear regression allowed estimates of Chlorophyll-*a* for fluorescence profiles obtained during the cruise.

Preserved zooplankton samples were sorted in the laboratory and all euphausiids removed, identified and counted. *E. mucronata* accounted for more than 90% of total euphausiids in all samples. All stages juveniles and adults were identified and counted, but our analysis did not include eggs and nauplii.

RESULTS

Oceanographic data

Oceanographic conditions during the study period, 18-20 December 1996, were characterized by a nearshore upwelling area, with a major focus in the

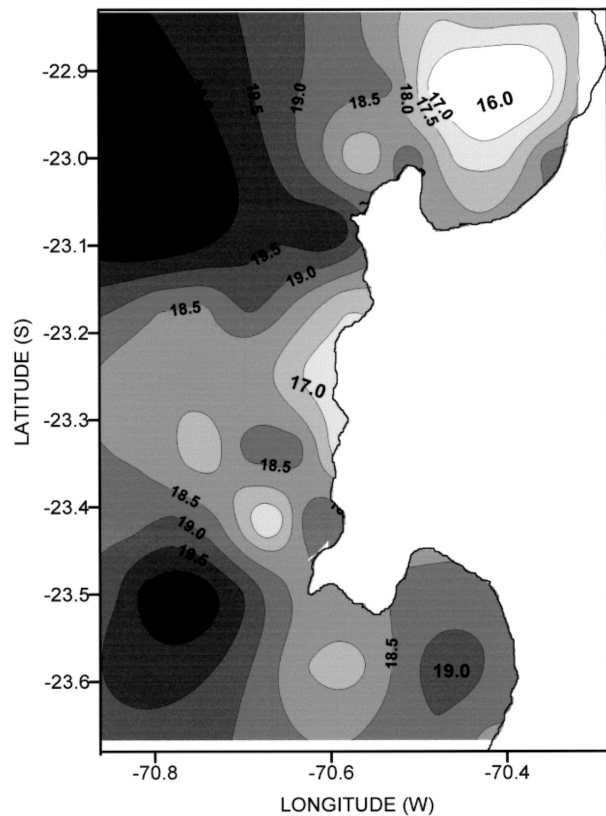


FIG. 2. – Sea surface temperature distribution during the 17-21 December 1996, showing the lenses and filaments of upwelling nearshore. The contours were constructed after interpolation of 53 measurements indicated in Fig. 1.

northeast area, possibly influencing the Bay of Mejillones and other focuses across the Peninsula. The off-shore area appears dominated by a warm water mass (Fig. 2). The surface temperature gradient was near 5°C and the mean temperature reflects spring conditions for this latitude (Sievers and Silva, 1982). The general oceanographic conditions are summarized in Table 1. Salinity values (<34.80 psu) agree with a dominance of Sub-antarctic waters (Sievers and Silva, 1982), while surface oxygen shows some oversaturation levels in areas with high Chla. Coast-oceanic sections in the northern bay, across the Peninsula and in the southern bay (Fig. 3) show that upwelling occurs close to the northern point of the Peninsula and nearshore at the front and in the southern bay.

TABLE 1. – Summary of oceanographic conditions in surface waters during active upwelling (December 1996) in Peninsula Mejillones, northern Chile. SST= Sea surface temperature, SAL=salinity, CHLa = Chlorophyll-*a*.

Variable	Mean	SD	Minimal	Maximal	n
SST (°C)	18.4	1.06	16.0	20.9	53
SAL (psu)	34.60	0.230	34.05	35.11	53
OXYGEN (ml l ⁻¹)	6.48	0.667	5.26	7.95	53
CHLa(µg l ⁻¹)	2.23	1.120	1.12	6.37	53

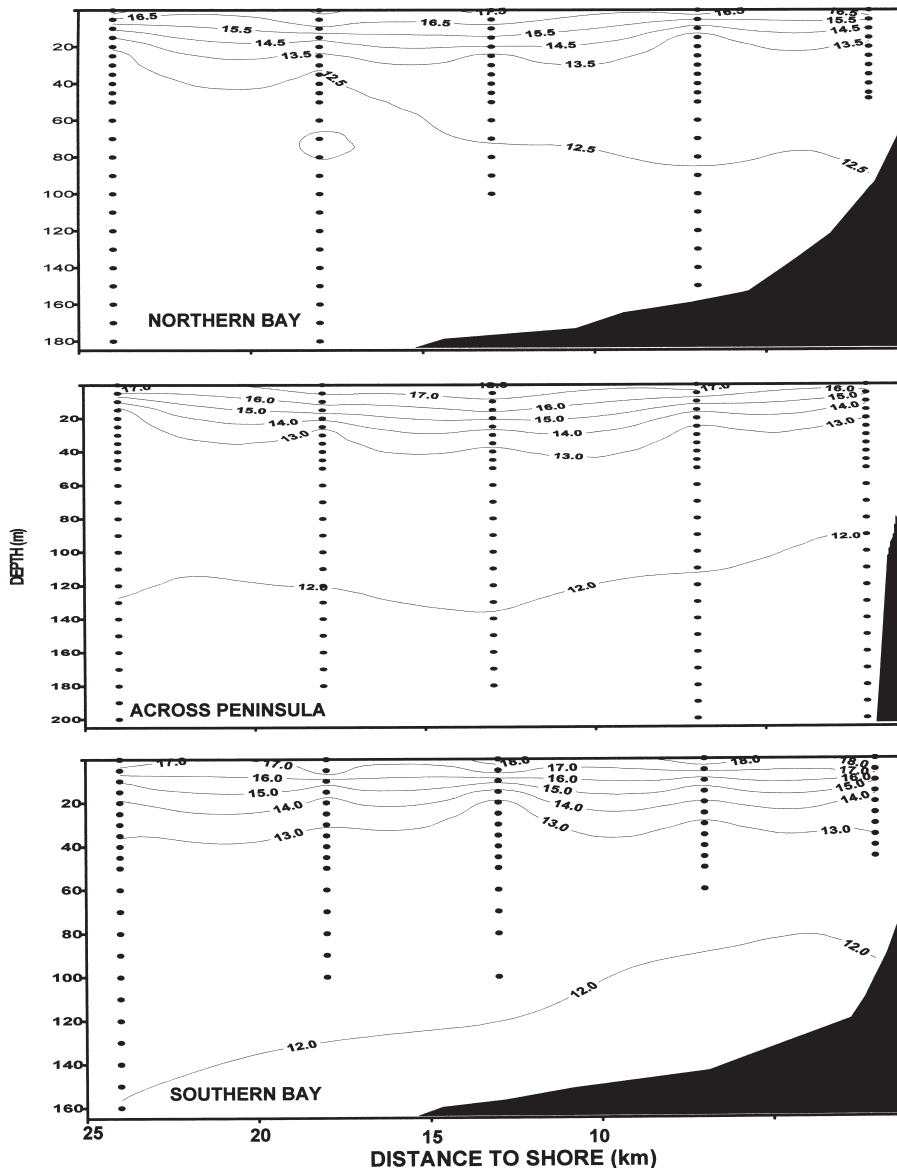


FIG. 3. – Transversal sections of temperature in Peninsula Mejillones during December 1996. The northern bay is Mejillones, the south is Bay of Antofagasta and across Peninsula is the central part of the Peninsula shown in Fig. 1.

The oxygen minimal layer (OML), here defined as $0.5 \text{ ml O}_2 \text{ l}^{-1}$, remains deep offshore and rises in the upwelling centers located nearshore, especially at the northern bay of Mejillones (Fig. 4). There seems to exist a strong association between the location of the upwelling centers and depth of the OML. A stepwise multiple regression with depth of the OML as a dependent variable revealed that this variable is negatively correlated with SST ($F = 9.12$, $p < 0.01$), although not with Chla ($F < 1$, $p > 0.05$).

Surface Chlorophyll-*a* (Chla) distribution appears associated with cold upwelled waters, with a major concentration at the northern area and

nearshore across the Peninsula (Fig. 5). There was a strong negative correlation between Chla and sea surface temperature (SST) ($F = 29.823$, $p < 0.01$). Surface Chla levels ($\sim 6 \mu\text{g l}^{-1}$) are not very high, although vertical profiles constructed with mean values for each of the three areas, indicate that Chla maxima are indeed located around 20 m, near the bottom of the thermocline, reaching maximal values greater than $15 \mu\text{g Chla l}^{-1}$ (Fig. 6).

Spatial distribution

Individuals of *E. mucronata* were found in all locations around the Peninsula (Fig. 7). Integrated

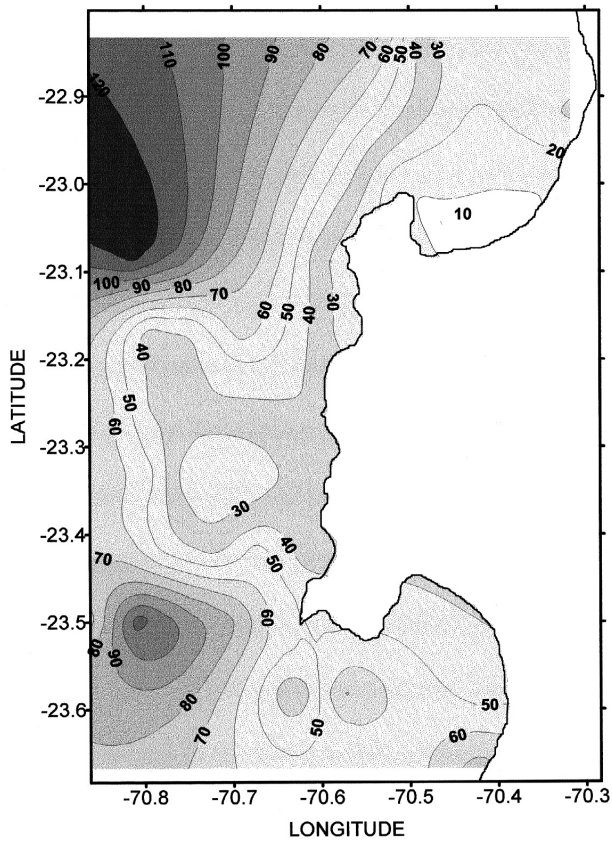


FIG. 4. – Distribution of the depth of the Oxygen Minimum Layer (m), here defined as the depth of $0.5 \text{ ml O}_2 \text{ l}^{-1}$. Contours were constructed after interpolation from vertical profiles at 53 stations (in Fig. 1).

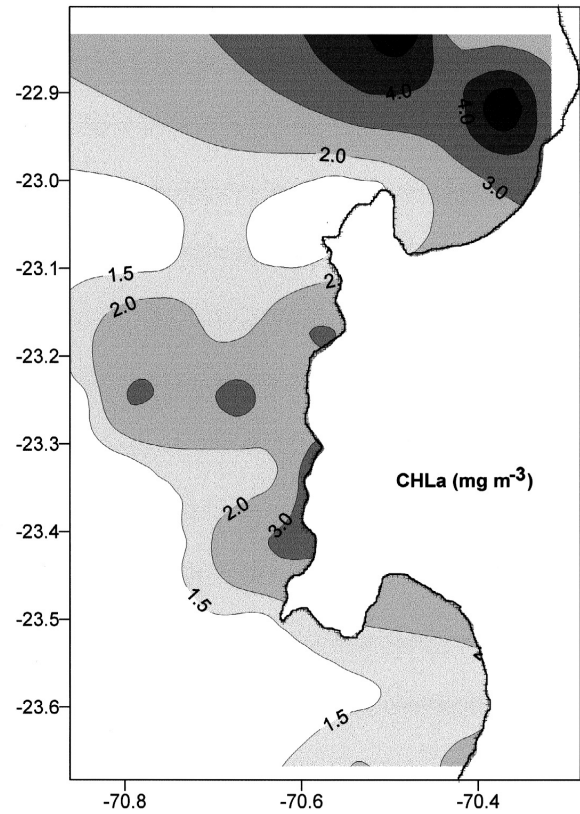


FIG. 5. – Surface distribution of chlorophyll-*a* concentration in Peninsula Mejillones during 17-21 December 1996.

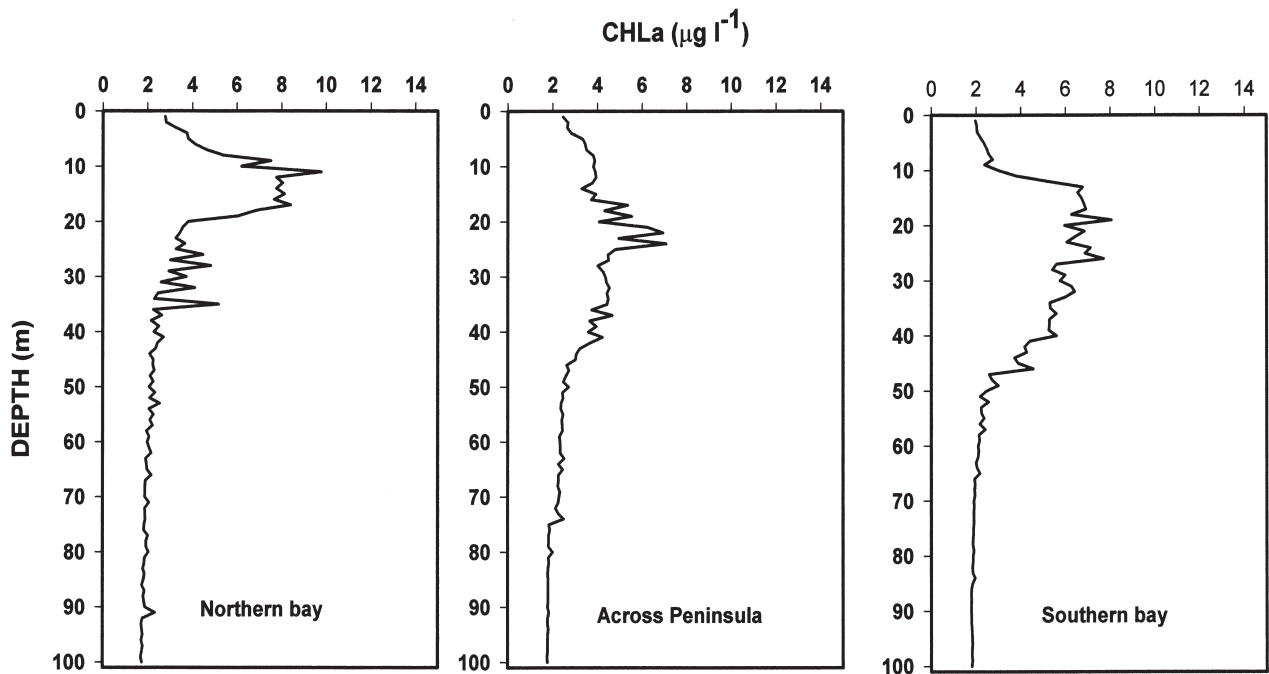


FIG. 6. – Vertical profiles of Chlorophyll-*a* concentration in three areas of Peninsula Mejillones. Each profile was obtained from mean values out of at least 10 stations for each area.

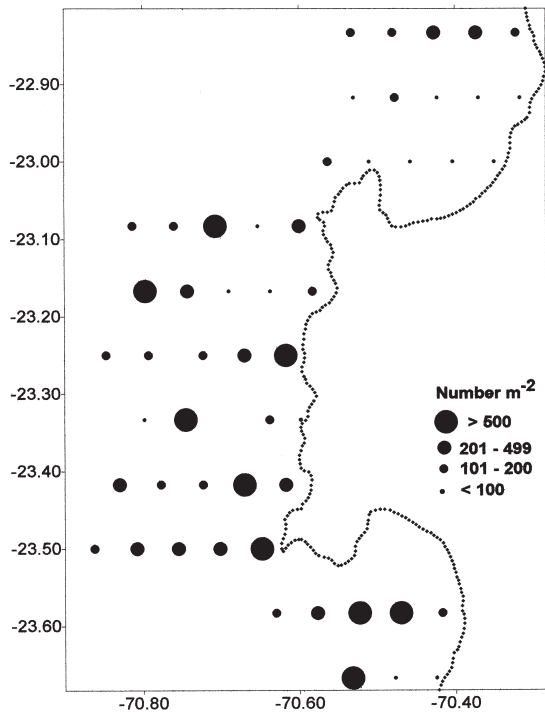


FIG. 7. – Distribution of individuals *Euphausia mucronata* around Peninsula Mejillones. Abundances are from integrated values from 200 m to surface.

numbers over depth show greater concentrations towards the south, while the population is very scarce at the northern bay of Mejillones (Fig. 7). Mean numbers of individuals per meter cube, both at the upper (0-50 m) layer and lower (50-200 m) layer confirm a tendency for greater concentrations in the southern area, specially in deep waters (Fig. 8). Samples were either taken during the night or day, but there were no differences in abundance between such samples ($F_{1,53} = 0.8, p > 0.05$), suggesting that abundance of individuals in either layer was independent of a night/day effect.

However, the use of a vertical distribution index (V) (Huntley and Escritor, 1991) as,

$$V = \ln(n_1/n_2),$$

where n_1 is abundance in upper stratum, and n_2 is abundance in the deeper one, shows that vertical distribution is a function of time of the day, in which animals remain in the upper stratum at night and tend to aggregate in the deeper stratum during the daylight hours (Fig. 9). Diel vertical migration, however seems quite variable among localities

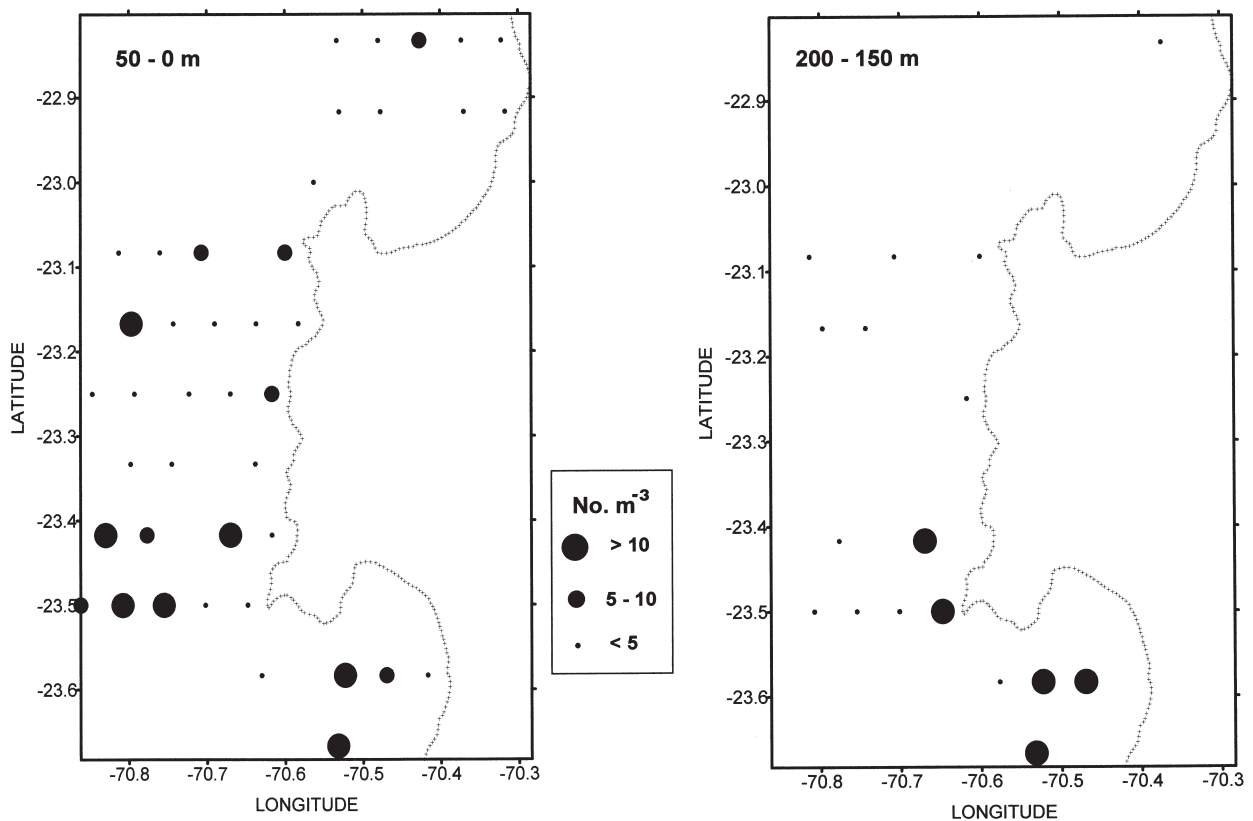


FIG. 8. – Distribution of individuals *Euphausia mucronata* around Peninsula Mejillones in two strata: 50-200 m and 0-50 m.

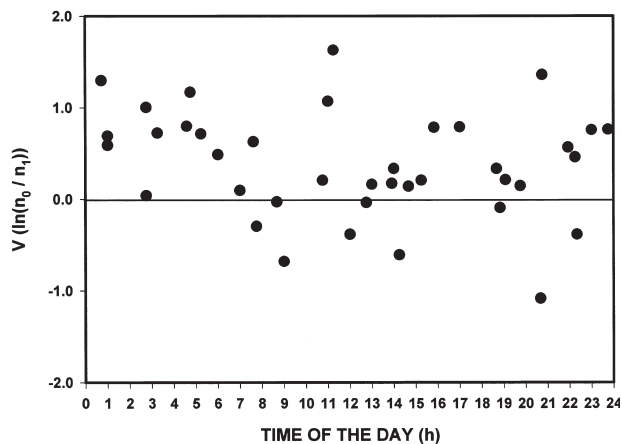


FIG. 9. – The vertical distribution parameter (V) as a function of time of the day of *Euphausia mucronata*. V was estimated from abundance of individuals (No. m^{-3}) in the upper 50 m layer and in the deep layer 50–200 m. During daytime, between 6:00 AM and 20:00 PM, abundances appear greater than during nighttime.

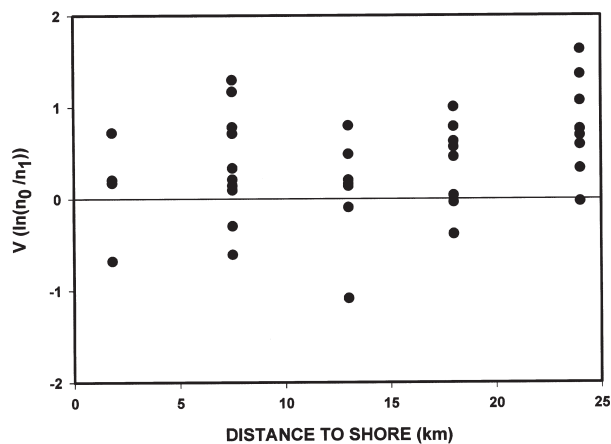


FIG. 10. – The vertical distribution parameter (V) as a function of distance to shore in *Euphausia mucronata*. V was estimated from abundance of individuals (No. m^{-3}) in the upper 50 m layer and in the deep layer 50–200 m. There was a significant ($p < 0.05$) positive correlation between V and distance to shore.

and shows a slight, but significant positive correlation ($p < 0.05$) with distance to the coast (Fig. 10).

In order to establish eventual association among oceanographic variables and abundance, log-transformed abundance of *E. mucronata*, integrated in the water column, was tested against oceanographic variables through stepwise multiple regression (step= 1 to retain one variable) (Table 2). There was a positive correlation between abundance of *E. mucronata* and depth of the OLM, defined as $0.5 \text{ ml O}_2 \text{ l}^{-1}$. This indicates that the species is more concentrated in areas where the OLM is deeper. Conversely, in places where the OLM appears too shallow low numbers of euphausiids are to be found.

TABLE 2. – Stepwise multiple regression ($P=0.1$ to retain variables) to test the effect of oceanographic variables on abundance and distribution of *Euphausia mucronata* around Peninsula Mejillones, during active upwelling on December 1996. Abundance was expressed as \log_e of number of individuals per meter square integrated from 200 m to surface.

Variable	P.Corr.	F-ratio	P
SST	-0.031	0.048	>0.05
Salinity	0.003	0.001	>0.05
Oxygen	-0.113	0.649	>0.05
Sigma-T	0.068	0.230	>0.05
Chla	-0.103	0.532	>0.05
ZOML		5.017	0.029 *

This is more remarkable at the northern bay, in which *E. mucronata* is almost absent and the OLM rises up to the depth of 10 m inside the Bay of Mejillones.

DISCUSSION

Euphausiids are known to actively perform diurnal vertical migration (Brinton, 1979; Roe *et al.*, 1984). The capacity to stay in deep waters during the day and swim to the deeper layer at night may play a significant role in maintaining populations in nearshore areas under upwelling circulation regimes (Peterson *et al.*, 1979; Wroblewski, 1982). Upwelling circulation implies a surface Ekman layer with strong offshore transport and a compensating deep current towards the shore (e.g. Wroblewski, 1982). Therefore, differential currents in the vertical plane in conjunction with vertical migration can be used to maintain position within coastal areas. However vertical migration of euphausiids has been seen to depend on their stage of development. For instance, *Euphausia lucens* eggs and nauplii do not migrate at all, while older stages go into deep waters during the day (Pillar *et al.*, 1989). This indicates that the probability of being advected offshore is not equal for all stages, and early stages are more likely to be washed offshore. However in the horizontal plane, presence of fronts and alongshore currents may also help either maintain, or transport individuals in upwelling regimes (Pillar *et al.*, 1989; Wroblewski, 1982). All these observations reveal a strong influence of currents on distribution of euphausiids in coastal upwelling areas.

The influence of the OML as a factor regulating distributional patterns of zooplankton has also been reported from distinct areas of the world's oceans. Vertical distribution of zooplankton is strongly asso-

ciated with the OML in the north subtropical eastern Pacific (Longhurst, 1967 for review). This has also been described in the Red Sea (Weikert, 1980), as well as in the Peruvian upwelling system (Judkins, 1980). In all situations some species are able to enter the OML and during vertical migration must cope with abrupt diurnal changes in oxygen concentration from $< 1 \text{ ml l}^{-1}$ to 5 ml l^{-1} (Longhurst, 1967). Some species however may limit their vertical distribution under the presence of low oxygen (e.g. Chen, 1986). This might result from increased mortality under low oxygen affecting vertical distribution (Roman *et al.*, 1993).

Low oxygen in shallow waters, usually just below the thermocline, is a general characteristic of coastal upwelling areas (e.g. Bradhorst, 1959; Wyrki, 1962). In northern Chile, the OML is able to enter the upper 50 m nearshore (e.g. Morales *et al.*, 1996a) limiting vertical distribution of anchovy larvae (Morales *et al.*, 1996b). Therefore *E. mucronata* must either cope with low oxygen ($< 0.5 \text{ ml l}^{-1}$) during daytime or restrict the extension of vertical migration to well oxygenated waters. Our results show that individuals can be found in oxygen conditions as low as 0.2 ml l^{-1} below 50 m, but a greater number of individuals tend to aggregate in areas where the OML is sufficiently deep, so that vertical migration is not limited by low oxygen. Although those places where the OML remains deep are mostly located offshore, the relationship between depth of the OML and distance from the shore is not weak. This is because upwelling lenses and filaments occur nearshore, but not uniformly along the coast. Thus places where the OML is also deep nearshore appear suitable for aggregations of *E. mucronata* as well. Thus the spatial distributional pattern of this species may not be directly associated with upwelling lenses in surface waters, but with presence of the OML in subsurface waters.

Although *E. mucronata* is present all around the Peninsula (Fig. 7) it is more abundant in the southern area characterised by less food but deeper OML. It is remarkable that the southern aggregation is much more noticeable in the deeper 50-200 m layer (Fig. 8) and towards the north the population extends only in the upper layer. Food appears more concentrated in the north area, where upwelling seems more active and also because the major current alongshore moves the upper layer northward (Sievers and Silva, 1982). Thus the interaction between vertical and horizontal distribution merges as an adaptation to avoid places

where the OML is too shallow to prevent vertical migration, but still remaining in nearshore areas around upwelling lenses associated with higher food levels. This implies a certain capacity of individuals to maintain aggregations independently from currents during upwelling. The lack of a positive correlation between abundance of individuals and location of upwelling lenses, or filaments, indicates that such capacity is possible.

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