Daily vertical migration of dense deep scattering layers related to the shelf-break area along the northwest coast of Baja California, Mexico

Carlos J. Robinson and Jaime Gómez-Gutiérrez
Laboratorio de Ecología de Pesquerías, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Apartado postal 70-305, CP 04510, Mexico, DF and Departamento de Plancton y Ecología Marina, Centro Interdisciplinario de Ciencias Marinas, Apartado postal 592, CP 23000, La Paz, Baja California Sur, Mexico

Abstract. Echo signals were collected with a Simrad 200 kHz transducer across the shelf-break features off the northwest coast of Baja California (30°05’-30°42’N, 115°50’-116°26’W) during two diel cycles (July 1995) with the objective of describing vertical migrations of two dense deep scattering layers (DSL) found near the shelf break. DSL records were made within an area ±50 m in the neritic zone, ±200 m at the shelf break and ±1000 m depth in the offshore station. Using an Isaacs-Kidd midwater net and Bongo nets, we inferred that the DSL were composed mainly of juveniles and adults of the euphausiids Nyctiphanes simplex Hansen and Euphausia pacifica Hansen. These aggregations have a close interaction with the ocean bottom during the daytime and display a vertical migration, rising near to the surface at night where a progressive horizontal dispersion then occurs. The DSL measured ~3.5-6.0 km horizontally during the night. The ascent and descent migrations of the DSL were significantly fitted to a polynomial function of the second order, suggesting different swimming behavior during these two processes. Vertical migrations of the DSL were between 60 and 90 m. During the descent migration, maximum instantaneous speeds reached ~0.7 cm s⁻¹, and during the ascent, maximum instantaneous speeds were ~0.3 cm s⁻¹. These coastal euphausiid species, along with other macrozooplankton and nektonic organisms, have a daily close interaction with the ocean bottom and also with the pelagic environment, suggesting that they play an important role providing food for demersal and pelagic organisms on the slope and shelf break in the upwelling region off the northwest coast of Baja California.

Introduction

The community structure in the pelagic ecosystem is composed of planktonic and nektonic organisms that display complex trophic interactions and form aggregations in tridimensional space. These shoals have been studied extensively using echosounders and have been recognized as deep scattering layers (DSL). The DSL are generally biological in origin, usually disperse at night, and gather in aggregations during the day, migrating toward the surface. Contrary to earlier views, DSL shoals are essentially dynamic structures, varying as a function of the organisms and temporal and geographic scales.

Spatial scales, size of the aggregations, migration velocity and behavior of the DSL, including several taxa, have been described (see the review by Ritz, 1994), including the northern part of the California Current System (Pieper, 1979; Smith et al., 1989). Although these kinds of studies had been scarce in the southern part of the System, where strong seasonal environmental changes could modify the zooplankton community structure and presumably the dynamics of the DSL, recent observations in zooplankton and micronekton ecology using echosounders have been successfully implemented (Smith et al., 1989; Robinson et al., 1995, © Oxford University Press
C.J. Robinson and J. Gómez-Gutierrez

Acoustic techniques are non-invasive and can detect the larger zooplankton, which are capable of swimming out of the way of nets, and the daily changes in the formation and dispersion of dense aggregations of the DSL. Vertical and horizontal echosounder viewing can increase the precision of abundance estimates and knowledge of the behavior of the patchiness of pelagic organisms. Identification of aggregation mechanisms is of major importance for our understanding of energy flow in the marine food web (Ritz, 1994).

Recent research has recognized the shelf break as a boundary that separates inshore and shelf species from oceanic species, revealing the boundary between shelf and oceanic circulation in the Eastern Current Systems (Genin et al., 1988; Barange et al., 1992; Pillar et al., 1992; Barange, 1994; Gómez, 1995; Johnson, 1995). Isaacs and Schwartzlose (1965) and Smith et al. (1989) have emphasized the interactions between the pelagic DSL and the ocean bottom on the continental shelf, shelf break and slope, and proposed that this enriched region is worthy of more detailed study because the most intensive upwelling processes are usually associated with the continental shelf break, where upwelling fronts occur.

In this study, we recorded the daily DSL dynamics using two kinds of nets (Isaacs-Kidd and Bongo) and hydroacoustic devices over the shelf break along the northwest coast of Baja California. DSL dynamics included migration speed to the surface during the night and a progressive horizontal dispersion not previously described for this area, a region with intense upwelling activity. Seasonal differences along the west coast of Baja California yield maximum upwelling intensities from March to June and seasonal warming from July to November (Bakun and Nelson, 1977).

**Method**

In July 1995, on board the R/V 'El Puma', two transects, each 18 km long, perpendicular to the coast, and separated by 65 km, were located off the northwest coast of Baja California, Mexico (30°05'-30°42'N, 115°50'-116°26'W) (Figure 1). Each transect was set to cover three zones, each ~6 km long: a neritic zone, which covers the shallower part of the transect (<80 m); a slope zone covering all the shelf break (~200 m); and the oceanic zone, the deep (>1000 m) and offshore part of the transect. Along each transect, we established three oceanographic stations. Two were at the extremes of each transect and one in the middle. During ~24 h, continuous recording of the water column using hydroacoustics was carried out. Our path started at the neritic station, went to the oceanic, then reversed the route to the middle station to obtain data there, and finishing at the neritic station ~3 h later. Ship speed along the transect averaged 11 knots. At each station, the temperature of the water column was recorded using an Inter-Ocean SO4 CTD. The reported time is Pacific Standard Time. In transect one, observations started at 13:00 h (2 July 1995) and finished at ~12:00 h (3 July 1995). At transect two, observations started at 14:00 h (4 July 1995) and finished at 14:00 h the following day. Local dawn during summer is ~06:00 h and dusk is ~20:00 h.

A Simrad EY-200 echosounder with a working frequency of 200 kHz was used. For analysis, we used a Hydro Acoustic Data Acquisition System (HADAS,
Fig. 1. Map of the study area, indicating the sampling stations covered in July 1995 within the two transects along the northwest of Baja California, Mexico.

Version 4.01) developed by Lindem and Houari (1988). This latter is an echo-counting analysis system that transforms the received echo distribution into area densities and hence abundance estimates. The system is based on a combination of hardware and computer software that together have the capability of digitizing and storing hydroacoustic transects. This program uses a modification of the Craig and Forbes (1969) algorithm to remove the beam-pattern effect. Because we used a time-varied gain of 40 LogR, analysis of echo counting for individuals and target-size distribution was possible. Results for echo counting are presented as individuals per hectare (ind. ha\(^{-1}\)). Pulse duration was set at 0.3 ms. Before the cruise, the echosounder was calibrated with a standard 13 mm copper sphere (-45 dB). HADAS used with a Simrad EY-200, 200 kHz, is able to record echoes between -37 and -57 dB, detecting dense aggregations of euphausiids, the gas bubble of physonect siphonophores, mesopelagic crustaceans and fish. Organisms that are aggregated into patches or layers return more scattered sound per unit volume than the same organisms would if distributed evenly throughout a larger volume (Smith et al., 1989). Therefore, we assume that this echosounder detects zooplankton patches rather individual animals. Moreover, smaller targets like dense copepod and euphausiid patches have been previously recorded (Whisner et al., 1988).

Isaacs–Kidd net midwater trawls were performed at depth and locations where echosounder information, displayed on the computer screen in real time, showed the presence of the dense DSL. A modified Isaacs–Kidd midwater trawl net (cod end liner of 500 \(\mu\)m mesh and mouth area of 2.5 \(\times\) 2.5 m) was trawled for ~30 min at 6 knots. These samples were used as a qualitative sampling of the DSL, preserving only 1 l of the total catch. To analyze them, they were divided with a Folsom splitter into aliquots not larger than one quarter. The maximum volume filtered with the Isaacs–Kidd midwater net was ~78,750 m\(^3\). Zooplankton samples
were collected by means of Bongo nets fitted with 300- and 500-μm-mesh nets towed obliquely from 200 m to the surface at the oceanic and slope stations. At the neritic station, Bongo nets were towed from 10 m above the bottom to the surface. About six samples were collected at each oceanographic station, obtaining ~18 samples per transect. Samples were preserved in 5% formalin buffered with sodium borate. Zooplankton biomass was determined by volumetric method and normalized to milliliters per 1000 m$^3$~1 week after we concluded the oceanographic survey. Because most of the Isaacs-Kidd samples were euphausiids, the juveniles and adults of euphausiids collected in the Bongo net were sorted and identified. Bongo net samples were analyzed in their entirety.

Results

Environmental conditions

Along both transects, the temperature profile showed an increase in temperature from the neritic towards the oceanic area, a typical pattern found in upwelling areas along Baja California. The mean of the monthly upwelling indices obtained from Punta Eugenia (27°N, 116°W) during 1995 (NOAA, http://www.pfeg.noaa.gov/products/upwelling.html) indicated that the highest upwelling indices were recorded during June and July (221 and 126 m$^3$ s$^{-1}$ per 100 m of coastline) showing positive anomalies (June 26 and July 12). These values signify a net volume transported offshore in the surface Ekman layer and support our hydrographic observations of active upwelling during the period studied. An isotherm of 14°C was found near the surface in the neritic zone of transect one and offshore in transect two where a temperature of <14°C dominated the continental shelf (Figure 2A and B). A profile obtained at the neritic, slope and oceanic stations showed temperature declining evenly from 15°C at the surface to 9.5°C at 200 m in transect one, and from 14 to 10°C in transect two. The thermocline in transect one was found between 25 and 30 m depth, and in transect two between 30 and 35 m depth (Figure 2A and B).

Hydroacoustic records

Figure 3A and B shows the location of the DSL in a diel cycle over the shelf break along the transects. During the night, the length of the DSL was ~6 km in transect one and 3.5 km in transect two. During the day, the DSL were near the bottom, where it was not possible to make a reliable estimation of their lengths. Both DSL were near the shelf-break regions. The DSL showed an undulating form during sunrise and sunset, probably affected by internal waves, indicating that organisms are contending with a more dynamic environment than normally encountered in the open ocean. Some of the catch obtained using Isaacs-Kidd and Bongo nets showed an unusual abundance of euphausiids, in the samples, for this area and season. However, the echosounder probably recorded an abundance of dense minipatches of macrozooplankton rather than an abundance of individuals. The presence of confirming replicate echograms during 24 h was interpreted as a semipermanent patchiness located in the area. The core of the
DSL of both transects during all 24 h was found in layers with a temperature of <11°C and below the thermocline (Figures 2A and B and 3A and B).

Once the dimension and position of the DSL were obtained, an area of ~7 km was selected in the echograms for analysis. For transect one, the selected area was from 85 m depth to 2 km after the disappearance of the bottom in the echogram (>200 m). For transect two, it was from 70 m depth to 2 km after the disappearance of the bottom. The water column along these areas was divided into layers of 10 m depth, starting at 10 m and ending at 140 m, and analyzed using HADAS. All the hydroacoustic analyses were carried out using target strength measuring -53 to -57 dB. This echo strength range was used based on (i) results obtained in >400 Isaacs-Kidd midwater trawls that we have made along the west coast of Baja California since 1992 and (ii) comparing the catch with echo analysis obtained using the same frequency, the same calibrated echosounder and the same variables to acquire hydroacoustic data. Accordingly, this target strength corresponds to zooplankton aggregations, mainly euphausiids, which are common in the area (Gómez, 1995; Gómez and Robinson, 1997).

In both transects, there were pronounced differences in the general appearance of aggregations between day and night (Figure 3A and B). These echograms show that, in general, the aggregation behavior of the zooplankton
leaves to compact and dense aggregations near the ocean bottom during the day, and more diffuse and less detectable aggregations over the water column during the night. This behavior was also confirmed by hydroacoustic analysis. Higher backscatter along the water column was obtained during the day in both transects (Figure 4A and B).

To explore vertical migration rates, we used an analysis method based on the 50% cumulative relative abundance criterion, explained as follows: starting from the shallower layer, the cumulative relative frequency of abundance was obtained down the water column. We used the depth where 50% of the cumulative frequency was found to monitor diel variations of the DSL. Figure 5A and B
Fig. 4. Backscattering abundance expressed as the sum of individuals per hectare along the water column. To obtain these data, the water column was divided into layers of 10 m depth, starting at 10 m and ending at 140 m. (A) Transect one; (B) transect two.

shows variations in depth of the 50% cumulative frequency along the diel cycle in both transects. In transect one, note the increase in depth of the DSL around 23:00 h (Figure 5A). Along transect two, there was also an increase in depth at ~22:00 h (Figure 5B). Once the position of the 50% cumulative relative abundance of the DSL was obtained at different hours, speed rates of ascents and descents were calculated, pooling the observations between 21:00 and 03:00 h for both transects (Table I). A polynomial function of second order (Sokal and Rohlf, 1981) was fitted to the data using the following function:

\[ Y = a_1 + b_1 X + b_2 X^2 \]

where \( Y \) is the predicted depth of 50% cumulative frequency of abundance, \( b_1 X \) is the local time and \( b_2 X^2 \) is the time squared. The fitted polynomial equation calculated was: depth = 216 + 31.17 time – 207.7 time^2 \( (r^2 = 50.1, F = 8.02, \text{d.f.} = 14, P = 0.006) \). Observed and predicted values are shown in Figure 6A, indicating a different pattern in the descending and ascending movements of the DSL. Using the polynomial equation, we calculated the instantaneous speed (cm s\(^{-1}\))
Fig. 5. Variation of the 50% cumulative frequency of abundance along the diel cycle. The upper part of the bar represents 25% cumulative frequency and the lower part is 75% in (A) transect one and (B) transect two.

Table I. Vertical position of the 50% cumulative frequency abundance used to calculate ascending and descending instantaneous speeds of the DSL.

<table>
<thead>
<tr>
<th>Transect one</th>
<th>Transect two</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth where the 50% was detected</td>
<td>Depth where the 50% was detected</td>
</tr>
<tr>
<td>150</td>
<td>125</td>
</tr>
<tr>
<td>110</td>
<td>100</td>
</tr>
<tr>
<td>85</td>
<td>75</td>
</tr>
<tr>
<td>70</td>
<td>50</td>
</tr>
<tr>
<td>70</td>
<td>100</td>
</tr>
<tr>
<td>125</td>
<td>100</td>
</tr>
<tr>
<td>140</td>
<td>145</td>
</tr>
</tbody>
</table>
Fig. 6. Depth of the 50% cumulative frequency of abundance along a diel cycle. (A) Data for both transects were pooled and fitted to a polynomial function of the second order (dotted points). Bars indicate 95% confidence intervals of predicted values. The triangles are the observed depth in transect one and the asterisks are the observed depth in transect two. (B) Predicted instantaneous speed of the DSL using the polynomial function.

do the DSL. Results show speeds of 0.5-0.7 cm s\(^{-1}\) between 03:00 and 06:00 h, decreasing progressively to 12:00 h. Ascent movement was slower, with speeds below 0.25 cm s\(^{-1}\) between 12:00 and 22:00 h (Figure 6B).

To investigate whether there was a homogeneous distribution of abundance of the DSL along the transects, a \(\chi^2\) test was performed. To do this, the areas already analyzed for vertical distribution were divided into eight similarly sized horizontal segments (~0.8 km each). Segments were numbered from one to eight, starting at the neritic side of the area. Abundance was obtained using HADAS in each division down the water column from 10 to 100 m depth. First, the analysis was applied to all eight segments. Next, both segments at the extremes were
eliminated and the test was carried out on the remaining six, and finally on only four segments. Results show that in transect one, there is a tendency for the distributions to become more homogeneous during the night; however, significant differences were obtained using only four segments. In transect two, though, there was no tendency in any of the segments (Table II).

The echograms also show the presence of stronger echoes during the night when the DSL was well above the bottom. This was evident in transect one at 02:00 h and at 19:00 h in transect two (Figure 3A and B). An echo analysis of these echograms shows target strengths between -37 and -45 dB, which had been associated with anchovies (*Engraulis mordax* Girard) (Robinson *et al.*, 1995). However, the proportion of abundance of these echoes was quite low, <10% of the total range analyzed (-37 to -57 dB).

**Isaacs-Kidd and Bongo net sampling**

The Isaacs-Kidd net was used to sample the DSL that had been recorded hydroacoustically between stations. All trawls were performed during the night in both transects. In transect one, we made six trawls between 19:00 and 04:00 h. In transect two, we made five trawls between 19:00 and 05:00 h. These data were used in qualitative terms to determine the population structure of the main species responsible for the scattering record obtained from the echosounder. Therefore, only a small subsample was analyzed in each trawl. In transect one, a dense aggregation formed by two euphausiid species, *Nycitiphanes simplex* Hansen (*n* = 231) and *Euphausia pacifica* Hansen (*n* = 174), was found. Most of the population structure caught with the Isaacs-Kidd net were juvenile and adult *N.simplex* (9–17 mm total length) and *E.pacifica* (8–21 mm). The population structure of *N.simplex* was dominated by males and *E.pacifica* by females (Figure 7A and B).

In transect two, euphausiid species *N.simplex* (*n* = 491) and *E.pacifica* (*n* = 151)
were also found. Most of the population structure were also juvenile and adult *N. simplex* (8–12 mm) and *E. pacifica* (8–20 mm). The population structure of *N. simplex* and *E. pacifica* was dominated by males, although females were larger than the males in *N. simplex* (Figure 7C and D). In addition, three adult specimens of *Thysanoessa spinifera* Holmes were found in this transect. Isaacs–Kidd net samples also included, although in less abundance and biomass, anchovies *Engraulis mordax* Girard, squid *Loligo* spp. and the red crab *Pleuroncodes planipes* (Stimpson).

In transect one, the highest zooplankton biomass using Bongo nets was found over the continental shelf (275 ml per 1000 m$^3$) and the slope (125–175 ml per 1000 m$^3$) with the zooplankton biomass decreasing in the oceanic sector of the transect (<100 ml per 1000 m$^3$). The highest biomass was found early in the morning at the coastal station and at about midnight at the slope station (Figure 8A). In transect two, the smallest biomass was found over the continental shelf (<10 ml per 1000 m$^3$) with the highest biomass at the slope and oceanic stations about midnight (200 ml per 1000 m$^3$) (Figure 8B). Four euphausiid species were found in the Bongo net trawls, dominated by *N. simplex*, followed by *E. pacifica*, *Nematoscelis difficilis* Hansen and *Euphausia gibboides* Ortmann.
Fig. 8. Diel variation of the zooplankton biomass caught with Bongo nets (500-μm-mesh net) in transect one (A) and two (B) in the coastal, slope and oceanic area of each transect along the northwest coast of Baja California, Mexico. Numbers of samples per transect were not similar; there were 18 samples in transect one and 27 samples in transect two.

Discussion

The DSL found in this study were dominated by two euphausiids in almost similar proportion, *N. simplex*, a marginal neritic species of the Eastern Tropical Pacific, and *E. pacifica*, a subarctic species of the California Current terminus, although Bongo net samples indicate that copepods and siphonophores were also abundant. Both euphausiid species have been recognized as facultative omnivores (Theilacker *et al.*, 1993) that can proliferate during active upwelling. However, we could not test niche separation between the species in these dense DSL. These DSL found between Ensenada and Punta Baja had a particular vertical distribution pattern.

The DSL we observed have a close interaction with the ocean bottom during the day and a pelagic behavior during the night, suggesting that they may play an important role as food for both demersal and pelagic organisms in the slope and shelf break in the upwelling region off the northwest coast of Baja California. Interactions between dense DSL and the ocean bottom at continental shelf, shelf...
DVM of dense deep scattering layers

break and slope have been found in several upwelling regions (Isaacs and Schwartzlose, 1965; Genin et al., 1988; Simard and Mackas, 1989; Barange, 1994). The importance of the shelf break in the biological enhancement of productivity is well documented (Santander-Bueno, 1981; Barange and Stuart, 1991; Gómez, 1995; Torgersen et al., 1997). This region is an interesting and important area as it is the boundary between the deep ocean circulation that changes slowly and the shallow shelf circulation that responds rapidly to changes in forcing (Johnson, 1995). The principal physical effects attributed to the presence of the shelf break are the existence of a secondary upwelling zone located just seaward of the shelf break and close to the bottom, and the existence of a circulation cell above the continental slope (Lill, 1979). The shelf width significantly affects the upwelling rate, with a greater rate for a smaller width (Cai and Lennon, 1993). In the area studied, the shelf width is narrow compared to the southern part of Baja California (i.e. Bahia Vizcaino 28°N, Bahia Ulloa 25-27°N), suggesting favorable topographical conditions for shelf-break upwelling.

A close relationship of N. simplex with the bottom during the day was suggested by Elorduy and Caraveo (1994) in Bahia de La Paz along the southwest coast of the Gulf of California, because it is an important item in the stomach content of the demersal whitefish Caulolatilus princeps Jenyns. Robinson et al. (1995) found, along the west coast of Baja California, a close relationship between anchovy (Engraulis mordax Girard) abundance and dense aggregations of euphausiids. Moreover, the stomach contents of the anchovies revealed large amounts of euphausiids. According to our hydroacoustic records, there is a close relationship between the aggregations and the shelf break, although what controls this behavior is not well understood. Reproductive behavior has been proposed for daytime surface swarms of N. simplex (Gendron, 1992); however, it is obvious that these species display complex migration patterns and patchiness behavior that have not previously been reported. It is well known that many zooplankton species are able to modify their diel rhythm to existing environmental factors (light, gravity, oxygen) and the inherent behavioral pattern that is dependent on the maturity of the specimens (including also endogenous factors like sex, age and biological rhythms) (Fragopoulu and Lykakis, 1990). Dispersion of the DSL during night-time may be stimulated by hunger to avoid intraspecies competition, as reported in shoaling fish species (Robinson, 1995). Field data suggest that N. simplex and E. pacifica feed on zooplankton (primarily copepods) at the greater depth during the day, but primarily on phytoplankton near the surface during the night (Theilacker et al., 1993). Food concentration is assumed to influence the diel vertical migration only during the ascent of the organisms. During their descent, they do not feed and only try to reach darkness and safety. In large swarms, mysids collected significantly more food than those in small swarms when food is patchy. In a conflicting situation of limited food and threat from a predator, survival demands that swarms become more tightly cohesive even though food capture suffers as a result (Ritz, 1994). In this study, tightly bound DSL were found over the shelf break, possibly as a strategy to avoid epipelagic predators, migrating to feed during the night and spreading over the continental shelf, and to a lesser degree in the oceanic zone. However, there is evidence that migrations
do not take place under circumstances of limited food availability (Wishner et al., 1988). We cannot reject the hypothesis that these euphausiid species feed on the detritus found on the ocean bottom.

In this study, we observed how DSL were distributed throughout the diel cycle in the inshore–offshore axis. Hydroacoustic data showed some mismatching with zooplankton biomass obtained with the Bongo net. Zooplankton biomass estimated from nets can be highly affected by plankton patchiness; therefore, comparison with continuous hydroacoustic records along a transect should be interpreted carefully. In general, in the two transects, high zooplankton biomass values were recorded near the slope area where hydroacoustic recording indicated dense plankton aggregations. Results of the $\chi^2$ test in transect one suggested that individuals are distributed homogeneously towards night. However, the relationship of these movements with environmental conditions was not clear. *Nyctiphanes simplex* and most *Euphausia* spp. usually cross the thermocline, indicating why these aggregations easily spread out over the water column, while other species like *E. gibboides* and *Nematoscelis difficilis* remain at or beneath the thermocline (Brinton, 1967; Simard et al., 1986; Lavaniegos, 1996). These diel vertical migration patterns have been observed with other euphausiid species like *Meganyctiphanes norvegica* (M. Sars), which did not migrate through the thermocline, whereas *Thysanoessa rachii* (M. Sars) does (Bergstroem and Stroemberg, 1997). William and Fragopoulu (1985) and Fragopoulu and Lykakis (1990) reported instead that the seasonal thermocline can be an influence in different diel vertical migrations (e.g. a tendency to aggregate at the thermocline layer). Moreover, temperature discontinuity alone does not seem to limit migration of *Nyctiphanes couchii* populations. In this study, DSL cores were found in a region where vertical profiles indicate lower temperature (<11°C).

Diel vertical migration plays a determining role in the downward flux of particulate organic matter (Angel, 1985). The significance of this has been emphasized recently. According to Andersen and Nival (1991), in fact, by feeding in surface layers and defecating at depth, migrating organisms could accelerate the fecal pellet flux. To be important, such a phenomenon must have the following characteristics: (i) the migration rate of organisms must be fast or faster than the sinking rates of its fecal pellets; (ii) gut retention time must be long enough to allow the animal the maximum depth before defecation; (iii) the amplitude of the migration, related to the migration speed, must be great and the pellets must be large. For this reason, it is important to demonstrate what are the diel vertical migration pattern and the speed of at least some key species like the euphausiids *N. simplex* and *E. pacifica*.

Vertical migration speeds of the DSL have been estimated using nets and different hydroacoustic devices. Smith et al. (1989) reported maximum migration rates over the San Diego Trough off southern California, estimated using an uncalibrated ADCP 307 kHz, on the order of 5–8 cm s$^{-1}$ during the ascent and 3–4 cm s$^{-1}$ during descent. Heywood (1996) reported vertical speeds of zooplankton measured from the ADCP between 2 and 6 cm s$^{-1}$ in the northeast Atlantic, Wiebe et al. (1992) estimated swimming speeds of 1–6 cm s$^{-1}$ for copepods and euphausiids, and Roe et al. (1984) reported that speeds varied...
from 1 to 4 cm s\(^{-1}\) both upward and downward. Our estimations were 10 times smaller than previous studies, estimating maximum speeds of 0.7 cm s\(^{-1}\) during descent and <0.25 cm s\(^{-1}\) for ascent. Lower migration speeds can be explained because the DSL was over the shelf break (<100 m depth), and moved vertically between 60 and 90 m, indicating relatively more horizontal than vertical movement. Our method is an average approach (50% of cumulative abundance) of the diel vertical migrations of the whole DSL so that specific migration speeds of the faster euphausiids can be buffered by lower migration speeds of copepods and other smaller scatterers. It is known that euphausiids move together and the copepods move more progressively, with portions of the population moving at different rates (Wiebe et al., 1992). Therefore, in our work, estimations can be considered as an average of faster-swimming animals like euphausiids and slower-swimming animals like copepods. In fact, our estimations are similar to larger upward migration speeds for copepods (0.8–2.5 cm s\(^{-1}\)) (Enright, 1977a). Our findings represent a different diel vertical migration speed to that described for offshore regions (e.g. Smith et al., 1989; Heywood, 1996), which were made in regions of water depths of ~1000–4000 m. In offshore regions, depth distributions, vertical and horizontal dimensions of the aggregations, and gaps between aggregations are relatively consistent (Smith et al., 1989). Our data over the continental shelf suggest a more variable DSL patchiness dynamic and a close relationship with the ocean bottom. Food distribution and feeding may be an alternative explanation for low speeds. Over the continental shelf and shelf break, a high concentration of food over all the water column can promote small-range vertical migrations in comparison to oligotrophic oceanic environments. Pearre (1979) claimed that simple counts of organisms as a function of time and depth or sonic scattering records can yield only minimal estimates of the range or velocity of vertical migrants. As we mentioned before, we estimate an average of the vertical velocity of the whole DSL. We did not estimate individual animal swimming speeds which usually tend to be high, up to 10 cm s\(^{-1}\) for \textit{E.pacifica} (Torres and Childress, 1983), whereas those for populations observed in the field are typically much smaller, 2 cm s\(^{-1}\) for \textit{Euphausia krohni} (Brandt) (Angel, 1985). Under field conditions, it is difficult to estimate individual speeds. Enright (1977a) reported sustained high-speed upward migration of copepods; however, it is not probable that zooplankton maintain high speeds for long periods (several hours) every day because this behavior has been associated with predation avoidance. In addition, different species and life stages [ontogenic vertical distribution \textit{sensu} William and Fragopoulu (1985)] should have different speeds over the diel cycle.

To date, few models consider migration. Some of these are wholly theoretical (Iwasa, 1982; Gabriel and Thomas, 1988), whereas others incorporate migration via the grazing term for the migrant species into a metabolic model (Enright, 1977b) or into ecosystem simulation models (Walsh, 1975; Herman and Platt, 1983). Possibly, the most complete model for diel vertical migration made by euphausiids, particularly \textit{M.norvegica}, was proposed by Andersen and Nival (1991). The model consists of a two-order partial equation describing the temporal and spatial variation of the biomass of euphausiids. Migration is
expressed as a function of light (irradiance) and food concentration (phyto- and
zooplankton), which are considered as forcing variables. It simulates daytime
depths of 256–416 m, night-time depths of 8–64 m, migration amplitudes of
208–372 m, and an ascent and descent migration taking 3 h (maximum possible
speed of $-150 \text{ m h}^{-1} = 4.16 \text{ cm s}^{-1}$). Our maximum speeds estimated with our
hydroacoustic method could be used for this model, although they were consider-
ably slower (0.3–0.7 cm s$^{-1}$), explained because $N.simplex$ and $E.pacifica$ are much
smaller than $M.norvegica$. William and Fragopoulu (1985) reported mean
population migration rates of $N.couchii$ of $-14–18 \text{ m h}^{-1}$ (0.38–0.5 cm s$^{-1}$). Unfor-
tunately, the basic run of the Anderson and Nival model gives a symmetrical
ascent and descent, which was not recorded in our field data; in addition, it pos-
sibly does not fit well to neritic species displaying diel vertical migration of
60–90 m. Our polynomial equation simulates differences of ascent and descent
maximum speeds. Although Brinton (1962, 1967) reported that $N.simpex$
is mainly above 100 m (considered a short-distance migrant), some adults can be
distributed at 600 m. Most of the population of $E.pacifica$ is mainly in the upper
300 m; however, some individuals have been collected at 1000 m. This indicates
that these species could have a wider vertical migration then observed in the
present study.

The most common diel vertical migration behavior observed in zooplankton is
to ascend to the surface layer at dusk and descend to a deeper layer at dawn.
However, like the Andersen and Nival model, several studies have reported
migrations to be symmetrical (e.g. Plueddemann and Pinkel, 1989), and reverse
migrations ($sensu$ Ohman, 1990) do exist. According to the polynomial model of
the second order, ascent and descent were almost symmetrical; however, the
equation simulates a faster descent and a slower ascent. This agrees with experi-
ments carried out by Hardy and Bainbridge (1954), who demonstrated that down-
ward migrations are a result of active swimming and not passive sinking.

In addition, a particular behavior was observed in both transects, i.e. a slow
descent after arrival at the surface at dusk, with a second ascent to the surface
toward the end of the night, after the midnight descent (Cushing, 1951), also
called twilight migration by Heywood (1996). Although the behavior is not well
understood, these results indicate that migrating animals within layers do not
move in unison as proposed by Pearre (1979). From results obtained in these two
DSL, euphausiids and perhaps other macrozooplankton and nektonic organisms
form dense shoals with different dynamics observed as nocturnal upward and
downward movements before descending during the day.

Further investigations should be performed to explore the latitudinal changes of
the DSL along the west coast of Baja California and to evaluate whether these verti-
cal migration patterns related to the shelf break display seasonal variations, and to
carry out a more accurate assessment of the abundance of zooplankton aggrega-
tions in the variable environment and highly productive upwelling region over the
continental shelf and shelf break along the Pacific coast of Baja California.
DVM of dense deep scattering layers

Acknowledgements

Thanks to Dr Virgilio Arenas-Fuentes, all the people from the Laboratorio de Ecología de Pesquerías UNAM and to the RV ‘El Puma’ crew for assistance and comradeship at sea, and to Dr Ellis Glazier, CIBNOR, for his editorial help with the English language text. This research was supported by funds provided by the Dirección de Estudios de Posgrado e Investigación (DEPI 966584 y 970123) and by the Consejo Nacional de Ciencia y Tecnología (CONACyT 940511, N511-N9108). The authors are supported by Sistema Nacional de Investigadores (SNI) and the second author is also supported by Comisión de Operación y Fomento Actividades Académicas del Instituto Politécnico Nacional (COFAA-IPN) fellowships.

References


C.I.Robinson and J.Gómez-Gutiérrez


DVM of dense deep scattering layers


Received on November 10, 1997; accepted on April 23, 1998.