

Tidal current transport of epibenthic swarms of the euphausiid *Nyctiphanes simplex* in a shallow, subtropical bay on Baja California peninsula, México

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ABSTRACT: *Nyctiphanes simplex* is the most prominent neritic euphausiid along the southwest coast of the Baja California peninsula, México. It was thought that this species is usually distributed in areas deeper than 50 m. However, in the mouth of a subtropical bay (Bahía Magdalena, 28 to 50 m depth) using a 120 kHz split-beam echosounder, a submarine video camera, and a 1 m plankton net, we discovered that high-density swarms of adult *N. simplex* enter the bay near the seafloor during spring and summer but not in winter, even though flood current speeds were statistically indistinguishable among seasons. Euphausiid transport was modulated by their abundance over the continental shelf, their daily vertical migration, and the semidiurnal tidal currents. From 6 series of 48 h sampling runs along a 18 km long transect located through the mouth of the bay, we estimated a set of acoustic parameters to identify euphausiid swarms and distinguish them from aggregations of the abundant local micronektonic galatheid *Pleuoncodes planipes*. The euphausiid swarms were vertically segregated from the dense aggregations of *P. planipes*. Euphausiids that entered the bay were completely dispersed within strong spring tidal currents ($>125 \text{ cm s}^{-1}$) and subsequently formed dense aggregations inside the bay, where current speed decreased substantially. Euphausiid distribution inside the bay never extended farther than the continental-shelf water mass delineated by the tidal front. In the bay, adult *N. simplex* remained close to the sea-bottom day and night. We hypothesized that the large euphausiid and red crab biomass transported from the continental shelf into Bahía Magdalena may contribute significantly to the trophodynamics of this eutrophic subtropical bay.

KEY WORDS: *Nyctiphanes simplex* · Acoustics · Euphausiid · Epibenthic aggregation · Swarm formation · Tidal currents · Bahía Magdalena · México

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INTRODUCTION

Nyctiphanes simplex Hansen is the most abundant neritic euphausiid species along the continental shelf of the southern part of the California Current System, the Gulf of California, and the Humboldt Current System (Brinton 1962, Brinton & Townsend 1980, Gómez-Gutiérrez et al. 1995, Brinton et al. 2000). When using conventional Bongo sampling nets towed from 5 to 10 m above the seafloor to the sea surface, previous

studies had concluded that *N. simplex* usually inhabited areas deeper than 50 m, suggesting that this species avoided shallow environments (Gómez-Gutiérrez 1995, De Silva-Dávila & Palomares-García 2002). In another study, also using standard Bongo nets to survey throughout the mouth of Bahía Magdalena (24° N, 112° W), we reported that *N. simplex* larvae (calyp toes and furciliae) but not juvenile and adults occasionally enter the bay, transported by tidal currents (Gómez-Gutiérrez et al. 2001). Contrary to our expect-

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tations, when we used a submarine video camera, a scientific echosounder, and a zooplankton net in this present study, we discovered that dense epibenthic swarms of adult *N. simplex* commonly enter through a relatively shallow (28 to 50 m depth) section of the main mouth of this subtropical bay.

Gómez-Gutiérrez (1995) and Gómez-Gutiérrez et al. (1996) reported that the abundance, population structure, and secondary production of *Nyctiphanes simplex* over the continental shelf of Bahía Magdalena demonstrates the formation of dense swarm densities in spring and summer (average 1075 and 2520 ind. 1000 m⁻³) when the cold and rich phytoplankton water mass of the California Current (CC) is intense. The abundance decreased dramatically in the autumn and winter (average 178 ind. 1000 m⁻³) when the water column is warmer, well mixed, and contains low phytoplankton concentration because of the retreat of the CC toward the north. This seasonal population-density variability could be associated with the amount of euphausiids that potentially enter the bay with the tidal currents.

The planktonic organisms use several strategies to stay in certain regions of shallow bays and estuaries. Among the best known mechanisms are tidally oriented, daily vertical-migration (vertical migration of zooplankton in response to local tides), position maintenance of zooplankton, or high net population growth rates (Kimmerer et al. 1998, Forward & Tankersley 2001, Gibson 2003). The role of tidal currents in the transport and swarm formation of euphausiids is in general poorly understood; however, this was recently studied for the micronektonic red crab *Pleuroncodes planipes* Stimpson in Bahía Magdalena (Robinson & Gómez-Aguirre 2004, Robinson et al. 2004). Cottée & Simard (2005) studied the daytime, 3-dimensional distribution of *Thysanoessa raschi* M. Sars and *Meganyciphanes norvegica* M. Sars in the St. Lawrence Estuary, Canada, over a semidiurnal tidal cycle during summer and hypothesized that the formation of dense aggregations (>500 g m⁻³ wet weight) were formed owing to the combined effect of semidiurnal tidal currents, local topography, and negative phototaxis of euphausiids. We explored the oceanographic coupling of tidal currents, temperature, raw fluorescence as a proxy for chl *a* concentration, and swarming formation to discuss the transport of the subtropical euphausiid *Nyctiphanes simplex* over the continental shelf and the mouth and inner part of Bahía Magdalena.

Zaytsev et al. (2003) reported that Bahía Magdalena is the largest bay along the west coast of the Baja California peninsula with the steepest continental-shelf slope and the narrowest continental shelf (88 m drop in depth per 11 km). They hypothesized that an upwelling process near the inlets of these bays, cou-

pled with tidal flooding and mixing processes, may transport biological material, grazing organisms, and nutrients into the bay because of the narrow continental shelf. We tested this hypothesis experimentally by studying how seasonal environmental conditions and tidal current-patterns affect the transport of euphausiids inside the bay in conjunction with the relatively well-known population dynamics of this species along the southwestern part of the Baja California peninsula. Our first goal was to estimate acoustic parameters to detect, identify, and distinguish dense *Nyctiphanes simplex* swarms from another abundant micronektonic crustacean in the region, the red crab *Pleuroncodes planipes*. Our second goal was to describe the mechanisms of how *N. simplex* is transported into the bay by local currents, and determine how this process affects these euphausiids trapped by the currents. Robinson et al. (2004) and Robinson & Gómez-Aguirre (2004) showed how *P. planipes* tend to avoid warm water moved by the receding tide (ebb tides) that might pose a risk of becoming stranded on the beach, as does occur in this bay every year (Aurioles-Gamboa et al. 1994). We assumed that *N. simplex* and red crabs interact in such a way that the euphausiids avoid an overlap in distribution with the larger aggregations of the voracious, omnivorous red crab. Our study showed a distinctive pattern of epibenthic *N. simplex* aggregation in shallow waters, not observed in other studies of euphausiid swarming-formation; this supposedly increases chances of mating and finding food and, as an ancillary benefit, may lead to the distraction of predators which become confused by a multitude of prey (Hamner 1984, Strand & Hamner 1990, Gendron 1992, Ritz 1994, Hamner & Hamner 2000, Mufti & Weise 2004, Cottée & Simard 2005). This study demonstrates the highly-flexible ability of *N. simplex* to modify its vertical migration and swarm-formation behavior in correspondence with local tidal currents, and how this species behaves during its relatively short stay inside the bay; furthermore, we demonstrated that euphausiids do not complete their life cycle in this shallow-bay environment.

MATERIALS AND METHODS

Sampling of environmental conditions. Acoustic and submarine videotape surveys and euphausiid collections were completed during 4 oceanographic cruises (1 to 18 December 2003, 16 March to 2 April, 29 June to 16 July, and 1 to 18 December 2004) over the continental shelf and in the middle part of Bahía Magdalena, Baja California Sur, México (24° 30' N, 112° 30' W) on board the R/V 'El Puma' (Universidad Nacional Autónoma de México) (Fig. 1A). Bahía Magdalena is a eutrophic sub-

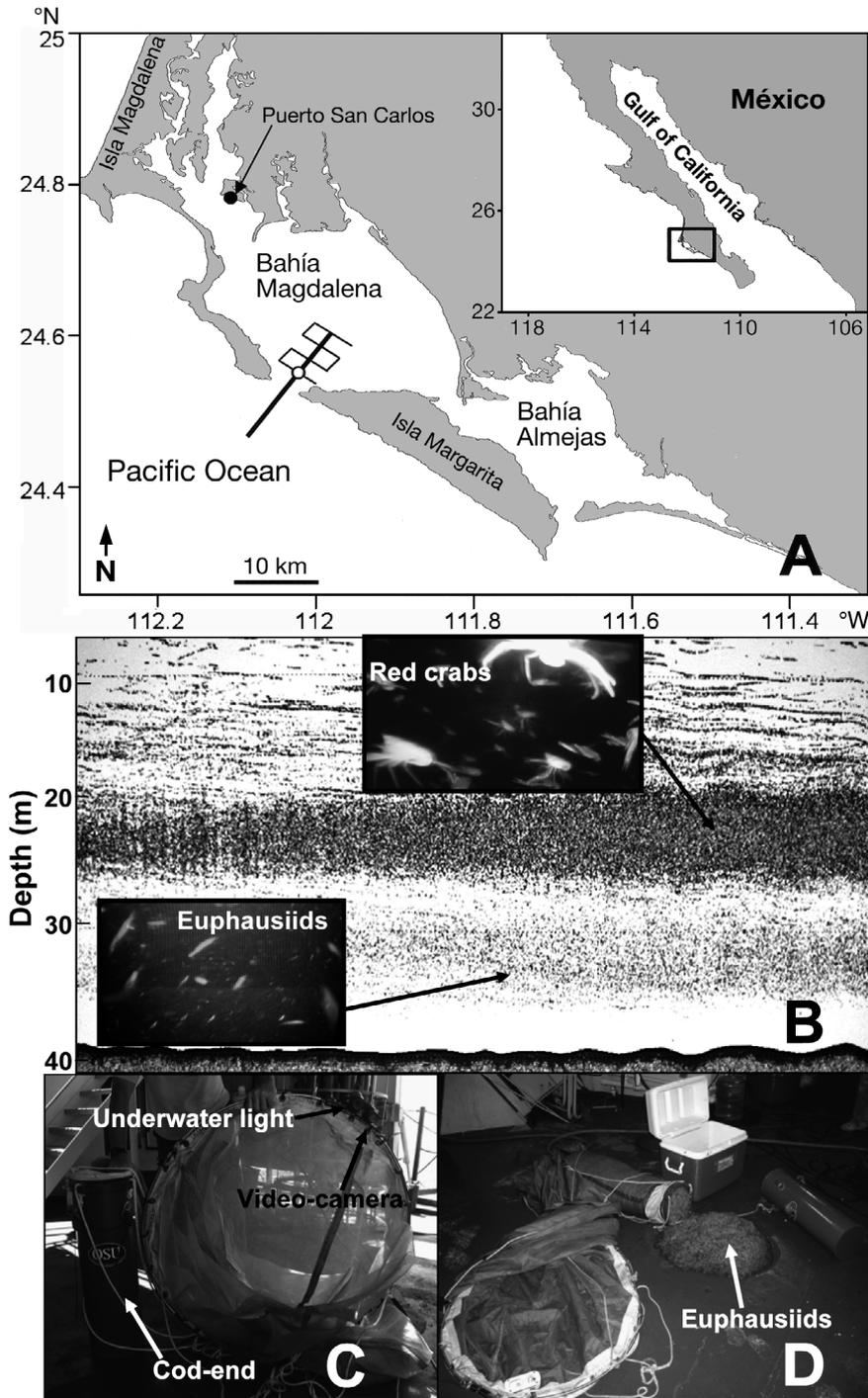


Fig. 1. (A) Bahía Magdalena. Bold line through mouth of bay: 48 h transect line, traversed during spring and neap tides in December 2003, March, July, and December 2004. Thin parallel lines: 'circuit' where continuous 4 m depth temperature and fluorescence were monitored over 48 h. O: 24 h anchorage station sampled every hour during spring and neap tides. (B) Echogram of dense scattering layers in mouth of Bahía Magdalena, detected using a Simrad EY-60 echosounder during slack tide: dense aggregation of the pelagic red crab *Pleuroncodes planipes* at 25 m; swarm of euphausiid *Nyctiphanes simplex* at 35 m. (C) Zooplankton net (1 m diameter) used to sample near seafloor, equipped with a submarine video camera, and underwater light. (D) The euphausiid catch was usually abundant and composed of a monospecies *N. Simplex*. Sporadically, high-density swarms were observed and collected during March and July

tropical bay with a tidal wave-energy-dominated system with a main mouth 4 km wide (Zaytsev et al. 2003). Our oceanographic cruises included 3 sampling strategies.

Sampling through the mouth of Bahía Magdalena: During each oceanographic cruise we made two 48 h surveys, each during spring and neap tides, along an 18 km long transect oriented through the mouth of Bahía Magdalena (Fig. 1A) to record the acoustic scattering layer of planktonic and nektonic organisms. Along the transect, the 4 m depth temperature ($^{\circ}\text{C}$; measured with a SeaBird microcat CTD) and fluorescence as a proxy for chl *a* concentration (measured with a Turner Designs 10-AU-005-CE fluorometer) were recorded every 5 s from seawater pumped from the intake located at the bow of the vessel. Simultaneously, a SonTek 250 kHz Acoustic Doppler Current Profiler (ADCP) was used to measure current velocity and direction. ADCP transducers were fixed to the vessel's hull at 4 m depth. Vertical resolution was 2 m with a pulse interval of 5 s. In order to identify the species for acoustic signals during each transect, we sporadically stopped to quickly submerge a high-resolution Multi SeaCam 1060 video camera (Deep Sea Power & Light; low-light black and white camera with an $f = 2.8$ mm lens and depth of field from 10 cm to infinity, equipped with a DVD videorecorder) to depths where the echosounder showed a dense scattering layer.

During the 3 oceanographic cruises conducted during 2004, euphausiid swarms were sampled using a 1 m diameter net that was 5 m long, and constructed of black 300 μm mesh. The cod end was constructed with gray PVC, and was of 0.215 m diameter and 0.70 m height. This net was equipped with an underwater lamp (Ikelite Pro-Video-Lite II system, 50 W) to attract euphausiids. The submarine video camera mentioned above was attached to the net ring (Fig. 1C).

Euphausiid total length was measured from the posterior part of the

eye to the tip of the telson, and during each cruise gender and maturity stage of all specimens was determined to obtain seasonal changes in size frequency distribution and population structure. The specimens were separated into 5 categories: juveniles, immature females (females with gonad development Stage I to III), mature females (females with pink gonad Stage IV ready to spawn, ovigerous females, and spent females), immature males (without spermatophore), and mature males (with spermatophore).

At several of the March and July 2004 sampling locations, we captured extremely high densities of euphausiids (Fig. 1D). On such occasions we deployed the video camera alone (without net) attached to a weight (20 kg) to avoid over sampling of euphausiids with the net. In several locations, the euphausiid swarms were in contact with the seafloor. We collected these epibenthic swarms, which were detected with the help of the echosounder and simultaneously observed with the underwater video camera.

Sampling at an anchorage station in the mouth of Bahía Magdalena: During spring and neap tides of each oceanographic cruise, we made a 24 h acoustic survey, zooplankton collections, and submarine video camera observations at an anchorage station located at 24° 33.34' N, 112° 01.07' W (Fig. 1A). These observations helped us to identify the acoustic targets and to study euphausiid swarming behavior: swarm compactness and swimming orientation of individual organisms recorded with the video camera. We selected the anchorage station from spring tides in March 2004, because this was our best example of how euphausiids and red crabs were simultaneously and heavily aggregated but in different depth layers (almost monospecific swarms), and later began to disperse demonstrating a relatively large variety of swarming behavior. In March, July and December 2004 we corroborated the presence of both common and abundant species at the anchorage station with ground-truth video camera and net samples.

Continuous sampling within Bahía Magdalena (circuits): After these 2 sampling strategies were completed, we monitored the 4 m depth fluorescence, temperature, current speed and direction continuously (every 5 s) and simultaneously recorded the acoustic scattering layer with 3 pulses s^{-1} over 48 h during spring and neap tides, along 4 transects within Bahía Magdalena that were ~6.5 km long and separated from each other by 1.8 km (Fig. 1A). The average duration of each circuit was about 3.5 h. The raw fluorescence data (V) measured with the fluorometer (excitation 340 to 500 nm, emission >665 nm) were used as a proxy for chlorophyll concentrations.

Acoustic identification of euphausiid swarms. During December 2003 and March and July 2004, we used

a Simrad EY-60 split-beam echosounder. The operational frequency was 120 kHz with a nominal beam transducer width of 7°. The transducer was fixed on the vessel's hull at 4 m depth. Ping rate was set to 3 pings per second and pulse duration 0.1 ms. Calibration was conducted before each oceanographic cruise in Mazatlán, México (23° 16' N, 106° 26' W), home port to R/V 'El Puma', according to Simrad ER-60 operation manual guidelines (Simrad 2003). The reference target was a copper sphere supplied by Simrad (120 kHz, 23 mm diameter, target strength [TS] = -40.4 dB). For acoustic data analysis we used the SONAR-4 software version 5.9. During December 2004, no acoustic data were recorded. Because euphausiid samples were not collected during December 2003, we used samples from December 2004 to determine the winter *Nyctiphanes simplex* population structure.

The volume backscattering coefficient (s_v) is a measure of the efficiency with which the echosound is scattered back to the source, and is defined by MacLennan et al. (2002) as:

$$s_v = \frac{\sum \sigma_{bs}}{V}$$

where σ_{bs} is the backscattering cross-section (m^2) of the discrete targets in the volume (V). We used the logarithmic version of this coefficient (mean volume backscattering strength, S_v) expressed in decibels, defined by MacLennan et al. (2002) as:

$$S_{vdB} = 10 \log_{10}(s_v)$$

The area backscattering coefficient (s_a) is the backscattering below an area (MacLennan et al. 2002), and it is described as:

$$s_a = \int_{z_1}^{z_2} s_v dz$$

where z_1 and z_2 are the depth of the echo integration. The software SONAR-4 calculates s_a with a scaling area factor, which in the present study was hectares with corresponding integration layer of 10 m. Thus, with this software s_a is calculated as:

$$s_a = 4\pi \times (100 \text{ m})^2 \times 10^{s_v \text{ mean}/10} \times (10 \text{ m})$$

In Bahía Magdalena there are dense aggregations of both *Pleuroncodes planipes* and *Nyctiphanes simplex*. Mean carapace length of the pelagic phase of *P. planipes* is about 2.5 cm (benthic phase is >3.2 cm) (Gómez-Gutiérrez & Sánchez-Ortíz 1997), which is significantly different from adult euphausiids with mean 1.3 cm total length (Gómez-Gutiérrez 1995, this study). However, dense aggregations of euphausiids may produce a backscattering strength similar to or stronger than a single red crab. Therefore, acoustic identification and separation of both species can be complicated. The analysis

of s_v is an appropriate method to discriminate these targets because it is standardized to a volume of 1 m^3 . We then assumed that the back scattering strength per volume is stronger for red crab than for euphausiids.

During the anchorage-sampling protocol, we made detailed analyses of echograms at depths where well-identified monospecific swarms of *Pleuroncodes planipes* or *Nyctiphanes simplex* were detected. To do this, we first used our experience in observing echograms in the area (which amounts to more than 10 yr), then confirmed identification of those echoes using an *in situ* submarine video camera or zooplankton catch obtained with the 1 m-diameter zooplankton net with the submarine video camera attached to the ring of the live net. Next, echograms were stored in the computer and analyzed using SONAR-4. This program is able to calculate s_v values from stored echograms for every ping in vertical layers of 50 cm thickness.

The aim of this analysis was to determine the ranges of s_v values for both species under the following patchiness conditions: *Pleuroncodes planipes* in dense aggregations and well-dispersed, and *Nyctiphanes simplex* in dense swarms and also well-dispersed. This acoustic characterization was a frame of reference to estimate and compare euphausiid and red crab abundance among oceanographic cruises under similar aggregation conditions. Therefore, it is possible that less-dense aggregations of euphausiids or red crabs than our observed may not be detected with our selected acoustic parameters, thereby perhaps underestimating total abundance. The main acoustic reference for dense monospecific swarms of *N. simplex* and *P. planipes* was observed during a 24 h anchorage station at 35 m and at 25 m layer depth (24° 32.98' N, 112° 01.14' W; 30 March 2004, between 21:00 and 22:00 h). A selected section of this echogram (~30 min of records) is presented in Fig. 1B and shows 2 well-separated scattering layers, one composed of dense red crab aggregations and the second of dense euphausiid swarms. The dispersed euphausiids were detected when swarms began to separate. On 31 March at 14:55 h at the same anchorage station, only dispersed red crabs were observed with the video camera system and were recorded acoustically.

Using the s_v analysis, *Nyctiphanes simplex* swarms were acoustically identified and separated from *Pleuroncodes planipes* aggregations (Table 1). The most significant difference in s_v values was between dispersed euphausiid swarms and dense aggregations of red crabs (Mann-Whitney *U*-test, $p < 0.05$). Aggregated *N. simplex* and dispersed *P. planipes* provided similar yet statistically-distinguishable values of s_v (Mann-Whitney *U*-test, $p < 0.05$, Table 1).

To estimate the *Nyctiphanes simplex* distribution and abundance we filtered the s_v values from the echograms recorded during 48 h surveys in the spring and neap tides of each oceanographic cruise. We used only the values recorded for aggregated *N. simplex* (ranging from first quartile $q_1 = -66.2$ dB to third quartile $q_3 = -61.2$ dB). With those values, we were able to calculate the back scattering area (s_a) as described above. The analyzed acoustic area was about 3500×10 m and began 2 m above the sea floor (Fig. 8B).

TS in decibels is the logarithmic version of σ_{bs} and, after MacLennan et al. (2002), is expressed as:

$$TS = 10\log_{10}(\sigma_{bs})$$

As far as we know, the TS of subtropical euphausiids including *Nyctiphanes simplex* has not been directly measured. We did not measure field TS values of *N. simplex* with SONAR-4 because most of the targets observed in the echograms were from multiple individuals, even in the most dispersed situation. We therefore used the relationship of known average total length of the euphausiids detected by sound during our study, but scaled to measured target strength for a slightly larger euphausiid species as:

$$TS = 20\log(\text{mean total length}) - 75.7 \text{ dB}$$

This relation was calculated for the euphausiid *Euphausia pacifica* Hansen (measured total length ranged from 11 to 19 mm; however, this species may reach up to 25 mm total length), which has a similar body morphology but is slightly larger than *Nyctiphanes simplex* and was detected with a 102 kHz frequency (MacLennan & Simmons 1992). Accordingly, the estimated TS of a single *N. simplex* of total length 13 mm (Fig 9A–D) should be approximately -73.4 dB.

Table 1. *Nyctiphanes simplex* and *Pleuroncodes planipes*. Mean volume backscattering strength (S_v ; dB) recorded over 48 h on 30 March 2004 at anchorage station near mouth of Bahía Magdalena. n: number of pings analyzed; q_1 : first quartile (25% of total observations); q_3 : third quartile (75% of total observations)

Species and form of aggregation	n	Median	Min.	Max.	q_1	q_3
<i>N. simplex</i> dispersed	10854	-66.7	-69.9	-61.0	-67.9	-65.0
<i>N. simplex</i> aggregated	7854	-63.9	-69.9	-55.1	-66.2	-61.2
<i>P. planipes</i> dispersed	4556	-58.7	-64.1	-43.4	-60.8	-55.8
<i>P. planipes</i> aggregated	4556	-58.1	-65.1	-46.2	-60.9	-55.5

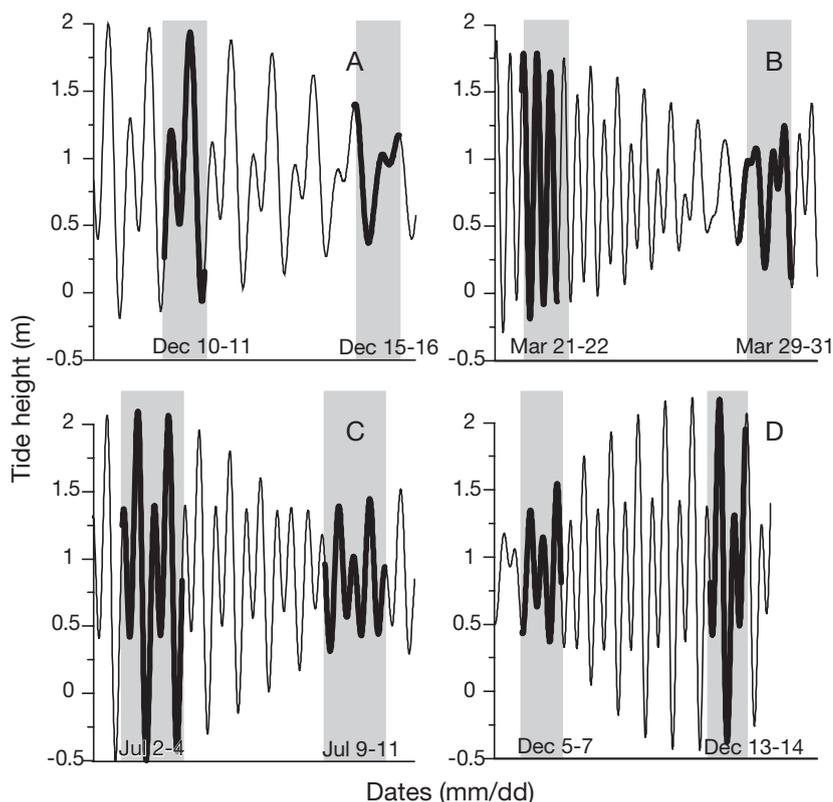


Fig. 2. Seasonal tidal height in Bahía Magdalena. (A) December 2003, (B) March 2004, (C) July 2004, (D) December 2004. Grey areas: periods during spring and neap tides when biological and physical variables were recorded

Next we calculated a backscattering cross-section $\sigma_{bs} = 4.5 \times 10^{-8} \text{ m}^2$ using the above mentioned TS with the following equation:

$$\sigma_{bs} = 10^{(TS/10)}$$

As an alternative, we used the average TS value of -91.5 dB reported for the Antarctic euphausiid species *Euphausia superba* Dana (corresponding for an individual *E. superba* of 13 mm total length) to estimate *Nyctiphanes simplex* abundance (Demer & Conti 2003, 2004). As total length of adult *E. superba* ranges between 45 and 65 mm, a total length of 13 mm likely represents the length of a larvae furcilia Stage VI (8 to 15.5 mm) or small juveniles (Brinton et al. 2000), which are probably more slender and occur in different densities to adult *N. simplex*. However, when using a TS of -91.5 dB , the calculated backscattering cross-section $\sigma_{bs} = 7.08 \times 10^{-10} \text{ m}^2$ would represent an abundance of *N. simplex* about 38 times greater than that estimated with the TS of -73.4 dB from *Euphausia pacifica*. Finally, the density of targets expressed as the number per unit volume ($\rho = \text{ind. m}^{-3}$) between depths z_1 and z_2 (in this present study, $z_2 - z_1 = 10 \text{ m}$) was obtained as in MacLennan et al. (2002):

$$\rho = s_a / \sigma_{bs}$$

We plotted euphausiid abundance (standardized to ind. m^{-3}) estimated acoustically during spring and neap tides for each oceanographic survey and compared that with the modeled tidal height predicted by software JTides version 4.8 (www.arachnoid.com/JTides/). Observational and modeled tidal information indicates that the tidal regime in Bahía Magdalena is mixed and semidiurnal.

RESULTS

Seasonal changes in tidal height and current speed

In Bahía Magdalena there is a semi-diurnal tidal pattern with maximum range of 2.5 m, but the magnitude of the first and second daily peaks and lows change significantly both seasonally and during spring and neap tides (Fig. 2A–D). The semidiurnal pattern (timing) associated with range and tidal height played a significant role in the transport of plankton and micronekton through the mouth of the bay not only on a diurnal time-scale (inflow and outflow), but also when it was compared between spring and neap tides. However, current speeds measured with the ADCP recorded during spring tide (at flood) were statistically indistinguishable among seasons (Kruskal-Wallis, $p > 0.05$) (Fig. 3). Highest current speeds (up to 125 cm s^{-1}) were recorded near the mouth of the bay, perhaps as result of a funneling effect caused by the abrupt change of topography from $\sim 90 \text{ m}$ depth to $\sim 40 \text{ m}$ at the mouth of the bay (Zaytsev et al. 2003). That current speed did not change seasonally indicates that, hydrodynamically, tidal currents could potentially transport a similar amount of planktonic and nektonic organisms through the mouth of the bay independent of season. Thus, currents are not a limiting factor of organism transport through the mouth of the bay.

However, as mentioned later, our biological information indicates that local eutrophic conditions during March and July promote large zooplankton and micronekton biomass production, favoring their transport into the bay, whereas during the oligotrophic conditions that prevail during December (both years) a significantly smaller biomass is moved through the mouth of the bay.

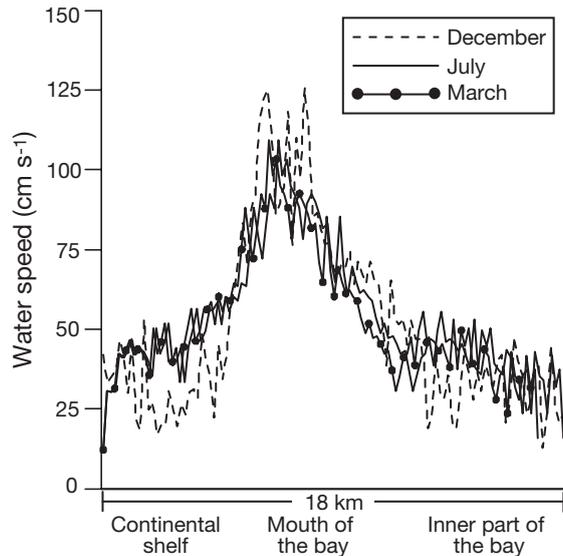


Fig. 3. Seasonal current speed measured at 15 m along the oceanographic transect (18 km long) through mouth of Bahía Magdalena during maximum flood phase in spring tides

Seasonal changes in 4 m depth temperature during spring and neap tides (circuits)

The continuous 4 m depth temperature (T_4), recorded throughout the mouth and within Bahía Magdalena along 4 transects monitored over 48 h at each tidal phase (spring and neap tides), showed a clear seasonal signal, with the first quartile (q_1 , 25% of total observations) and third quartile (q_3 , 75% of total observations) of T_4 ranging between 15.8 and 18.2°C in March 2004, 15.6 and 20.4°C in July 2004, and between 21.3 and 22.4°C in December 2003 and 2004 (Fig. 4A). Variability in T_4 was relatively large in March and July during spring and neap tides, and thermal condition variability was smaller and more homogeneous during December of both years (Fig. 4A). During March and July 2004, median T_4 were significantly lower during spring tides than during neap tides (Mann-Whitney U -test, $p < 0.05$). The opposite was observed during December 2003 and 2004, with a significantly lower T_4 during neap tide than during spring tide (Mann-Whitney U -test, $p < 0.05$). Overall, T_4 variability was less pronounced during both Decembers than during the March and July oceanographic cruises in both tidal states (Fig. 4A).

Seasonal changes in 4 m depth fluorescence during spring and neap tides (circuits)

The 4 m depth fluorescence (F_4) as a proxy of the chl a (chl a_4) showed typical moderate levels during March 2004, with q_1 and q_3 values between 5 and 9 volts in

spring tides and increasing during neap tides to 7 and 14 volts of fluorescence. This difference probably reflected a reduction in phytoplankton export from the bay to the continental shelf during neap tides (Mann-Whitney U -test, $p < 0.05$). During summer (July 2004), F_4 peaked during spring tides with q_1 and q_3 (14 to 22.5 volts of fluorescence) associated with a lower T_4 . During neap tides, significantly lower F_4 values (11.5 to 14.5 volts of fluorescence) were recorded than during spring tides (Mann-Whitney U -test, $p < 0.05$). However, those F_4 values were within the range observed during neap tides in March. During winter low F_4 values prevailed, usually < 9 volts of fluorescence in December 2003, and < 6 volts of fluorescence in December 2004 (Fig. 4B). During both months of December, significantly higher F_4 values were recorded during neap tides than during spring tides (Mann-Whitney U -test, $p < 0.05$). It is interesting that during March and July high variability (q_1 and q_3) was recorded between and within spring and neap tide periods, whereas during December in both years, F_4 values were homogeneous during a 48 h period throughout the area surveyed (Fig. 4B).

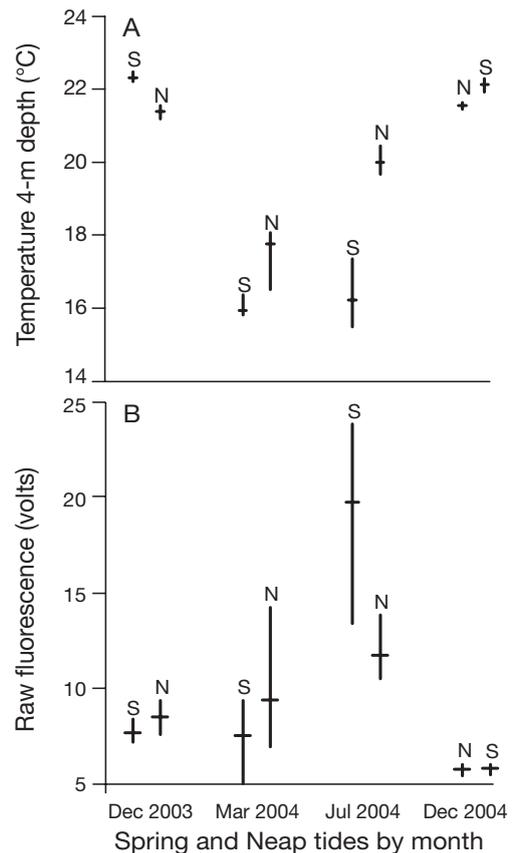


Fig. 4. Seasonal median, q_1 and q_3 of continuous (A) T_4 and (B) raw fluorescence $_4$ as a proxy for chl a_4 along circuits (Fig. 1A) in December 2003, March, July, and December 2004. S: spring tides; N: neap tides

Patterns of distribution of 4 m depth temperature along transect

Tidal fronts were easily detected visually and instrumentally (using the spring tide continuous T_4 along the transect through the mouth of Bahía Magdalena during flood and ebb conditions) in March and July 2004, but they were not observed in December 2003.

T_4 showed that in winter (December 2003), temperature was homogeneously warm (22 to 23°C) along the entire hydrographic line with an almost imperceptible thermal front located over the continental shelf of Bahía Magdalena (Fig. 5A). During March 2004, the thermal front exhibited a dramatic T_4 gradient ($\Delta \sim 3^\circ\text{C}$) near the mouth of the bay during ebb tides and within the bay during flood tides. The tidal front moved approximately 6 km inside the bay between tidal phases. T_4 was lower over the continental shelf than within the bay because of wind-induced upwelling that tended to cool the deeper part of Bahía Magdalena during maximum inflow (Fig. 5B). In July 2004, the thermal front was even stronger than during March ($\Delta \sim 4^\circ\text{C}$), and the tidal front also moved about 6 km inside the bay between flood and ebb tide phases. However, T_4 was higher over the continental shelf than within the bay during ebb tides, and T_4 was lower over the continental shelf than within the bay during maximum flood tides. This was probably caused by the combined effect of higher solar radiance (causing an intense and shallower thermocline) and stronger upwelling events over the continental shelf moving recently-upwelled water into the bay (Fig. 5C).

Advection of plankton and micronekton by tidal currents

Although it is sometimes difficult to identify a functional group of organisms directly from echograms, the dense scattering layer (SL) analysis provides an insight into how those aggregations migrate vertically and are transported horizontally by local currents. As an example of plankton and micronekton transport through the mouth of the Bahía Magdalena associated with tidal height, we show the tidal-height cycle, indicating with a bold line and sequential letters (A–L) the periods when acoustic information was recorded during a 48 h sequence of echograms (spring tides, 17 to 19 March 2004) (Fig. 6). On each echogram is shown the initial and final times used to delimit the acoustic data set (Fig. 7 A–L). The mouth of the bay is identified by the abrupt rise of the seafloor to a depth of about 35 m. All echograms showed a dense SL, composed of macroplanktonic and micronektonic organisms, in the deeper region over the continental shelf (~90 to 60 m

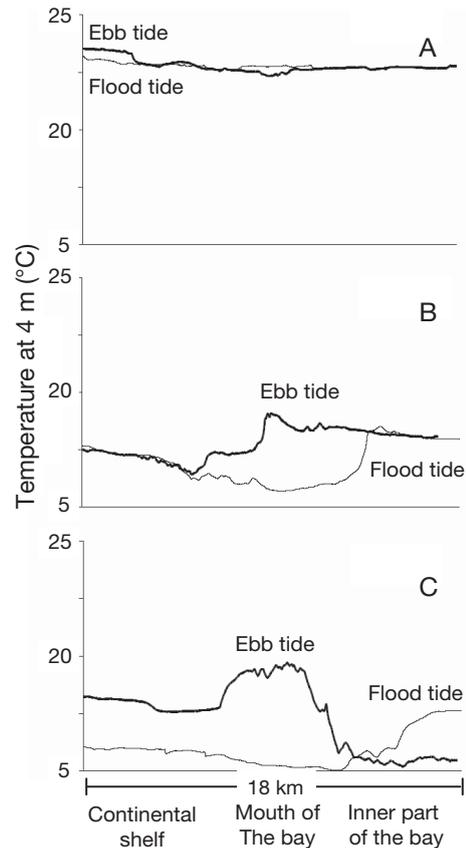


Fig. 5. Seasonal T_4 recorded continuously through mouth of Bahía Magdalena (18 km transect) in (A) December 2003, (B) March 2004, and (C) July 2004. Bold line measured during outflowing (ebb) spring tides; thin line recorded during inflowing (flood) spring tides. Location of tidal front according to tidal phase detected by abrupt changes in T_4

depth). During the nighttime sections of the echograms, the SL migrated upward to near surface layers (<25 m depth), whereas during the day the SL was deeper (>50 m depth). If the plankton-nekton upward nighttime-vertical migration coincided with the inflowing tide, part of this dense SL was transported into the inner-most part of the bay delimited by the tidal front (Fig. 7E,H). However, this also occasionally occurred during the day when a relatively dense SL was recorded near the mouth (Fig. 7K). Most commonly, if the inflowing tide occurred during the day, when most of the organisms were usually in deeper waters, a relatively small amount of pelagic organisms were transported into the bay only within the region near the mouth (<3 km inside the bay) (Fig. 7B). This distribution also occurred at night when the tidal height started to increase immediately after an ebb tide (Fig. 7). During strong, diurnal ebb tides, the SL was scarce in the mouth and inner region of the bay (Fig. 7I,L) or only moderately abundant (Fig. 7A,F,G). During nighttime ebb tides, dense scattering layers were recorded in the

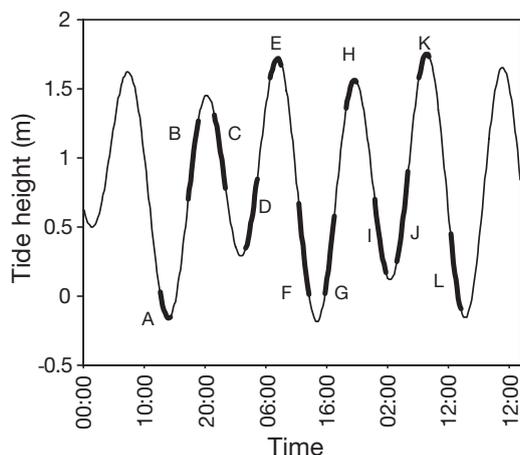


Fig. 6. Tidal height in Bahía Magdalena, 17 to 19 March 2004 (spring tides). Bold line: periods when sound-scattering layer was recorded using a split-beam echosounder (see echograms in Fig. 7)

mouth of the bay when the pelagic organisms were being transported out of the bay (Fig. 7C).

As predicted by the tidal height pattern, the massive SL intrusion inside the bay occurred twice per day, but this process was quite asymmetrical because of the combined effect of the daily vertical migration of the pelagic organisms (dependent on time and light intensity) and the tidal current speed and direction pattern (current velocity). The identification of the main components of those dense SLs at specific places along the oceanographic transect were deduced from video analysis and samples collected with a zooplankton net in regions where the echosounder indicated a dense SL. All this information showed that aggregations of *Pleuroncodes planipes*, *Nyctiphanes simplex*, and the copepod *Calanus pacificus* Brodsky comprised a large portion of the total acoustic signals recorded. Small pelagic schools (Pacific sardine *Sardinops sagax* Jenyns, and Pacific mackerel *Scomber japonicus* Houttuyn) were also observed and were distinguishable from the plankton, because fish schools are smaller and acoustic signals were well above those obtained from plankton and red crabs.

Seasonal changes in euphausiid abundance and advection of swarms during spring and neap tides estimated by echosounding

Euphausiid swarms were commonly recorded acoustically and with the video camera during March and July 2004 as dense near-bottom aggregations (between 1 and 10 m above the seafloor near the mouth of the bay) both day and night, or as dense midwater aggregations (40 to 100 m) over the continental shelf. During both December cruises, euphausiid swarms

were observed less frequently and with smaller density than in spring and summer cruises. A typical echogram in March (Fig. 1B), recorded at the anchorage station in the mouth of Bahía Magdalena, shows dense aggregations of *Pleuroncodes planipes* at midwater depths and dense monospecific swarms of *Nyctiphanes simplex* near the seafloor. During July, the *P. planipes* aggregations were again observed with comparable abundances; however, the euphausiid aggregations were relatively smaller and less frequently observed than in March. Over the continental shelf of Bahía Magdalena and at offshore stations (>100 m depth), *N. simplex* migrates vertically on a daily basis, showing near-surface dense aggregations at night and dispersed aggregations during the day (Robinson & Gómez-Gutiérrez 1998a). However, in the mouth of Bahía Magdalena, the euphausiids were invariably observed as epibenthic aggregations without any evidence of typical daily vertical migration. Results of the density of targets (ind. m⁻³) when using the average TS for *Euphausia pacifica* (-73.4 dB) were plotted as a function of time and compared with tidal height (Fig. 8 A-F). If using a TS of -91.5 dB, predicted by the stochastic distorted-wave Born approximation model (SD-WBA) for *Euphausia superba* individuals of average total length 13 mm (Demmer & Conti 2003, 2004), the abundances of *N. simplex* estimated acoustically would be 38 times greater than those shown in Fig. 8.

In general, euphausiid abundance inside the bay was directly associated with tidal height, except during spring tides in the July 2004 cruise when no apparent association was observed. During December 2003 (spring tides), euphausiid abundance was usually <100 ind. m⁻³ (Fig. 8A). No acoustic data were recorded during neap tides on this cruise. Dense euphausiid swarms (up to 160 ind. m⁻³) entered the bay in March 2004 during spring tides (Fig. 8C), but abundance was substantially reduced (<40 ind. m⁻³) during neap tides (Fig. 8D). In spring tides of the July 2004 cruise, acoustic abundance of euphausiids did not show any association with tidal currents (Fig. 8E). It is possible that euphausiids were swimming in a more dispersed manner than in March, or were out of our range of the volume analyzed for S_v . The abundance of euphausiids within the bay in July increased again during neap tides, and was closely associated with tidal current transport (Fig. 8F).

Population structure of *Nyctiphanes simplex* swarms inferred from zooplankton net collections

Seasonal euphausiid abundance was corroborated by field data from euphausiids collected with a zooplankton net. In March 2004, euphausiids were col-

lected in 17 out of 23 (74%) zooplankton net tows made during the 18 d cruise ($n = 1338$ euphausiids). In July, euphausiid swarms were less frequently collected in the mouth of Bahía Magdalena, but they were more

common and abundant over the continental shelf. We collected euphausiids in 10 out of 19 (53%) stations sampled during the 18 d ($n = 501$ euphausiids). In December 2004, euphausiids were extremely difficult to col-

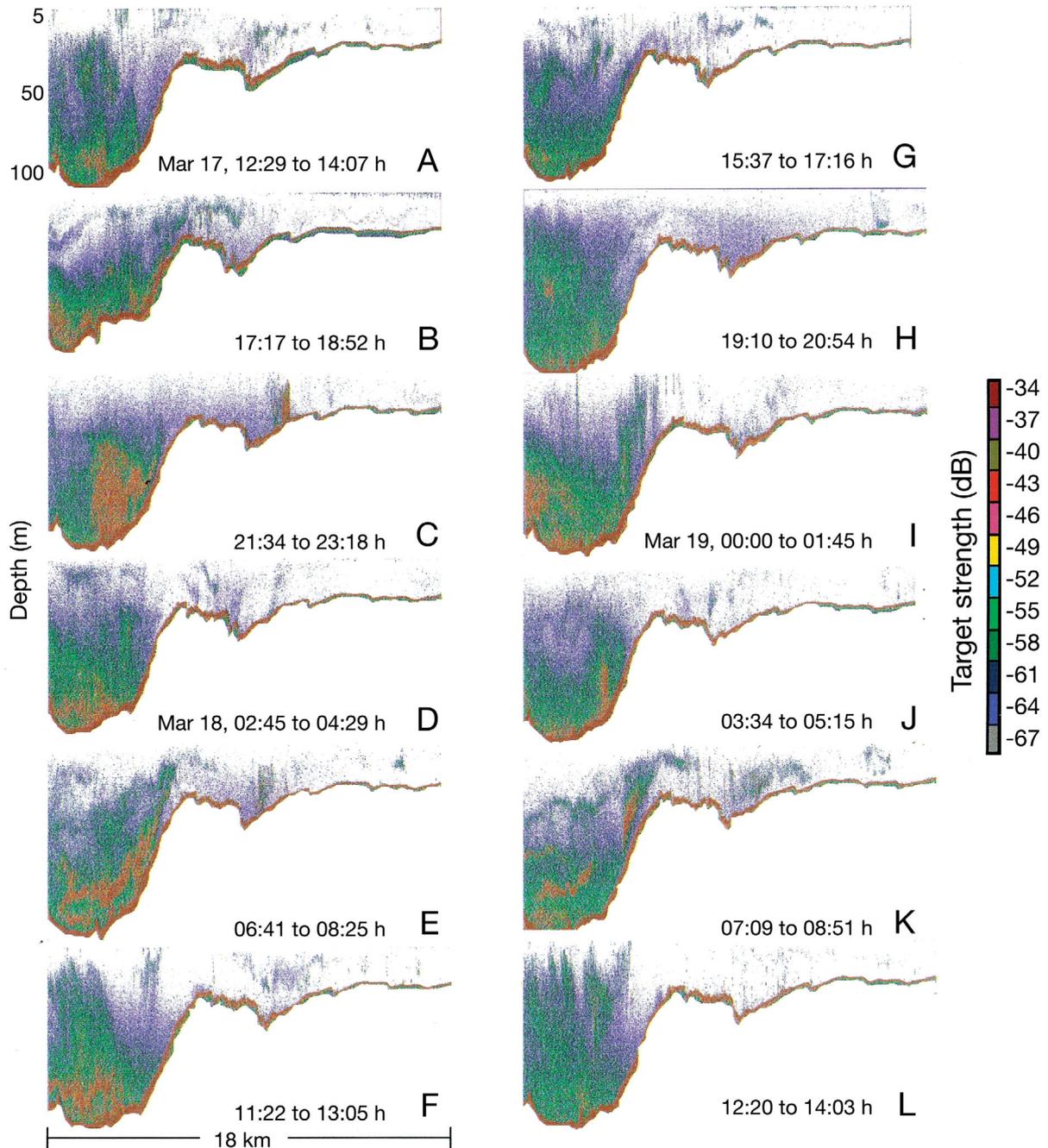


Fig. 7. A 48 h sequence (17 to 19 March 2004) of echograms recorded through the mouth of Bahía Magdalena during spring tides. Echograms show scattering layer (SL) composed of a myriad of zooplanktonic and nektonic organisms that entered the bay with strong flood-tide currents (up to 125 cm s^{-1}). SL was mainly composed of aggregations of pelagic euphausiid *Nyctiphanes simplex*, calanoid copepod *Calanus pacificus*, pelagic red crab *Pleuroncodes planipes*, and schools of Pacific sardine *Sardinops sagax* and mackerel *Scomber japonicus*. Initial and final local time shown on each echogram and tidal height shown in Fig. 6 demonstrate that (1) during ebb tide (outflow) the SL is retracted to the mouth and (2) during inflow (high tidal height) the SL enters the inner part of the bay

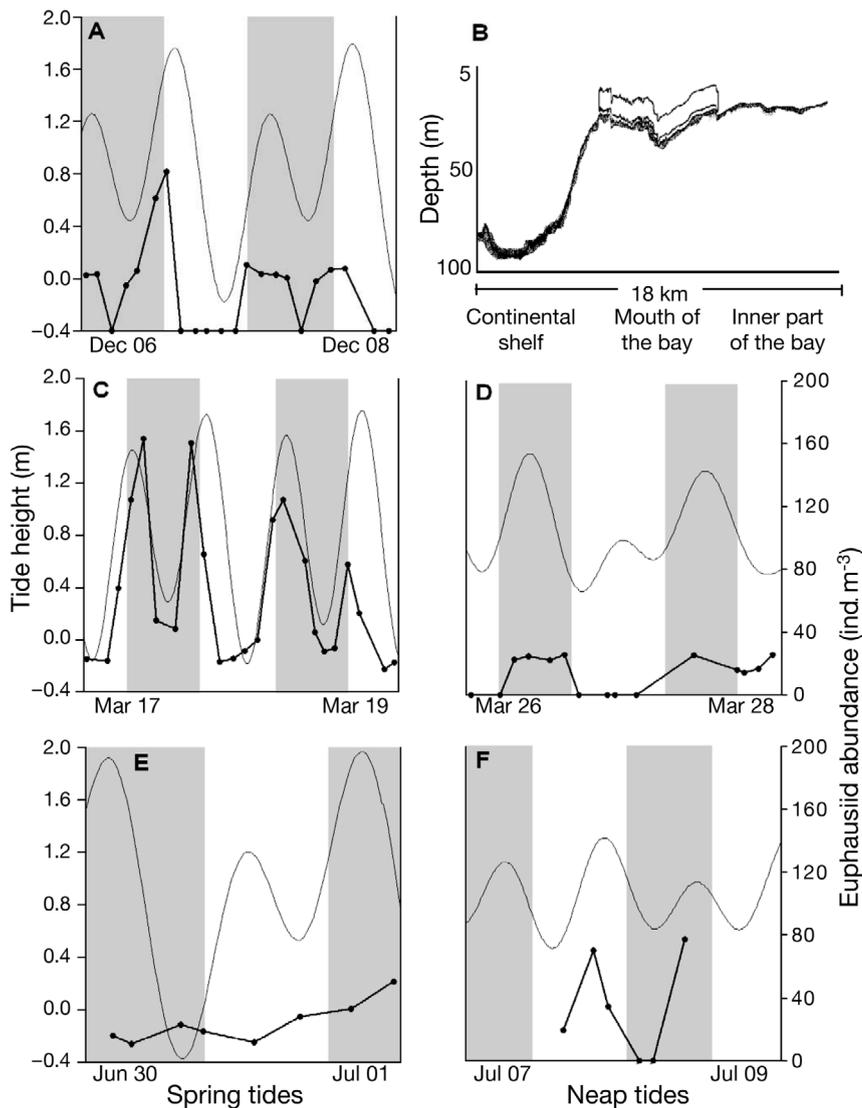


Fig. 8. *Nyctiphanes simplex*. Epibenthic swarms in mouth of Bahía Magdalena, detected using acoustic parameters obtained from observations of dense monospecies swarms at a 24 h anchorage station. Dense swarms entered during flood tides and receded from the bay during ebb tides in (A) December 2003 (spring tides), (C, D) March 2004 (spring and neap tides), (E, F) July 2004 (spring and neap tides). (B) Topography of mouth of Bahía Magdalena where acoustical sampling transect was made, showing the section and depth where acoustical analysis was performed. Grey areas indicate night sampling periods

lect because they did not form dense aggregations and because they were mostly located outside the bay over the continental shelf. We collected euphausiids in low densities at 16 stations ($n = 268$ euphausiids) from a total of 33 (48%) zooplankton samples collected during December 2004.

During March and July, the euphausiid population structure was comprised of a large proportion of animals in the reproductive stage (females with pink gonads in meiosis stage filling the cephalothorax until the first abdominal segment, and males with spermatophores)

(Fig. 9A,B,D,E). When comparing stations located over the continental shelf and the mouth and inner part of Bahía Magdalena, in March we collected larger animals within the bay than over the continental shelf. In July, the size structure was similar in both regions (Fig. 9B,E). In December 2004, the euphausiids collected were substantially smaller than those in the previous 2 oceanographic cruises (Fig. 9C,D). Although reproductive euphausiids were present in similar proportions in both regions, smaller organisms were observed in the mouth of the bay than over the continental shelf (Fig. 9C,F). Juveniles were opportunistically collected and Fig. 9 does not reliably reflect their field abundance. The total length at first maturity for *Nyctiphanes simplex* males and females is about 8 mm (Fig. 9), and the larger euphausiids collected measured 18.6 mm total length.

Video camera observations of swarming behavior of *Nyctiphanes simplex*

The number of video camera deployments and total hours of video recorded was significantly greater in March 2004 than in the other oceanographic cruises, even excluding the March 2004 49 h of continuous video recording at the anchorage station (40 m depth). Excluding this experiment, the number of casts and hours of video per cruise in 2004 were: March cruise, 42 casts, 27 h; July cruise, 12 casts, 8 h; December 2004 cruise, 1 casts, 18 h. In the mouth and inner part of the bay, we observed swarms of *Nyctiphanes simplex* adults swimming exclusively close to the seafloor. The swarming behavior of *N. simplex* was associated with the tidal-current speed. During flood tides, with current speeds up to 125 cm s^{-1} , the euphausiids were dispersed and moved semi-passively with the current. They were detected with the video camera and their characteristic fast and linear swimming-pathways clearly distinguished them from smaller and more passive zooplankton. After the tidal height reached maximum inflow (slack tide) the current speed decreased substantially. In the innermost part of

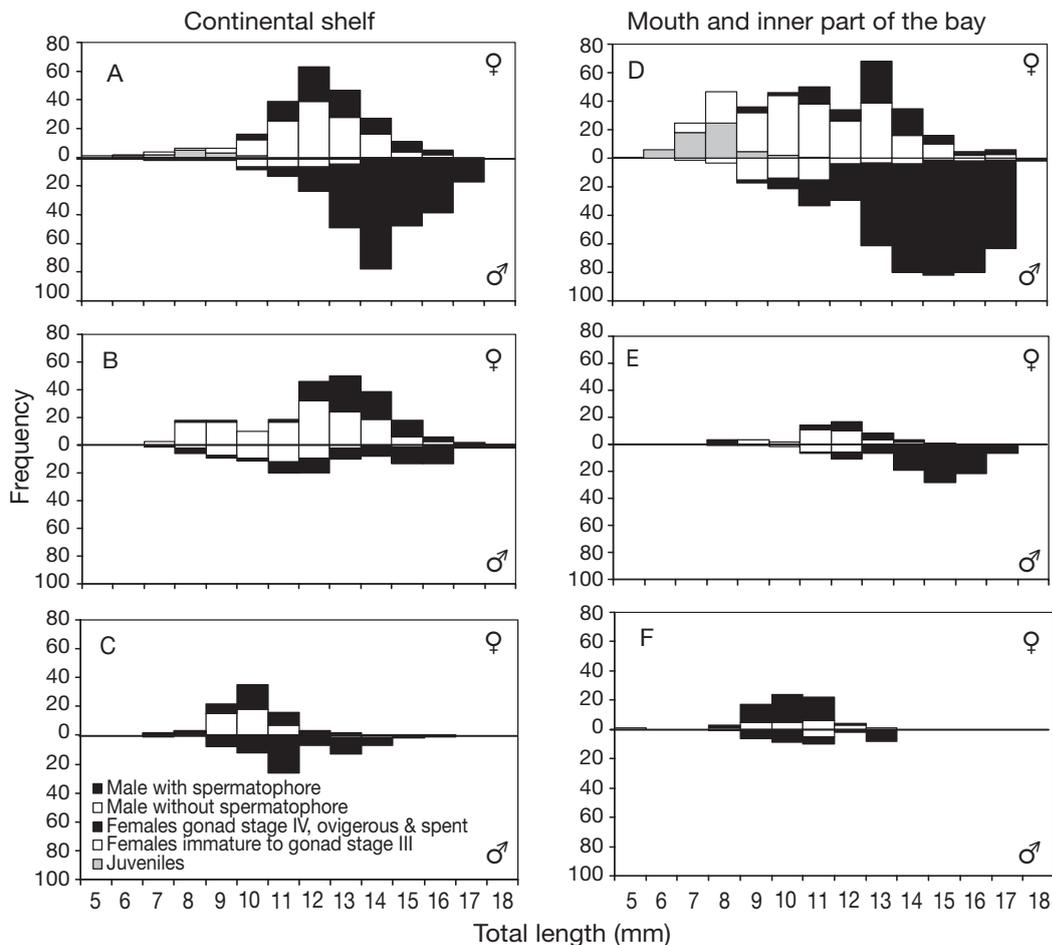


Fig. 9. *Nyctiphanes simplex*. Size-frequency distribution and population structure for specimens collected over continental shelf in (A) March ($n = 511$), (B) July ($n = 345$), and (C) December 2004 ($n = 160$) and specimens collected in mouth and inner part of Bahía Magdalena in (D) March ($n = 847$), (E), July ($n = 156$), and (F) December 2004 ($n = 108$)

the bay, the *N. simplex* swarms were more aggregated and swam continuously in an eddy-like motion near the seafloor, with no evidence of polarized swimming among individuals within the swarm, which means that each euphausiid usually had a different swimming pathway—much like that of an individual in a bee swarm rather than in a uniformly-oriented swimming school of fish (Ritz 1994). Unlike *Euphausia superba*, where the schools are usually thin in at least 1 dimension (Hamner 1984), *N. simplex* swarms exhibited relatively small spherical or cylindrical swarms where individuals located in the center may move to the border of the swarms occasionally. The coherence of the swarms lasted for hours, particularly during nighttime. Interaction among adults within the swarm was probably related to reproduction, as evidenced by population structure in this region (Fig. 9A–F). However, we did not directly observe the mating process owing to the video camera resolution and apparent chaos within the swarm. Euphausiid swarms were not observed during December 2003 and 2004.

DISCUSSION

Seasonal variability in environmental conditions

Traditionally, it has been thought that seasonal and interannual changes in sea surface temperature and chl *a* patterns in Bahía Magdalena were the greatest source of variability (Palomares-García & Gómez-Gutiérrez 1996, Lluch-Belda et al. 2000, Palomares-García et al. 2003), rather than circadian or daily sampling at an anchorage station (Aceves-Medina et al. 1992, Palomares-García & Vera-Alejandre 1995, Gómez-Gutiérrez et al. 1999a, Robinson & Gómez-Aguirre 2004) or along a hydrographic line through the mouth or inner part of Bahía Magdalena (Gómez-Gutiérrez et al. 2001, Zaytsev et al. 2003, Robinson et al. 2004). On a seasonal time-scale, variability in temperature and fluorescence as a proxy for chl *a* patterns observed in the present study was similar to that reported in previous studies, with lower temperatures and chl *a* during spring, a moderate increase in tem-

perature and a sharp peak in chl *a* during the spring-summer transition, and warmer and relatively oligotrophic conditions during autumn and winter (Gómez-Gutiérrez et al. 2001, Palomares-García et al. 2003). However, we recorded T_4 and F_4 as a proxy for chl a_4 with high-frequency sensors over shorter time-scales, associated with diurnal and tidal time-scale variability, and found significantly higher hour- to day-scale variability than previously reported. We were surprised that during spring tides of the July cruise, T_4 was significantly colder and F_4 much more highly elevated within the bay than during neap tides. This is an unprecedented observation for Bahía Magdalena, because T_4 between these 2 tidal periods was highly variable, exceeding well-known seasonal variability that has a time-scale of months. Observed variability in T_4 between spring and neap tides could not be explained solely by upwelling intensity, because spectral variability derived from the coastal upwelling index is usually 0.5 cycles d^{-1} (Zaytsev et al. 2003), which is significantly longer than spectral variability recorded during our tidal-scale study (>1.5 cycles d^{-1}).

This has significant ecological implications for resident pelagic and plankton organisms in the bay, as environmental conditions change abruptly within days. However, such rapid environmental differences associated with spring and neap tides were apparently restricted to summer. During March, the combination of intensification of the cold CC, moderate solar radiation and high wind speeds, which induces upwelling over the continental shelf, did not cause significant changes in T_4 and F_4 during spring and neap tides within the bay. However, during July, when the CC is less intense and solar radiation significantly increases, there were marked changes in temperature between spring and neap tides within the bay. This was caused by a funneling effect and the intrusion of cold upwelled waters ($<17^\circ\text{C}$) into the warmer and shallower waters in the bay, which was more intense in spring than in neap tides. During December, the CC usually retracts toward the north allowing the tropical north equatorial current to invade the continental shelf and part of Bahía Magdalena. This current significantly increases the temperature and forms a thick (~ 30 m), warm, well-mixed layer in the mouth of the bay (Gómez-Gutiérrez et al. 2001). Thus, waters from the continental shelf and the inner part of the bay were warm and statistically indistinguishable. The combined effect of local bottom topography (from 90 to 30 m depth along ~ 11 km), wind-induced intermittent upwelling events, and periodic tidal currents that enhance turbulent mixing processes near the mouth of Bahía Magdalena create conditions that enhance high rates of plankton production in spring and summer and high rates of plankton transport during flood and ebb tides.

Selective tidal stream of *Nyctiphanes simplex* in the mouth of Bahía Magdalena

Using a submarine video camera, we demonstrated that *Nyctiphanes simplex* exhibited a different aggregation behavior than previously observed: it formed dense epibenthic swarms in the shallower mouth of Bahía Magdalena modulated by tidal currents, which did not migrate vertically. This species is traditionally considered as a neritic, shorter daily vertical-migrator (Brinton 1962, 1967). However, recent studies have shown that *N. simplex* is highly flexible with regard to its daily vertical-migration (DVM) pattern, forming day-time surface swarms (Gendron 1992) or under-taking typical DVM that is concentrated over shelf-break areas (Robinson & Gómez-Gutiérrez 1998a, Gómez-Gutiérrez et al. 1999b). This indicates the existence of highly intraspecific and geographically-dependent population DVM behavior that is tuned to local mesoscale variability in environmental conditions. Occurrences of highly-abundant epibenthic euphausiid aggregations over continental shelves or in shallow waters have been attributed to (1) reduced current speeds that promotes retention of swarms for several days (Ressler et al. 2005), (2) funneling effects that increase the concentration of zooplankton over seamounts and banks (Genin 2004), or (3) the combining effect of tidal currents, local topography, and negative phototaxis of euphausiids (Cottée & Simard 2005).

We have evidence that part of the *Nyctiphanes simplex* population inhabiting the continental shelf of Bahía Magdalena seems to be trapped by tidal currents after being transported into the bay. The amount of euphausiids introduced into the bay is regulated by synchronization of the nighttime ascent of euphausiids over the continental shelf and the strong flood tidal currents. Obviously, these 2 processes do not occur symmetrically as strong flood currents might occur during daytime when euphausiids are deeper and beyond the influence of near-surface tidal currents. The highest current speed recorded with the ADCP was always in the mouth of Bahía Magdalena and was caused by the funneling effect. An interesting observation made during our study was that the speed of the strongest flood tide currents during spring tides was statistically indistinguishable among seasons. Thus, in theory a relatively similar amount of euphausiids should be introduced into the bay on a monthly basis if euphausiid biomass were constant over the continental shelf. Thus, variability would be explained just by physical advection from tidal currents.

However, advection is just part of the story, the other part being represented by seasonal variability in swarming formation. In March, high-density *Nyctiphanes simplex* swarms were frequently observed

with video cameras and recorded acoustically; the occurrence of such swarms moderately decreased in July, and became infrequent during December even when monitored with the ROV and a video camera (SeaBotix, with a color and black and white camera) (December 2004). Because *N. simplex* abundance, population structure, and secondary productivity pattern over the continental shelf of Bahía Magdalena is highly seasonal and influenced by CC environmental and current pattern variability (Gómez-Gutiérrez 1995, Gómez-Gutiérrez et al. 1996), the entrance of euphausiids into the bay is a highly dynamic process. Tidal currents introduce euphausiid swarms only when euphausiids are highly abundant over the continental shelf and when the daily vertical distribution coincides with inflowing tidal currents. During spring and summer, upwelling events pump elevated nutrient concentrations into the bay and promote elevated phytoplankton concentrations near the mouth (Zaytsev et al. 2003), even though this is a region with a low zooplankton resident-time during intense flood and ebb tides. Upwelling and downwelling events also play a role in cross-shelf transport of plankton. For example, relatively slow-swimming bivalve veligers do not behave as passive particles (they are not always swept offshore by upwelling or onshore by downwelling) but, contrary to prediction, when larvae are distributed below the thermocline they are swept onshore during upwelling and offshore during downwelling. When larvae are found above the thermocline, cross-shelf transport is as predicted (Shanks & Brink 2005). Observational studies describe a series of situations where zooplanktonic organisms migrating vertically in the water column on a background of tidal currents would experience considerable horizontal transport (Hill 1991, 1995, Forward & Tankersley 2001). However, these mechanisms may not work if zooplanktonic animals do not retain a migration behavior synchronized with the lunar semidiurnal tide in shelf waters, where horizontal transport by the M_2 tide component would not be expected (Marta-Almeida et al. 2006).

The by-product of day-night epibenthic aggregations of euphausiids suggests a behavioral DVM change, where euphausiids invade shallower waters and stay near the seafloor to avoid potential visual predators like seabirds, small pelagic fish, or red crabs near the surface. However, this apparent epibenthic distribution may also indicate that euphausiids transported to near the surface are actually preyed on significantly, which reduces their near-surface concentrations. *Pleuroncodes planipes* forms high-density aggregations during spring and early summer as part of its offshore-to-inshore reproductive migration (Aurióles-Gamboa et al. 1994, Gómez-Gutiérrez & Sánchez-Ortíz 1997), making them voracious grazers and

predators of phytoplankton and zooplankton (Aurióles-Gamboa & Pérez-Flores 1997). However, during autumn and winter when there is a warmer temperature regime and scarce food, red crabs migrate offshore or northward and almost disappear from Bahía Magdalena. This partially explains why red crabs were observed over the continental shelf in low abundance but not in the mouth or within the bay during either of the December oceanographic cruises. Red crabs selectively remain at midwater depths with frequent upward swimming movements with the abdomen flipping where highest flood current speeds (30 to 50 cm s^{-1}) occur in the mouth of Bahía Magdalena, but they tend to occur in greater concentrations in areas with lower current speeds near the seafloor during the receding tide (Robinson & Gómez-Aguirre 2004, Robinson et al. 2004). This contrasts with the rapid (<1 h) red crab DVM recorded over the continental shelf along the west coast of the Baja California peninsula (Robinson & Gómez-Gutiérrez 1998b). The highest current speeds during ebb tides occur between the surface and 15 m, and during flood tides between 10 and 20 m (Robinson & Gómez-Aguirre 2004). Euphausiid swarms were commonly recorded near the seafloor, and near-seafloor current speeds were considerably slower during both tidal phases (<25 cm s^{-1}).

Using continuous T_4 records through the mouth of the bay, we reported that water from the continental shelf moves about 6 km into the bay with the tidal front. Euphausiids never crossed the tidal front invading the bay water mass. This distance is within the range previously reported of 5 km (Robinson et al. 2004) and 8 to 10 km (Zaytsev et al. 2003). Kimmerer et al. (1998) demonstrated that in temperate estuaries, mysids and amphipods showed tidally-oriented vertical migration sufficient to override the net seaward flow to produce a net landward flux of organisms. Migration of copepods, however, was insufficient to reverse or even greatly diminish the net seaward flux of organisms, implying species-specific alternative mechanisms of position maintenance. Even *Nyctiphanes simplex* adults have relatively strong swimming abilities; video records showed that they were easily transported as semi-passive zooplankters through the mouth of the bay, particularly during spring tides. Euphausiids tended to form dense coherent swarms only during slack tides, when the euphausiids engaged in a more social behavior and formed dense swarms, perhaps related to reproduction as suggested by the high proportion of mature adults in zooplankton samples (Fig. 9).

The existence of epibenthic *Nyctiphanes simplex* swarms was first indicated by indirect evidence derived from the diet and stomach content of the demersal whitefish *Caulolatilus princeps* Jenyns in Bahía

de La Paz on the southwest coast of the Gulf of California (Elorduy-Garay & Caraveo-Patiño 1994). This teleost fish species is a passive predator that feeds mainly during daylight upon organisms associated with the seafloor. Therefore, the *N. simplex* DVM could be a regular food source for epibenthic zooplanktophagous predators. This episodic and epibenthic trophic interaction may occur in Bahía Magdalena when flood tides transport a large biomass of euphausiids into the bay, which then become available to autochthonous demersal predators.

During March 2004, the estimated euphausiid biomass that entered through the mouth of Bahía Magdalena during the 2 flood phases in spring tides (Fig. 8C) was about 74 t d^{-1} . This *N. simplex* biomass was calculated (assuming an individual TS of -73.4 dB for 13 mm total length) as the product of (1) current net inflow from the seafloor to 10 m above, where euphausiid swarms were usually observed, assuming a net inflow of $43\,000 \text{ m}^3 \text{ s}^{-1}$ during 12 h (this is one quarter of total net flow $172\,000 \text{ m}^3 \text{ s}^{-1}$ measured with our ADCP [19 to 23 March 2003 during spring tides]) along a cross-section of the mouth of Bahía Magdalena (6.5 km wide \times 40 m average depth) (SánchezMontante 2003); (2) the modal value of euphausiid abundance recorded acoustically during the 2 flood tide periods (20 ind. m^{-3} , Fig. 8C), and (3) euphausiid biomass, assuming an average individual euphausiid wet weight of 2 mg ind.^{-1} (average 13 mm total length) (Gómez-Gutiérrez & Robinson 1997). This is a conservative euphausiid biomass estimation flux, because standardized abundance estimated acoustically and episodically recorded up to 170 ind. m^{-3} ; in addition, previous studies suggest that acoustic methods produce estimates of euphausiid swarm density much below that of visual estimations (Hamner & Hamner 2000).

Our video camera records occasionally showed euphausiid aggregations with densities probably of the order of $>1000 \text{ ind. m}^{-3}$, estimated before they were attracted by the video camera light. Using TS for a euphausiid with an average total length of 13 mm, predicted with the stochastic distorted-wave Born approximation model (SDWBA) (Demmer & Conti 2003), the estimated biomass of euphausiids that enter the bay would be about 2812 t d^{-1} —equivalent to average euphausiid densities of 760 ind. m^{-3} . Although similarly high euphausiid densities were occasionally observed in individual swarms by the video cameras, it is unlikely that this high biomass actually represent the average abundance of euphausiids that enter Bahía Magdalena, because euphausiids tend to form patchy swarms. This clearly exemplifies the relevance of directly measuring TS of *N. simplex*, because biomass estimation strongly depends on the TS selected. Kaartvedt et al. (2005) estimated that a single

Meganctiphanes norvegica M. Sars swarm in the Norwegian Sea of about $380\,000 \text{ m}^3$ and numerical density of 200 ind. m^{-3} had a total biomass of 11 t. Thus, it is evident that a significant *N. simplex* biomass is frequently introduced into the bay with the flood tide currents. Our range of estimated euphausiid biomass was from 0.12 to 1.02 g m^{-3} (20 to 170 ind. m^{-3}), which is relatively smaller than previous acoustic estimations of euphausiid biomass over the continental shelf of the Bering Sea (0.7 to 21 g m^{-2} ; Coyle & Pinchuk 2002), or acoustic estimates of biomass that occasionally reached values that exceeded 500 g m^{-3} in the St. Lawrence Estuary that were equivalent to 1500 to $45000 \text{ ind. m}^{-3}$ (Cottée & Simard 2005).

Using hydroacoustic data, Everson & Bone (1986) and Demer & Conti (2003, 2004) demonstrated that *Euphausia superba* swarms remained unchanged in structure during daylight and throughout the night, even though density of swarms appears to change day-to-night because of a change in the orientation of krill in swarms. We observed that *Nyctiphanes simplex* swarms in the mouth of Bahía Magdalena remained relatively unchanged for periods longer than 6 h during our 24 h anchorage observations. Acoustic echograms may indicate apparently solid masses of euphausiids that (at least theoretically) may impose serious problems to individuals in the center, if euphausiids near the periphery harvest all the food. However, Hamner (1984) reported that most *E. superba* swarms were thin in at least 1 dimension and that some of their spread-out formations were in fact hollow domes. Epibenthic *N. simplex* swarms observed in Bahía Magdalena were moderately sized (3 to 20 m length) but never showed a well-synchronized swimming process among members of the aggregation, suggesting that individuals temporarily located in the center of a swarm may easily move to the periphery. This probably reflects different swarming behavior and dynamics between subtropical and Antarctic euphausiid species.

In summary, our study was conducted on a diurnal time-scale with equipment to record high-frequency variability, which was focused over a hydrodynamic mouth of a subtropical bay where tidal currents and inherent plankton DVM behavior modulates most vertical-horizontal transport of plankton aggregations. The euphausiid *Nyctiphanes simplex* is frequently trapped by tidal currents and temporarily enters the highly productive waters of Bahía Magdalena; however, it is thereby probably also exposed to bay-resident predators. The distribution of *N. simplex* near the seafloor during day and night in this area indicates a modification in the DVM known for the species, or may simply reflect of significantly higher predation rates in shallower waters. Possibly, similar epibenthic

swarms of other neritic euphausiid species episodically enter relatively shallow bays, which could be observed if studied with the adequate methodology and thus expand our knowledge of typical marine environments for euphausiids.

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