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Twilight vertical migrations of zooplankton in a Chilean fjord

Arnoldo Valle-Levinson [a,*], Leonardo Castro [b], Mario Cáceres [c], Oscar Pizarro [b,d]

[a] University of Florida, Gainesville, FL 32611, USA
[b] Programa COPAS Sur-Austral, Universidad de Concepción, Barrio Universitario s/n, Concepción, Chile
[c] Universidad de Valparaíso, Facultad de Ciencias del Mar, Av. Borgoño 16344, Viña del Mar, Chile
[d] Departamento de Geofísica & COPAS Sur-Austral, Universidad de Concepción, Chile

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ABSTRACT

Time series of acoustic backscatter and vertical velocity profiles were obtained at three sites along a Chilean fjord with the purpose of determining dominant structures of vertical migrations of the sound scattering layer. Ancillary data obtained with stratified net samples indicated that the sound scattering layer may have been dominated by euphausiids and decapods. Therefore, distributions of acoustic backscatter anomalies and vertical velocities were attributed to vertical migrations of predominantly these organisms. Migration patterns were dominated by twilight excursions in which organisms swam toward the water surface at sunset, spent <0.5 h at a depth near the pycnocline (∼10 m) and then swam downward to depths between ∼20 and ∼60 m. After congregating at those depths during night-time, organisms swam upward again toward the pycnocline at sunrise, spent <1 h near the pycnocline and swam downward to their day-time depths (>100 m). This migration strategy can also be termed 'semidiel migration' as two double excursions were linked to light levels. The reasons for this twilight migration remain uncertain. But it is possible that the up and down motion around sunset was related to predation avoidance, hunger–satiation state, ontogeny, seaward transport evasion, or reaction to the environmental shock from the pycnocline, or a combination of all or some of them. In contrast, the sunrise double excursion was probably linked to feeding requirements by organisms that need to spend the day at great depth with no food available. This study demonstrated the existence of semidiel patterns throughout the fjord and through prolonged periods. In addition, identification of this pattern by acoustic backscatter was complemented by direct vertical velocity measurements. It is proposed that twilight vertical migration is a common strategy in Chilean fjords.

1. Introduction

The paradigm of zooplankton's diel vertical migrations in oceans and lakes describes ascent of organisms to near the air–water interface at around sunset and descent at sunrise (e.g., Cushing, 1951; Hutchinson, 1967). A reverse vertical migration in which organisms spend daylight hours near the surface has also been documented for different species (see review by Cohen and Forward, 2009). Other vertical migration strategies have further been described to change seasonally, interannually or with ontogeny (e.g., Staby and Aksnes, 2011). All migration models have been derived through sampling with direct methods that use nets (e.g., Hutchinson, 1967), and pumps (Castro et al., 1993, 2007), or with indirect acoustic methods (e.g., Kaartvedt et al., 2009), or a combination of direct and indirect methods (e.g., Giske et al., 1990). In particular, acoustic methods record backscattering signals with echosounders (e.g., Staby et al., 2011) and with acoustic Doppler current profilers (e.g., Flagg and Smith, 1989; Zhou et al., 1994; van Haren, 2007). Acoustic methods have been able to fill in the gaps not covered by nets in terms of where in the water column and when a patch of planktonic organisms is located. Also, acoustic methods have allowed long term records of continuous measurements that conventional net sampling programs may not achieve. Acoustic approaches are also overwhelmingly used with acoustic Doppler current profilers to measure horizontal currents in the ocean. In addition to the acoustic intensity recorded by Doppler current profilers, an important piece of information they provide is the vertical velocity of backscatterers (e.g., Pleuddemann and Pinkel, 1989; Tarling et al., 2002). Values of vertical velocities obtained with Doppler shifts sometimes are not related to flow but can be linked to the rates of ascent and descent of organisms (e.g., Rippeth and Simpson, 1998; Zhu et al., 2000; Valle-Levinson et al., 2004).

Acoustic methods have also revealed several vertical migration schemes for aquatic organisms. For instance, more than year-long echosounder records have suggested different migration strategies

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* Corresponding author. Tel.: +1 352 392 9537x1479.
E-mail address: arnoldo@ufl.edu (A. Valle-Levinson).

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for mesopelagic fish (*Maurolicus muelleri*) at one location in a Norwegian fjord, Masfjord (Staby et al., 2011). The strategies identified were normal diel vertical migrations, reverse vertical migrations, crepuscular or twilight migrations superposed on the normal migrations (a double or semidiel migration), and interrupted night-time ascents. In particular, twilight or crepuscular vertical migrations have been recognized as viable strategies in different environments. In his seminal review, Cushing (1951) described 'midnight sinking' and 'dawn rise,' in addition to the typical ascent around sunset and descent after dawn, as identifiable stages in vertical migration patterns of planktonic crustacea. Twilight vertical migrations have been observed from shallow (<10 m deep) estuaries (Cohen and Forward, 2005a) to comparatively deep (depths >100 m) fjords (Tarling et al., 2002; Staby et al., 2011). In a North Carolina (U.S.) estuary <4 m deep, the migration pattern was effected by a marine copepod *Calanopia americana* (Cohen and Forward, 2005a,b). In that case, nighttime downward (sinking) motions and pre-dawn upward excursions were carried out over a span of >1 h and extended to and from the bottom. Reasons for these twilight migrations were attributed to a combination of absolute irradiance levels, rate of change of irradiance, and endogenous rhythms. In the Norwegian Masfjorden, twilight vertical migrations of postlarvae and juvenile of *Maurolicus muelleri* were attributed to a combination of irradiance conditions, hunger or satiation state of the organisms, and ontogeny (Staby et al., 2011). In the Clyde Sea, *Calanus finmarchicus* exhibited downward migrations following upward excursions around sunset (Tarling et al., 2002). This sequence of upward motions followed by downward excursions was attributed to an escape strategy by copepods from predation by euphausiids.

Studies on twilight vertical migrations reported to date have relied mostly on profile measurements at one point in a study area. This sampling limitation begs the question: are twilight migrations observable over prolonged periods and over extended areas in a fjord or estuary? The purpose of this study is to determine whether zooplankton twilight migrations are detectable, with acoustic methods, at different locations along a Chilean fjord or whether they are patchy. Twilight migrations in this fjord persisted throughout nearly 6 months of observations. During that entire period, the vertical velocities of the organisms were also documented with direct measurements obtained with acoustic Doppler current profilers (ADCPs). Two additional reasons for twilight vertical migrations are suggested in the Chilean fjord as a result of this work: seaward transport evasion and reaction to the environmental shock from the pycnocline.

2. Data collection

Three upward-pointing ADCPs were deployed near the head, in the middle of and at the mouth of Reloncavi Fjord (Fig. 1 and Table 1). A description of the fjord, including its morphology, bathymetry, tides, tidal flow, hydrography, precipitation, river discharge and wind regime, may be found in Valle-Levinson et al. (2007) and Castillo et al. (2012). Information relevant to this study consists in the fact that the fjord is commonly >100 m deep with tidal currents <0.2 m/s. This allows the development of year-round highly stratified water columns in the upper 10 m. Stratification is denoted by robust pycnoclines where salinity changes from values that can be anywhere between 0 and 10 g/kg at the surface to ≈32 g/kg at 15 m. Underneath 20 m deep, salinity changes negligibly.

The original purpose of the ADCP deployments was to determine the variability of subtidal velocity profiles (Valle-Levinson et al., 2014). That study found that the fjord may be sometimes influenced by a puzzling three-layered residual circulation structure with subtidal outflow throughout a surface layer above the pycnocline (also described in Valle-Levinson et al., 2007; Castillo et al., 2012). This study provides further intriguing findings and concentrates in the analysis of the echo intensity and the vertical velocity structures. Vertical velocities were related to migrating organisms and not to specific flow structures.

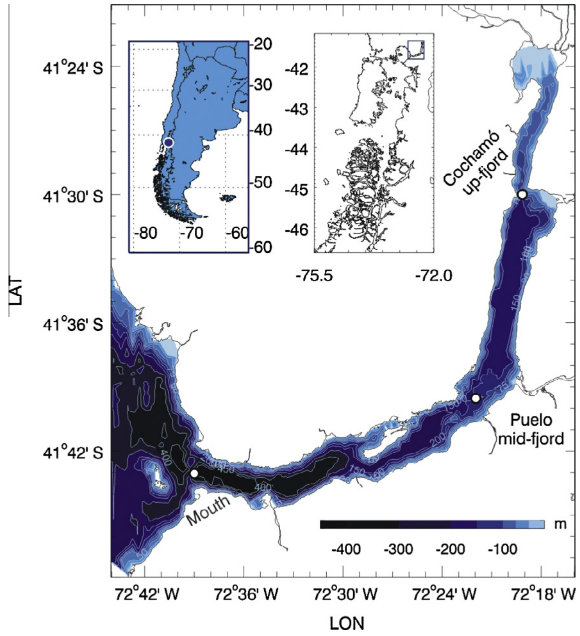

Fig. 1. Study area showing bathymetry of Reloncavi Fjord and location of 3 ADCP moorings at mouth, mid-fjord and up-fjord sites. Left inset shows a blue circle over the study area in the context of a portion of South America. Right inserts displays the northern Chilean Inland Sea with a rectangle outlining Reloncavi Fjord. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Characteristics of ADCP deployments. All instruments were pointing upward.

ADCP	Up-fjord	Mid-fjord	Mouth
Latitude	41°29.794′S	41°37.830′S	41°43.217′S
Longitude	72°19.176′W	72°20.802′W	72°37.534′W
Frequency (kHz)	614.4	307.7	307.7
Water column depth (m)	114	177	475
Instrument depth (m)	61	122	85
Bin size (m)	2	5	4
Record period (days)	219	155	123
Sampling interval (min)	15	15	15
Pings per interval	85	40	45
Nominal range (m)	60	120	120

A 614.4 kHz ADCP with a recording range of around 60 m was moored at Cochamo (41°29.794′S, 72°19.176′W) pointing upward. Its position was near the coastline constriction toward the head of the fjord (Fig. 1) over a water column depth of 114 m. The instrument itself was deployed on a taut-wire at a mean depth of ~61 m from July 13, 2006 (day 195) to February 16, 2007 (day 413). Data were recorded every 15 min in 2-m bins, representing ensemble averages of 85 1-s pings. This record location will be referred to as the "up-fjord" site. A second ADCP was taut-wire moored in the middle of the fjord (Fig. 1), where the channel changes orientation, off the region of the Puelo River discharge (41°37.830′S, 72°20.802′W). The ADCP operated with a frequency of 307.7 kHz pointing upward at a depth of 122 m (equivalent roughly to the instrument's range) over a water column of 177 m. Data were recorded every 15 min also from July 13, 2006 (day 195) to December 14, 2006 (day 349) in 5-m bins with 40 1-s bursts. This

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location will be referred to as the "mid-fjord" site. Finally, a 307.7 kHz ADCP (same operation range as the mid-fjord location) was deployed at the entrance to the fjord (Fig. 1 and 41°43.217′S, 72°37.534′W) pointing upward on a taut-wire mooring and logging 4-m bins with 45 1-s bursts. The recording interval was 15 min from July 15, 2006 (day 197) to November 14, 2006 (day 319). This instrument was located at a depth of 85 m over a water column of 475 m. The site will be referred to as "mouth."

All moorings were taut in such a way that their pitch and roll oscillations were minimal (<2° from the vertical). Therefore, mooring vibrations were not a factor in affecting the data collection. The wavelengths of the 307.7 and 614.4 kHz sound pulses emitted by the ADCPs were ~5 and 2.5 mm, respectively. Thus, the recording sound frequencies allowed identification of targets with size greater than those wavelengths. On this basis, the up-fjord instrument should have been able to capture smaller organisms than the other ADCPs.

As part of an accompanying study that provided ancillary data to this investigation, stratified zooplankton samples were obtained onboard the *R/V Agor Vidal Gormaz* at a mid-fjord station for a 24-h period on July 13–14 and November 6–7, 2006. Samples were collected every 3 h at four depth strata (0–25, 25–50, 50–75 and 75–100 m) with the aid of a Tucker Trawl net (1 m^2 mouth opening, 300 μm mesh, equipped with a flowmeter). Once on board, zooplankton samples were fixed in 10% buffered formaline and stored for later analyses. At the laboratory, the zooplankton samples were analyzed, the major functional groups were recognized, and the most conspicuous and largest organisms (>2 mm) were identified to the lowest taxonomical level and counted.

Measurements of irradiance are now customarily integrated to studies of diel vertical migrations (e.g., Benoit-Bird et al., 2009; Staby et al., 2011). Irradiance measurements can be related to the reaction of organisms to changes in light levels. The original purpose of this deployment, however, was to study the circulation in the fjord. Unfortunately, no irradiance or optical measurements were available. But findings from other studies related to plankton responses to light levels may be used as guidance for the interpretation of results obtained with the analysis of the data collected. In particular, the study of Staby et al. (2011) in a Norwegian fjord explored similar conditions to those investigated here. Obviously, no quantitative assessments can be accomplished here on the response of zooplankton to irradiance levels, but qualitative inferences may be drawn in terms of sunrise and sunset timings.

2.1. Data analysis

Velocity records obtained with the acoustic current profilers, specifically the mid-fjord and up-fjord locations, have been analyzed in Valle-Levinson et al. (2014). The main findings of that investigation were that the non-tidal velocity profiles showed a marked synoptic and fortnightly variability with a two- and three-layer structure. The analysis reported here concentrated (a) on the anomaly of the echo intensity I' (in relative units), produced through sound scattering by organisms, and (b) in the vertical velocities w (in cm/s) associated with vertical migrations by organisms. More precisely, the echo (or sound scattered) intensity I was normalized by determining anomalies $I'(z,t)$ relative to a mean echo intensity profile $\bar{I}(z)$ (e.g., Pleuddemann and Pinkel, 1989; Rippeth and Simpson, 1998):

$$I'(z,t) = I(z,t) - \bar{I}(z). \tag{1}$$

The variable $I(z,t)$ equals $10\log[\mathrm{RSSI}(z,t)]$, where RSSI is the received signal strength indicator recorded directly by the instruments. The mean echo intensity $\bar{I}(z)$ is depth-dependent and calculated over arbitrary periods (e.g., average over 1 month or over the entire deployment period). For temporal variations of I' at periods <1 day, results are essentially the same if $\bar{I}(z)$ represents a low-pass filtered record (period centered at 25-h) at each depth, or a monthly mean profile, or a deployment-long mean profile.

The first analysis performed was to plot contours of I' and w as a function of time and depth (Fig. 2) for each of the 3 stations and for selected 3-day periods. This allowed verification of whether I' displayed diel structures corresponding with simultaneous positive w (ascents) and negative w (descents). Data from stratified net sampling were then used to describe potential variations in vertical distribution of the major functional groups during the 24 h periods (Fig. 3). Centroids (weighted mean depths, *WMD*) were calculated

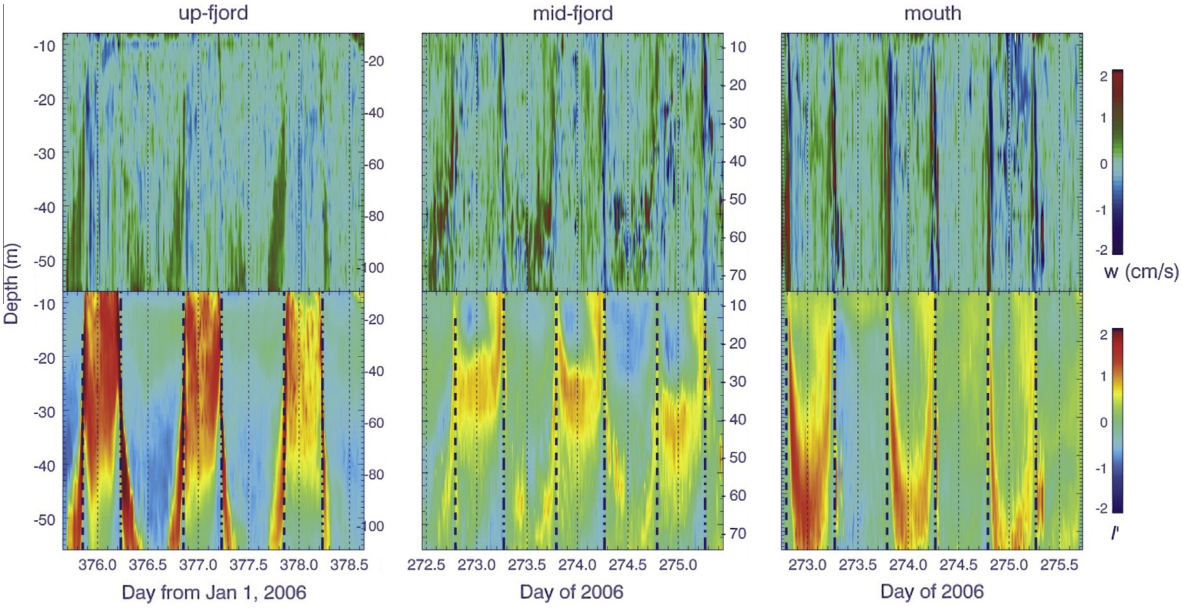

Fig. 2. Three-day segments of vertical velocity w (upper row) and acoustic backscatter anomaly I' (lower row) at each of the three sites observed in Reloncavi Fjord. In the lower row, dashed lines indicate times of sunset and dash–dot lines denote times of sunrise.

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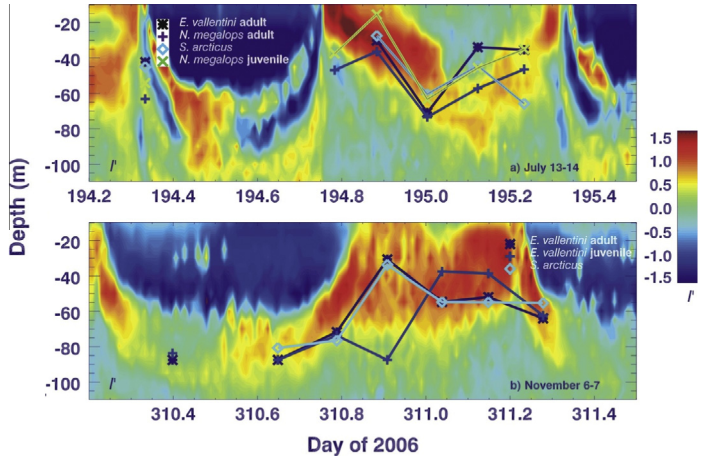

Fig. 3. Acoustic backscatter anomaly I' (in color) during 2 days of sampling with nets at the mid-fjord station. Centroids (as in Eq. (2)) of the dominant species collected with nets are pointed out for the two periods of measurements. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

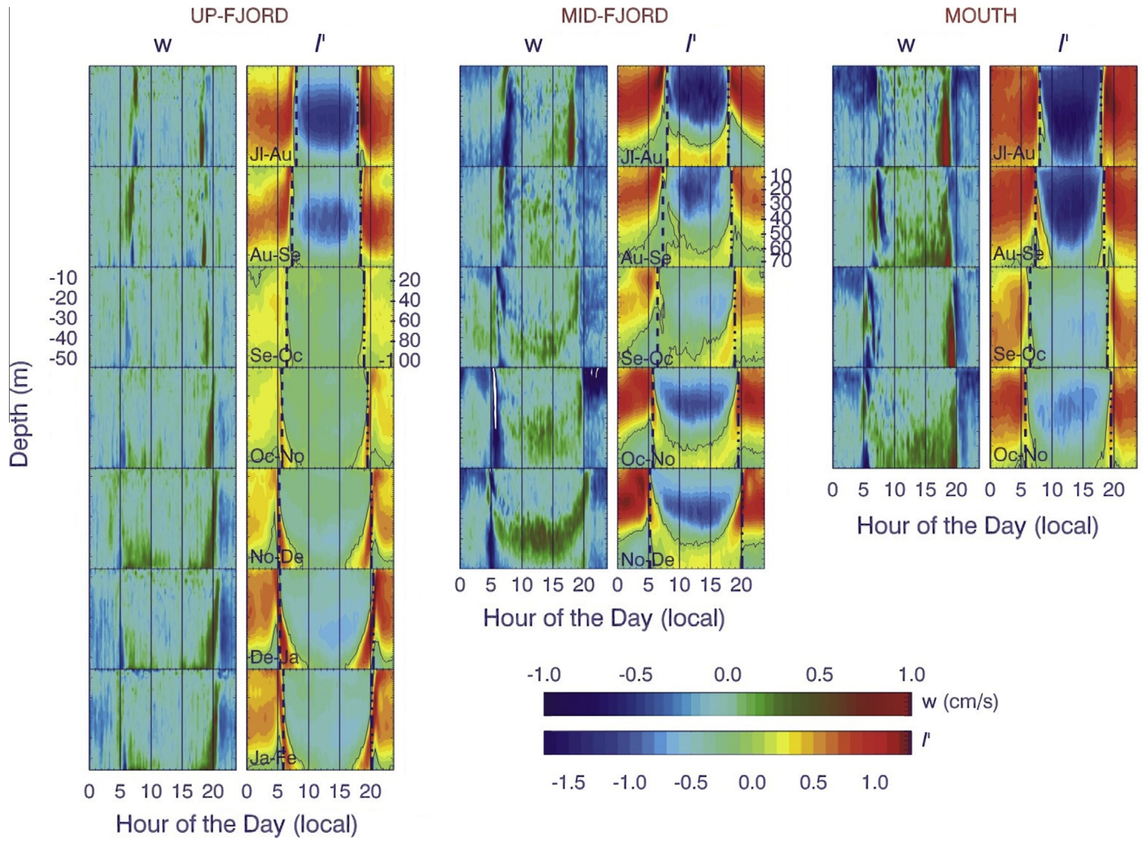

Fig. 4. Monthly means of w and I' (with respect to monthly mean) for each site as a function of depth and hour of the day. Times of sunrise are represented by a dashed line and times of sunset appear as dash–dot lines in the I' distributions.

for all zooplankton profiles based on the algorithms of Roe et al. (1984), Pillar et al. (1989), and Verheye et al. (1992):

$$WMD = \sum_i (n_i z_i) / \sum_i n_i, \qquad (2)$$

where n_i is the zooplankton density (n/m^3) at depth z_i. Abundance of selected zooplankton groups at all the different depth strata were estimated from each zooplankton profile and hour, and expressed as individuals/m^3.

Then, acoustic data were binned as a function of hour of the day, at 0.25 h increments, and position in the water column, following the sampling bin size (2–5 m, Table 1). Binned distributions were determined for each month of observation and for all 3 locations along the fjord (Fig. 4). This approach provided monthly mean distributions of I' and w in the water column as a function of hour of the day. Subsequent analysis involved determination of empirical orthogonal functions (EOF) of I' at each location in the fjord, separately, to identify dominant modes of spatial and temporal var-

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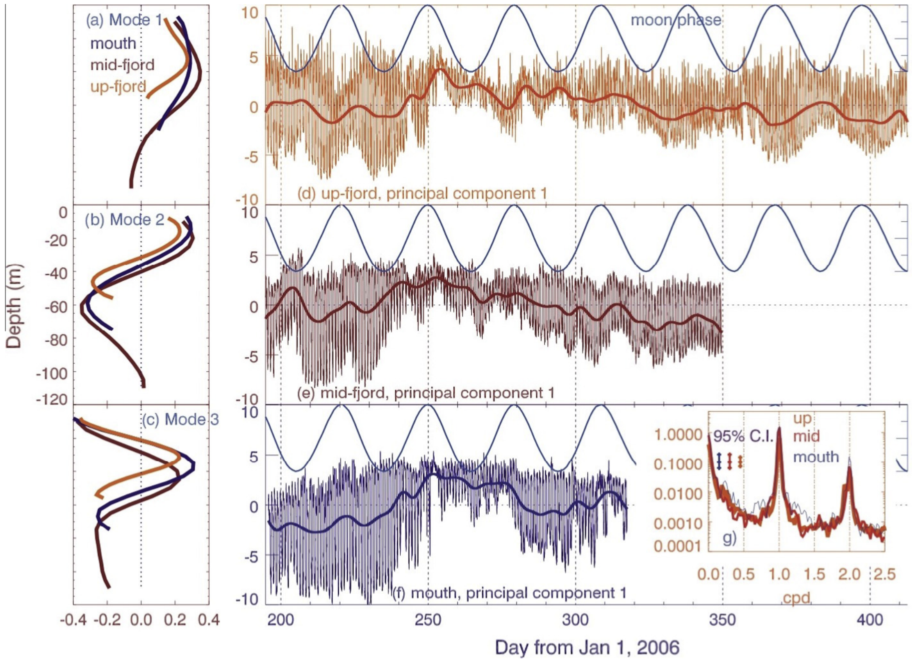

Fig. 5. Results of empirical orthogonal function analysis for I' (arbitrary units) at each of the 3 sites. Eigenvectors, denoting the spatial structure or vertical profile of I', are shown in (a), (b) and (c) for all sites. Mode 1 (and only Mode 1 associated with profiles in (a)) time series, or principal component, for I' is shown at each site in (d), (e) and (f). Oscillations are relative to the deployment-long mean. Thick lines indicate low-pass filtered versions of the same Mode 1 I' time series. Blue lines oscillating between 0 and 1 in the upper third of each time series frame describe the lunar phase, with 1 being Full Moon and 0 being New Moon. Power spectra of the 3 time series in (d), (e) and (f) (arbitrary units) are shown in (g). Mode 2 explained 8%, 12% and 14% of I' variability at mouth, mid-fjord and up-fjord stations, respectively. In the same sequence, Mode 3 explained 4%, 5% and 6% of I' variability. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

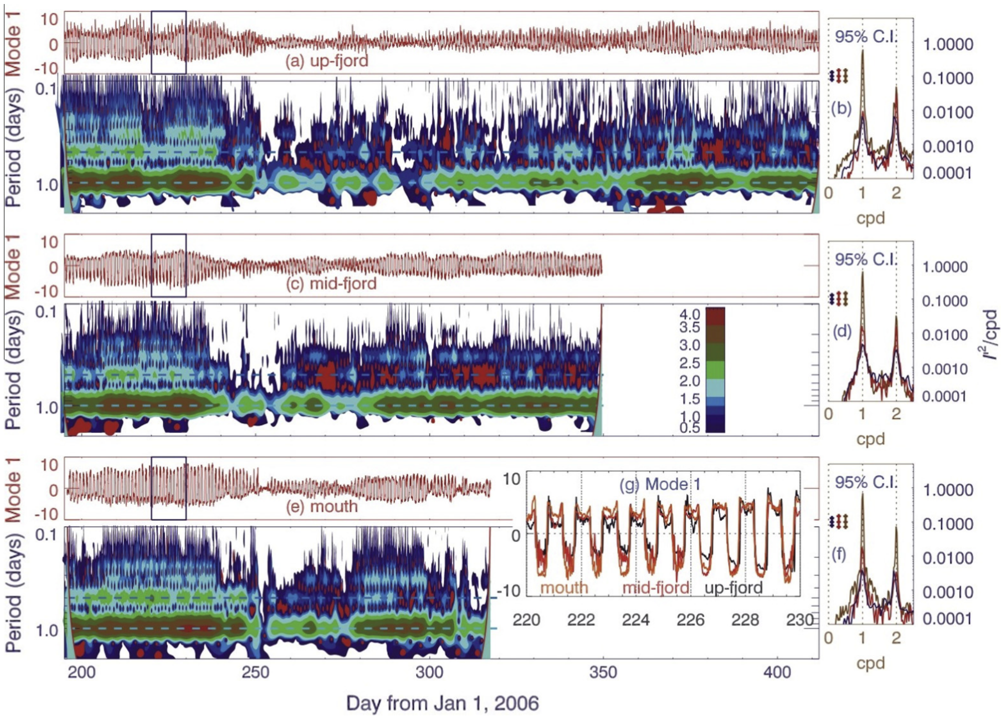

Fig. 6. Wavelet analysis of the principal component 1 obtained from a high-pass filtered version of I' for each fjord site. A 4th order Morlet wavelet is applied to the time series displayed in (a), (c) and (e) with the respective results appearing underneath. Wavelet amplitudes are displayed in color with the cone of influence barely appearing at the edges of each contour plot. Dashed lines feature variations with periods of 1 day and 0.5 day. Only wavelet amplitudes greater than 0.5 are displayed. Global spectra associated with the wavelet amplitudes are shown in (b), (d) and (f). A 10-day portion of the Mode 1 time series encased by a rectangle in (a), (c), and (e) is shown in (g) to illustrate the shape of the temporal variations and the semidiel cycle. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

iability in the signal (Fig. 5). The essence of an EOF analysis for I' is to construct the covariance matrix of all the I' time series of one site at all depths and solve the eigenvalue problem related to the covariance matrix (e.g., Emery and Thomson, 2004). Solution to this eigen-

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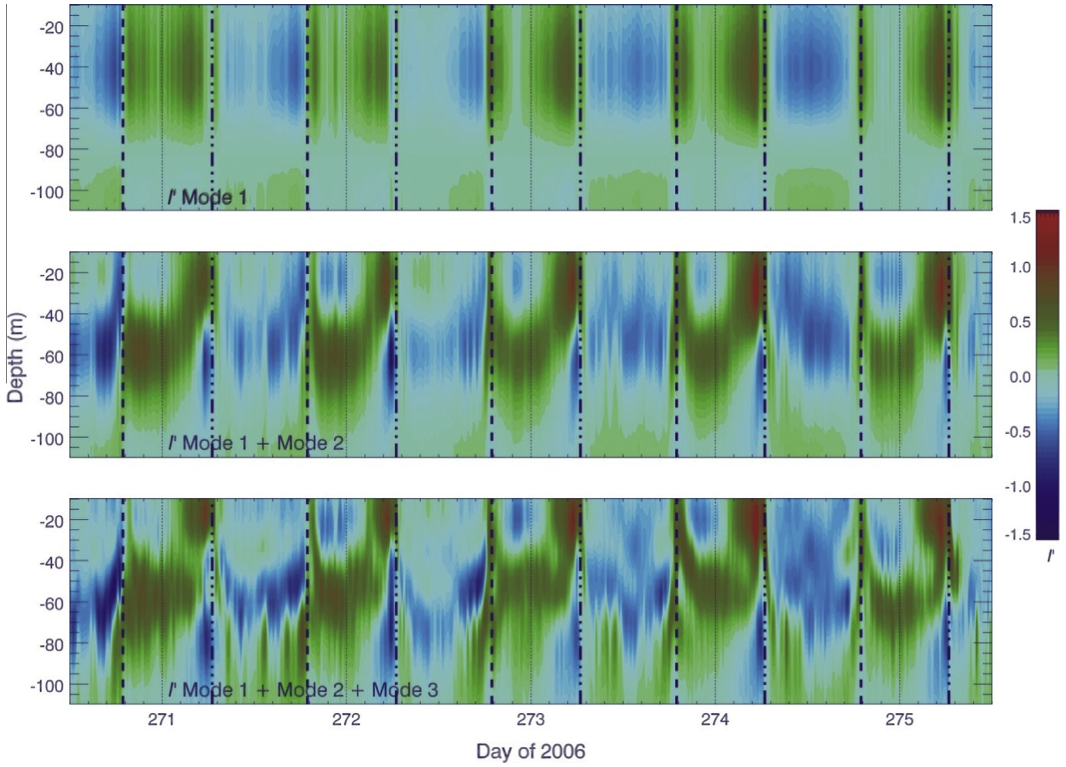

Fig. 7. Reconstruction of the original signal at "mid-fjord" with EOF Modes 1, 2 and 3 illustrating the importance of Modes 2 and 3 in explaining details of the vertical migrations at the transitions between day and night. Dashed vertical lines denote sunset and dash–dot lines indicate sunrise.

value problem yields a decomposition of the original time series of I' profiles into several EOF modes (typically 2 or 3 that explain most of the variance). These EOF modes consist of (i) representative I' profiles (spatial structure or eigenvectors), and (ii) representative temporal variability (or principal components) associated with each eigenvector profile. The eigenvectors represent dominant vertical structures of I'. Emphasis on the EOF application was on the eigenvalues (or % variability explained by each mode) and the temporal variation of the modes, or principal components.

The time series representing the principal component of Mode 1 at each site was further explored with wavelet analysis (e.g., Torrence and Compo, 1998). This analysis breaks down a signal into spectral distributions at each time of measurements (Fig. 6). In other words, periods of greatest variance in the signal are identified with wavelet analysis for each time at which measurements are taken. Dominant periods of variability (e.g., one cycle per day and/or two cycles per day) and their relative influence to the signal could then be identified for the entire period of observation.

Furthermore, results from EOF analysis were used to reconstruct the original I' signal and determine the qualitative influence of each mode on the total signal (Fig. 7). This allowed elucidation of the number of modes (beyond the percent of variability explained by each) that were able to represent the dominant migration pattern observed. Moreover, in order to portray a representative vertical migration cycle for the entire deployment, the distribution of maximum I' (histogram of I') was determined. Histograms of maximum I' for all depth classes were calculated as a function of the hour of the day (Fig. 8).

Spectral energies of vertical velocities as a function of depth were calculated for all stations sampled (Fig. 9). Spectra revealed the dominant periods of vertical excursions at all sites. Finally, the principal component of Mode 1 (I'_1) was also used to determine whether vertical migrations were related to times of sunrise and sunset or to tidal stage (Fig. 10). Times of ascents and descents of organisms were identified from the first derivative of I'_1 with respect to time $\partial(I'_1)/\partial t$. Ascents were assigned as the maximum of $\partial(I'_1)/\partial t$ for each day, while descents were identified as the minimum $\partial(I'_1)/\partial t$ for each day. These ascent and descent times were roughly equivalent to sign changes in the vertical velocity of the ADCP (w), although w-derived values were more equivocal than $\partial(I'_1)/\partial t$. Ascent and descent times were then compared to sunrise and sunset times, and to tidal stage. This analysis allowed identification of causal factors for the main diel migration.

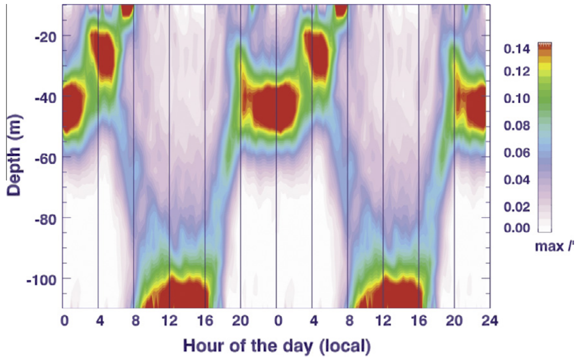

Fig. 8. Histograms of maximum I' for each time of the day, at 15 min intervals at the "mid-fjord" location for the entire deployment period. The units of the contours are counts or number of appearances of maximum I' relative to the total occurrences, at that depth and time. This can be interpreted as the distribution of organisms in depth and time.

3. Results

Cursory inspection of the time series of w and I' for selected 3-day periods at the three locations of measurements (Fig. 2) showed the expected diel pattern. During nighttime, near-surface I' values

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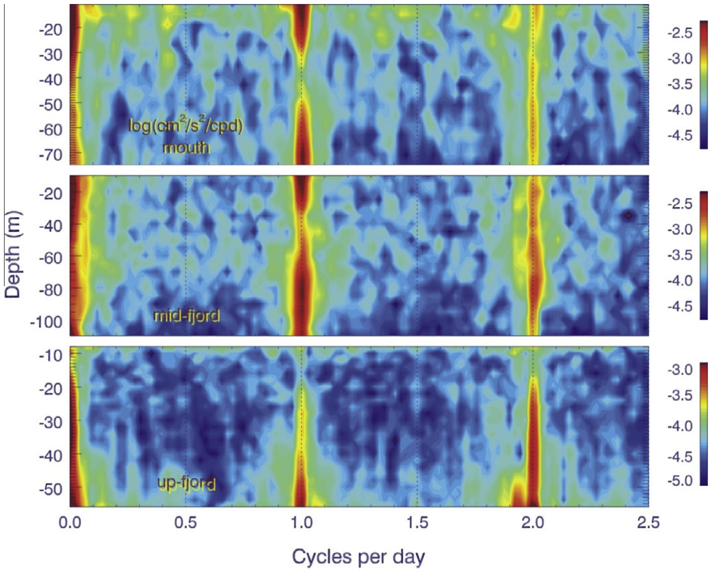

Fig. 9. Contours of the amplitude (log scale) of the power spectra of *w* as a function of depth for the entire data set at each fjord site. This figure illustrates the dominant pulses of *w* at 1 and 2 cycles per day.

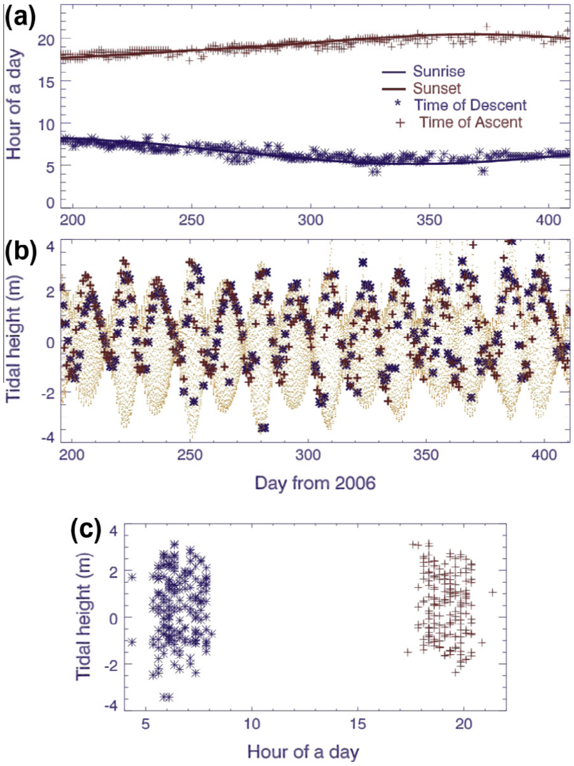

Fig. 10. Times of ascent and descent as identified by the maximum and minimum, respectively, time rate of change of the first principal component for the mid-fjord and up-fjord stations (the mouth station was too short). Ascents and descents are compared to (a) times of sunrise and sunset, showing excellent correspondence; (b) and (c) tidal height showing vertical motions independent of whether tide was falling or rising. Orange dots in (b) denote tidal height itself. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

were greater than daytime values, indicating high concentrations of sound scatterers near the surface at night, i.e., upward excursion of the scattering layer. Clearly, there were upward migrations coinciding with sunset times and downward excursions appearing at times of sunrise. These excursions occurred over a span of less than 1.5 h. Associated with the rapid changes of echo intensity values, upward and downward velocities were evident in the *w* record. Such variations in depth and time conformed to the paradigm of diel vertical migrations of zooplankton (e.g., Hutchinson, 1967; Cohen and Forward, 2009). But a detailed examination of the *I*′ and *w* records revealed that the cluster of scatterers also descended 20–40 m soon after reaching the shallowest depth following sunset. Similarly, the scattering layer ascended 20–40 m before sunrise, followed immediately by the typical sunrise descent. Vertical velocities associated with the twilight (semidiel or double) migration patterns of two ascents and two descents per day were between 0.02 and 0.03 m/s. Velocities were related to vertical excursions of 72–108 m in 1 h, or 108–144 m in 1.5 h throughout the observation records, except for a few winter days.

Stratified net sampling carried out during July and November, at time of mooring deployments, indicated that the sound scatterers were likely associated with euphausiids and decapods (mesopelagic shrimps). Sampling on July 13–14 2006 identified 3 euphausiid species with developmental stages longer than 2.5 mm (*Euphausia vallentini* adult and juveniles, *Nematoscelis megalops* adult and juveniles, *Euphausia mucronata* adult) and one species of decapods (the mesopelagic shrimp *Sergestes arcticus*). The most abundant at night were adult stages of *N. megalops* (38.9%), *S. arcticus* (34.4%) and adult *E. vallentini* (15.1%) with concentrations of up to 1.27, 0.59 and 0.37 individuals/m^3 respectively. Among larval fish, only *M. parvipinnis* showed postflexion larval stages but they were very scarce (0.7%) at night compared with euphausiids and shrimps. Sampling on November 6–7, 2006 found only two euphausiid species (*E. vallentini* adult and juveniles and *N. megalops* adult and juveniles) and also the mesopelagic shrimp *S. arcticus*. Among them, *S. arcticus* was dominant (76.3%) at night, followed by adult stages of *E. vallentini* (10.7%) and juveniles of the same species (9.3%) with maximum abundances at a single stratum of 2.8, 0.84 and 0.94 individuals/m^3. *M. parvipinnis*, a fish species previously observed in Chilean coasts and fjords (Landaeta and Castro 2002, 2006), was the most abundant postflexion fish larvae but were caught in very low numbers (0.023 ± 0.025 larvae/m^3 mean night abundance).

These low *M. parvipinnis* but high euphausiid abundances coincide with observations of fish gut contents (*Merluccius australis*) in

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this area during different seasons. Adults of *M. parvipinnis* have not been widely reported while euphausiids have been the numerically dominant item in their guts (Lillo et al. 2006). At both sampling dates in July and November 2006, the most abundant taxa (three crustaceans) showed diel changes with scarce presence in the upper 50 m during the day and increased numbers at night. At night, all taxa showed two clear ascent movements, one around sunset and the following just before sunrise (Fig. 3), coinciding with the I' signal. During November, the nocturnal ascending peaks in I' were likely related to adult *E. vallentini* and *S. arcticus*. At sunrise, migrations resulted from the combined presence of those two plus juvenile *E. vallentini*. A question that arose from examination of I' and w instantaneous records (Fig. 2) was: how persistent were these twilight migration patterns throughout the entire time of record? The first approach to answer this question was through monthly mean structures of I' and w as a function of depth and hour of the day.

Monthly mean distributions as a function of hour of the day clearly showed the twilight variability in vertical velocities w and backscatter anomaly I' (Fig. 4). Downward velocities with typical mean values of 0.01 m/s were preceded at sunrise by upward velocities. Similarly, upward velocities at sunset were followed by downward velocities. Vertical velocities suggested then a double vertical excursion (up and down) around sunrise and another one (up and down, again) around sunset. But it was the structure of mean I' that best defined the semidiel or twilight pattern. Within a period of $\sim$1 h before sunrise and after sunset, the greatest concentration of sound scatterers (maximum value of I') was found practically at the surface. Around midnight and between the brief times of near-surface residence, the greatest values of I' were typically between 20 to 60 m from the surface. This night-time location of maximum I' was observed consistently from month to month at all three fjord locations, indicating a persistent migration strategy rather than an oddity.

It is evident that the w and I' distributions were related to phototactic organisms because peak values changed as a function of the hour of the day from month to month. In the austral winter months (first two rows of frames in Fig. 4), nighttime congregation in the upper 50 m of the water column was longer than in spring and summer. As daylight periods grew longer, so did periods of negative near-surface anomalies in I'. Remarkably, the double-peaked patterns of w and I' were prevalent at the three stations of the fjord, indicating that organisms effecting twilight migrations were found from head to mouth of the fjord, and from winter to summer.

Analysis of empirical orthogonal functions (EOFs) provided information on the vertical structure of I' and its temporal fluctuations throughout the period of observation (Fig. 5). In the particular context of Fig. 5, I' was determined relative to the deployment-long mean profile of I (see Eq. (1)). Mode 1 explained 81% of the variability of I' at the mouth of the fjord, 70% at mid-fjord and 71% at the up-fjord location. The vertical structure of Mode 1 (Fig. 5a) had the same sign at the mouth and up-fjord locations, whereas it changed sign at the mid-fjord location. This means that I' either increased or decreased throughout the portion of the water sampled at the mouth and up-fjord sites, with the greatest changes occurring essentially in the middle of the range sampled. At the mid-fjord location, the sign change indicated that while I' increased near the surface, it decreased at the deepest levels sampled, and *vice versa*. The principal components or time series of I' Mode 1 for each of the three fjord sites (Fig. 5d, e, f) showed variations dominated by frequencies of 1 cycle per day. This could be gleaned from the spectra of Mode 1 time series at each of the three stations (Fig. 5g). Other I' Mode 1 oscillations had periods >10 days (also seen in Fig. 5g) and were likely related to weekly, monthly, and seasonal variations in organism concentrations and extent of vertical excursions. The character of the vertical excursions was depicted by the low-pass filtered records of Mode 1 time series (thick lines in Fig. 5d, e, f). Negative low-pass filtered values suggested that vertical migrations were centered below mid-water column, i.e., that ascents were shorter than when the values were near zero. Comparing moon phase to the low-pass filtered signals, it appears that there was no modulation by the moon phase (or ‘moonlight’) of the extent of the migrations, except at the up-fjord site during the last two moon cycles (after day 350). In that period after day 350 (Fig. 5d), full moon periods (moon phase = 1) caused the oscillations to be centered below zero, i.e., shorter than usual ascents. More details on the high frequency variations in time of the amplitude of the high-pass filtered principal component 1, may be drawn from wavelet analysis.

A wavelet analysis of the time series of Mode 1 principal component of I' (Fig. 6a, c, e) illustrated the presence of fluctuations with periods of 1 and 0.5 day throughout the observation period and at the three sites sampled. Isolated periods at the end of winter (around day 250, or September 7, in Fig. 6a, c, e) were characterized by the smallest oscillations of I', which is interpreted as a reduced concentration of organisms. Except for a few-day period around September 7 when vertical migrations were not evident, marked vertical migrations with periods of 1 and 0.5 days were present throughout the entire Mode 1 records at the 3 sites. Power spectra of I' representing the entire period of observations (Fig. 6b, d, f), and the integrated wavelet power spectrum over time (not shown), indicated two distinct oscillations with frequencies of one cycle per day and two cycles per day. The wavelet amplitudes (Fig. 6a, c, e) can be best understood by examining a portion of the temporal variability of Mode 1, or principal component of Mode 1 (Fig. 6g), which showed essentially the same shape for the three locations. A square-like wave emulated the paradigmatic diel migration with positive values representing relatively high scatterer concentrations and negative values indicating comparatively low concentrations. The square wave was modified at the crests by relatively rapid upward peaks (Fig. 6g). These peaks appeared soon after the transition from negative to positive principal component values, at sunset, and also just before the switch from positive to negative values, at sunrise. The vertical excursions (or peaks) that modified the diel migration paradigm were consistent with the twilight or semidiel structures depicted in Figs. 2–4. Remarkably, there were periods when the timing of the fluctuations coincided at the three fjord sites (Fig. 6g). This indicated that vertical migrations were effected throughout the fjord at the same time. Furthermore, the amplitude of the oscillations of principal component 1 at the three stations was roughly the same, which suggests coherent variations of organism abundance throughout the fjord.

Empirical Modes 2 and 3 explained much less variability of I' than Mode 1 but still they were influential in the variations observed. Mode 2 (Fig. 5b) exhibited vertical profiles that changed sign from surface to bottom. This was the mode that preferentially explained that while I' (or the concentration of organisms) increased near the surface it decreased at the depths sampled furthest from the surface, and *vice versa*. Mode 3 (Fig. 5c) showed a three-layer structure. The principal components of Modes 2 and 3 for I' were much more noisy than Mode 1 (not shown). Nonetheless, their power spectra indicate robust signals with frequencies of one and two cycles per day and the reconstructed signal illustrated their contribution to the vertical migration patterns.

The reconstructed signal of I' with the first three EOF modes at the mid-fjord site was illustrated over a period of 5 days to demonstrate their qualitative influence (Fig. 7). Only the mid-fjord site was exemplified here because the records covered the largest extent of the water column. The up-fjord and mouth sites, however, portrayed the same patterns. Mode 1 depicted abundance of scatterers near the surface at night and at great depths (>100 m) during day time. Instead of describing a 1–2 h transition of large I' between near-surface and deep waters at sunrise and sunsets, Mode 1 illustrated practically instantaneous transitions. Furthermore, the descent after the sunset's ascent and the ascent before the sunrise descent, as observed, was faintly displayed in this mode. Mode 2 provided the realistic transitions from shallow depth dwellings to deep congregations and *vice versa*. This mode was essential to represent the spatial structure observed. Similarly, Mode 3 portrayed relevant details around the times of ascent and descent and was not negligible in its contribution. The reconstructed signal of I' with the 3 EOF modes thus reinforces the semidiel twilight character of vertical migrations.

Additional evidence of the twilight structure of vertical migrations was illustrated by histograms of distributions of maximum I', for all profiles recorded, as a function of time of day from the entire data set (Fig. 8). Values of maximum I' for each profile are interpreted as maximum concentration of organisms. Their frequency distributions (or histograms) could be considered as the epitome or the paradigm of the vertical migration sequence at the study area. The histograms of I' as a function of time of day clearly showed the night-time residence of organisms at a depth centered at ~30 m from the surface, or ~20 m below the pycnocline. Such histogram distributions also depicted the brief (<~0.5 h) excursions to the pycnocline region (typically in the upper 10 m of the water column) around sunset and sunrise. These additional excursions were representative of two migratory cycles per day associated with times of appearance and vanishing of light in the water column. The twilight semidiel pattern was also confirmed by power spectra of vertical velocities w.

Spectra of vertical velocities (Fig. 9) were determined for all different depths at the three fjord sites sampled. Spectra at mid-fjord and mouth sites showed dominant fluctuations at 1 cycle per day and slightly lesser fluctuations at 2 cycles per day. Interestingly, vertical velocities at the up-fjord location had more energetic fluctuations at 2 cycles per day than at one cycle per day. The low frequency spectral energy that appeared in the vertical velocity spectra was related to the low-frequency modulation of the signal. This is likely associated with the month to month variations in scatterers effecting migrations. Low-frequency variations were not apparent in the spectra of I' of Fig. 6 because they were determined from high-pass filtered signals, i.e., I' represented the deviations from the low-pass filtered oscillations of backscatter anomaly. Low frequency variations do appear, however, in the spectra depicted in Fig. 5 because those were calculated with anomalies from the deployment-long mean profile.

4. Discussion

The twilight vertical migrations depicted here can be tied to light level conditions, in particular to sunrise and sunset (e.g., Ringelberg, 1995; Cohen and Forward, 2009). Some studies have mentioned that organisms may follow same levels of light intensity (isolume, Giske et al., 1990; Cohen and Forward, 2009), even though there are examples where this does not happen (e.g., Benoit-Bird et al., 2009). In some situations, lunar phase may be more influential than irradiance at the water surface in driving the vertical excursions of scattering layers. But studies on vertical migrations of *Maurolicus muelleri* (Staby and Aksnes, 2011) have identified close relationships with isolumes during the longest stretches of the twilight migrations. In the case of the scattering layer in Reloncavi Fjord, there was no clear relationship between vertical excursions and the phase of the moon except for the last 2 months of the up-fjord record (Fig. 5d). Therefore, these results may confirm previous assertions that there is no uniformity in the reasons for vertical migrations in organisms. This lack of uniformity may be also caused by variations in species composition, which could not be ascertained with the very limited net sampling performed. It was evident, however, that the bulk of the vertical migrations of the scattering layer (the diel structure) was tightly coupled to the times of sunset and sunrise (Figs. 2–4). Such timing could also be gleaned from the first derivative of Mode 1 principal component I'_1 with respect to time $\partial(I'_1)/\partial t$ (Fig. 10a). Ascents were assigned as the maximum of $\partial(I'_1)/\partial t$ for each day, while descents were identified as the minimum $\partial(I'_1)/\partial t$ (or most negative) for each day. It was evident that vertical motions were tied to sunrise and sunset times, as expected.

Vertical migrations may sometimes be linked to semidiurnal tides, as observed extensively in other systems and taxa (e.g., DeVries et al., 1994; Welch and Forward, 2001; Castro et al. 2011). In a shallow estuary, Morgan (1995) showed how vertical swimming ability of snail and crab larvae may effectively regulate the position relative to semidiurnal tidal cycles. Older larvae rose higher in the water column during flood tides resulting in upstream transport, and negatively buoyant snail eggs remained near the bottom during slack tides and were mixed during flood and ebb tides resulting in no-net transport. There is also evidence that some larvae use endogenous rhythms that favor flood-tide transport (e.g., DeVries et al., 1994; Welch and Forward, 2001). In the case of Reloncavi Fjord, vertical excursions did not necessarily follow semidiurnal signals (Fig. 10b, c). The timing of ascent and descent was independent of tidal height. It was evident that the phasing of semidiurnal tide and light–dark cycles shifted slightly each day and also clear that the timing of ascent and descent was intimately linked to light availability in the fjord (Figs. 3 and 10). Thus, migrations were not connected to the phase of semidiurnal tides as previously reported for ichtyoplankton in an area adjacent to this fjord (Castro et al. 2011). In fact, the mechanism of selective tidal stream transport (e.g., Hill, 1991; Queiroga et al., 1997, 2006), which favors net transport of organisms during flood tides, was not apparent in the largest and most abundant zooplanktonic species found in Reloncavi Fjord.

The results presented here may be differentiated from previous studies on twilight vertical migrations of zooplankton by several aspects. First, results indicate that twilight vertical migrations can actually be a dominant migratory mode for the organisms observed (maybe euphausiids and decapods). Second, results from the backscatter in the Reloncavi Fjord are the first in Chile to identify a twilight vertical migration pattern persisting for >3 months. While some of the taxa apparently producing the pattern were the same during July and November, other species and younger developmental stages of the original species strengthened the backscatter signal in the last month of record (compare October to January in Fig 4). Twilight vertical migrations, as described here, of *Maurolicus muelleri* in Masfjorden appeared intermittently at a single-point time series that extended for 15 months. In that case, species succession or alternation allowed more varied vertical migration cycles than those observed at Reloncavi Fjord. Third, results indicate for the first time that twilight vertical migrations can appear simultaneously over the entire length of the fjord as indicated by measurements at up-fjord, mid-fjord and mouth locations. Fourth, in distinction to other studies where twilight migrations are reported, this analysis supplements the backscatter signal measured by an ADCP with values of vertical velocities associated with organism vertical excursions. Vertical velocity measurements indicate that the pre-dawn ascents of plankton, followed by descents around sunrise, occur within a relatively short period (<1.5 h, Figs. 2–4). This is analogous to the echogram-derived assertions of Staby et al. (2011). Pre-dawn upward velocities measured by the ADCP clearly showed pulses that lasted only between 0.5 and 1.5 h and suggested that these upward excursions are indeed influenced by irradiation levels. Fifth, these

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results have been obtained with analyses that may not have been applied before to studies of vertical migrations of organisms, namely empirical orthogonal functions and wavelet analysis. These useful techniques were able to identify the times (a) when the scattering layer had greatest concentration of organisms and (b) when the twilight migration structure was most evident.

A relevant question for the particular case of twilight vertical migrations in Reloncavi Fjord is: what is the advantage of effecting the extra 30–50 m upward and downward excursions, twice each day? Departure of the typical diel vertical migrations paradigm through extra excursions seems puzzling. At dusk, there could be different reasons for this first downward added trajectory. Organisms could be swimming to be as close as possible to the surface in order to first eat and then (1) sink once they are satiated (e.g., Cohen and Forward, 2009) or (2) sink to avoid predation (e.g. Tarling et al., 2002) or (3) descend through a delicate balance between feeding and predation avoidance (Giske et al., 1990). Other options for the up-and-down extra excursion are as follows. (4) These crustaceans might be selective feeders so it is possible that they are following their food. Copepods themselves are known to effect twilight migrations (Cohen and Forward, 1995a,b). Evidence to date indicates that the species involved eat zooplankton but also that a large fraction of their diet (i.e. *E. vallentini*) usually is phytoplankton (diatoms), which reduces the support for this prey-chase hypothesis. (5) Crustaceans might like to congregate at the depth of maximum water temperature, analogously to juvenile fish (Giske et al., 1990; Giske and Aksnes, 1992) so when they get to the relatively cooler near-surface fjord waters, they swim down to relatively warmer waters. This hypothesis, although plausible during the winter season, may be difficult to support in spring when surface temperatures rise (e.g. Castillo et al., 2012) and yet the migrating pattern persists. (6) Upon swimming up, the crustaceans find the pycnocline (at ~10–15 m depth, or shallower e.g. Castillo et al., 2012; Valle-Levinson et al., 2007) to be a physical barrier or an abrupt change in salinity that makes them escape down to higher salinity waters. This idea is supported by the fluctuations of two cycles per day illustrated by vertical velocity spectra (Fig. 9). Twilight fluctuations are better defined at mid-fjord and up-fjord locations (semidiel peaks in Fig. 9), where the pycnocline is stronger, than at the mouth (Castillo et al., 2012). (7) When sensing the pycnocline effects, the organisms descend to ensure their permanence inside the fjord. This strategy would prevent them from being swept out of the fjord by the net outflow near the surface, typical of estuarine and fjord circulation (e.g., Valle-Levinson et al., 2007, 2014). (8) A combination of all or some of the above reasons might be causing the upward and downward motion associated with the overall dusk ascent.

The upward-and-downward excursion around sunrise may be caused by fewer reasons than the excursion around dusk. Only one can be proposed here, on the basis of previous studies. The expected scattering layer motion, following the paradigm of normal diel vertical migrations, should be downward after the organisms spend the night at depths of 30–50 m. But instead of proceeding directly downward they actually swim up, spend less than 1 h around the pycnocline and then go deep to their daylight depths. This excursion may be effected because the migrating group does not find food at 30–50 m deep during the night. Therefore, they need to go up for nourishment before the downward swim to the deep congregation during daylight hours. The upward excursion of zooplankton to the feeding strata just before sunrise might be more advantageous and clear in winter than in spring, as revealed by the strength in I' and by the movements of the centroid of the main large crustaceans (Figs. 3 and 4). This is because in winter the overall productivity of the area is low and largely supported by small sized organisms in the photic zone (microbial food web; González et al. 2011), which represent zooplankton food. In general, the potential optimization of feeding rates *versus* predation threats during dusk and dawn has also been referred to as 'antipredation window' (Clark and Levy, 1988), which still represents a viable explanation for the vertical excursions.

It is clear that this study in a Chilean fjord did not have all the information required to provide solid explanations for the reasons of the twilight vertical migrations depicted. The study was designed to investigate the circulation in the fjord but, unfortunately, not the biological phenomenon directly. However, the collected acoustic data provided valuable information to advance understanding on the character of scattering layers in the ocean, but particularly in fjords. Other targeted studies in Norwegian and Scottish fjords have provided reasonable interpretations that seem to be ratified by the data collected in the Chilean fjord. For instance, in both Masfjorden and the Clyde Sea, the nighttime sinking motion was halted at depths of 30–50 m, similar to the situation reported herein. Therefore, the twilight vertical migration structure in fjords is perhaps more pervasive and widespread than previously recognized.

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