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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.

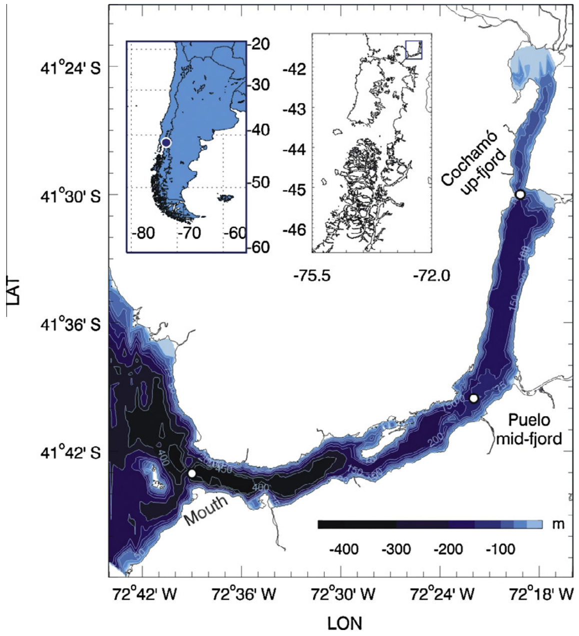

Fig. 1. Study area showing bathymetry of Reloncavi Fjord and location of 3 ADCP moorings at mouth, mid-fjord and up-fjord sites. Left inset shows a blue circle over the study area in the context of a portion of South America. Right inserts displays the northern Chilean Inland Sea with a rectangle outlining 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

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.

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