



## Research papers

## Short-term variations in mesozooplankton, ichthyoplankton, and nutrients associated with semi-diurnal tides in a patagonian Gulf

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## ABSTRACT

The relationships between the distribution of different zooplankton and ichthyoplankton stages and physical and chemical variables were studied using samples and data (CTD profiles, ADCP and current meter measurements, nutrients, mesozooplankton, ichthyoplankton) obtained from different strata during two 24-h cycles at two oceanographic stations in a Chilean Patagonian gulf during the CIMAR 10-Fiordos cruise (November, 2004). A station located at the Chacao Channel was dominated by tidal mixing and small increments in surface stratification during high tides, leading to decreased nutrient availability. This agreed with short periods of increased phytoplankton abundance during slack waters at the end of flood currents. Increases in larval density for all zooplankton and ichthyoplankton taxa corresponded to the flooding phases of the tidal cycle. When the larval density data were fit to a sinusoidal model, the regression coefficients were high, suggesting that tides are important features that modulate short-term variations in plankton abundance. All larvae did not vary synchronously with the tidal phase; rather, time lags were observed among species. The abundances of older individuals of the copepodite *Rhincalanus nasutus* and all zoea stages of the squat lobster *Munida gregaria* increased during night flood tides, whereas younger stages increased during daytime flood tides. At a station located at the Queullin Pass, which was dominated by vertical stratification patterns, the variations in peak larval density were better fitted to the semi-diurnal sea level fluctuations. Other evidence indicated internal tides below the pycnocline, which could promote larval transport in deeper layers. In the overall picture that emerges from this study, planktonic organisms from different habitats and phylogenetic origins seem to respond to the local tidal regimes. In some cases, this response might be beneficial, transporting these individuals inshore to areas that are rich in food during the peak biological production season.

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### 1. Introduction

Semi-enclosed coastal environments such as bays, estuaries, gulfs, and fjords are highly productive zones that, seasonally, show favorable living conditions for the earliest fish and invertebrate stages. During the high production seasons, the youngest life stages of organisms from offshore, the continental shelf, or coastal areas co-occur temporarily, taking advantage of elevated larval food availability, decreased turbulence, or warmer temperatures to enhance larval growth (Boehlert and Mundy, 1988; Epifanio, 1988; Castro et al., 1993, 2007; Landaeta and Castro, 2002, 2006; Palma et al., this issue). The presence of young stages in these coastal zones, however, is affected by coastal oceanographic processes (mixing, stratification, transport) that

may occur regularly or occasionally, disrupting typical vertical and horizontal distribution patterns. If these oceanographic processes occur regularly throughout the season, similar behavioral adaptations to local conditions may sometimes be observed, even in individuals produced in different areas (i.e., selective tidal stream transport to avoid exportation from highly productive zones, Queiroga et al., 1997, 2006). In other cases, alternative behavioral responses conducive to achieving, for instance, the similar final goal of retention, may also occur, even in species that have a close phylogenetic relationship.

The association between larval vertical migration and tidal currents has received attention in terms of changes in abundance within the tidal cycle (DeVries et al., 1994; Tankersley et al., 1995; Welch and Forward, 2001), as a mechanism for subsequent horizontal transport (Hill, 1991; Christy and Morgan, 1998), and as a response to endogenous swimming rhythms (Tankersley et al., 1995; Zeng and Naylor, 1996; Forward et al., 1997). The effect of tidal currents on the abundance of different larval stages

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on intra-tidal time scales in mixed and stratified systems has received less attention. Tidally mixed systems are characterized by weak or absent stratification and an early onset of the annual production cycle (Mann and Lazier, 2006), homogeneous distributions of chlorophyll-*a* (chl-*a*) concentrations in the water column (O'Reilly et al., 1981), and year-round primary production at levels lower than those in stratified systems. Changes in the typical food web of diatoms-copepods-larval fishes to a system dominated by small copepods and microplankton – a less efficient chain for providing food to young fish – have also been reported (Williams et al., 1994). On the other hand, changes in water-column stratification are known to affect copepod fecundity through changes in phytoplankton abundance and size (Peterson and Bellantoni, 1987), but there is also evidence of increased copepod abundances in stratified systems due to more nutritious and available phytoplankton (Sullivan, 1993). The classical vertical distribution pattern of zooplankton in the open ocean shows the highest abundances just above the pycnocline (Longhurst, 1981), associated with the maximum phytoplankton biomass (Ortner et al., 1980) or maximum phytoplankton productivity (Longhurst and Harrison, 1989). But in stratified systems induced by buoyant estuarine plumes, entrainment may induce changes in grazing patterns by enhancing biological productivity and larval transport through tidal currents in the up-estuary direction in lower layers (Norcross, 1991).

The northern zone of Patagonian fjords and channels in southern Chile (41.4–43°S, Fig. 1) is known for its high biological production, which increases in austral spring and summer (Iriarte et al., 2007; González et al., this issue). During these seasons, the input of freshwater with low nitrate, low

phosphate, and high silicic acid increases. Seasonal increments in rain and melting of ice from surrounding glaciers promote the stratification of estuarine waters, lowering their surface nitrate and phosphate contents but maintaining their high silicic acid contents (Silva, 2008) and increasing phytoplankton density (Iriarte et al., 2007).

A typical, two-layer pattern of estuarine circulation develops on the continental coastal margins of Ancud Gulf (Fig. 1) near the freshwater sources, with an upper layer flowing seaward and the layer beneath flowing landward (Sievers and Silva, 2008). The main source of freshwater emptying to the gulf comes from Reloncavi Estuary, a fjord-like inlet, known locally and hereinafter referred to as Reloncavi Fjord, where a plume of buoyant water develops a down-fjord surface current characterized by significant vertical stratification. The largest discharge into Reloncavi Fjord is provided by Puelo River, with an annual mean of 670 m<sup>3</sup>/s and variations between 150 and 3590 m<sup>3</sup>/s (Niemeyer and Cereceda, 1984). This river has the third highest discharge of all those emptying into the entire Chilean Inland Sea (41–56°S). A gulfward-flowing buoyant plume enters Reloncavi Sound and follows to the south mostly through Queullin Pass, the main way of exchanges between the two basins (Reloncavi Sound and Ancud Gulf). Other freshwater sources on the eastern side of the gulf play a less significant role in stratification. Stratification gradually decreases as the surface layer moves westward and southward into Gulf of Ancud (Silva et al., 1997). On the western side of this basin, Chacao Channel provides a way for water exchange with the shelf. This shallow, narrow passage is characterized by strong tidal currents (3–4 m/s) in its narrowest region (2 km) at Remolinos Rock (10 m depth), a pinnacle

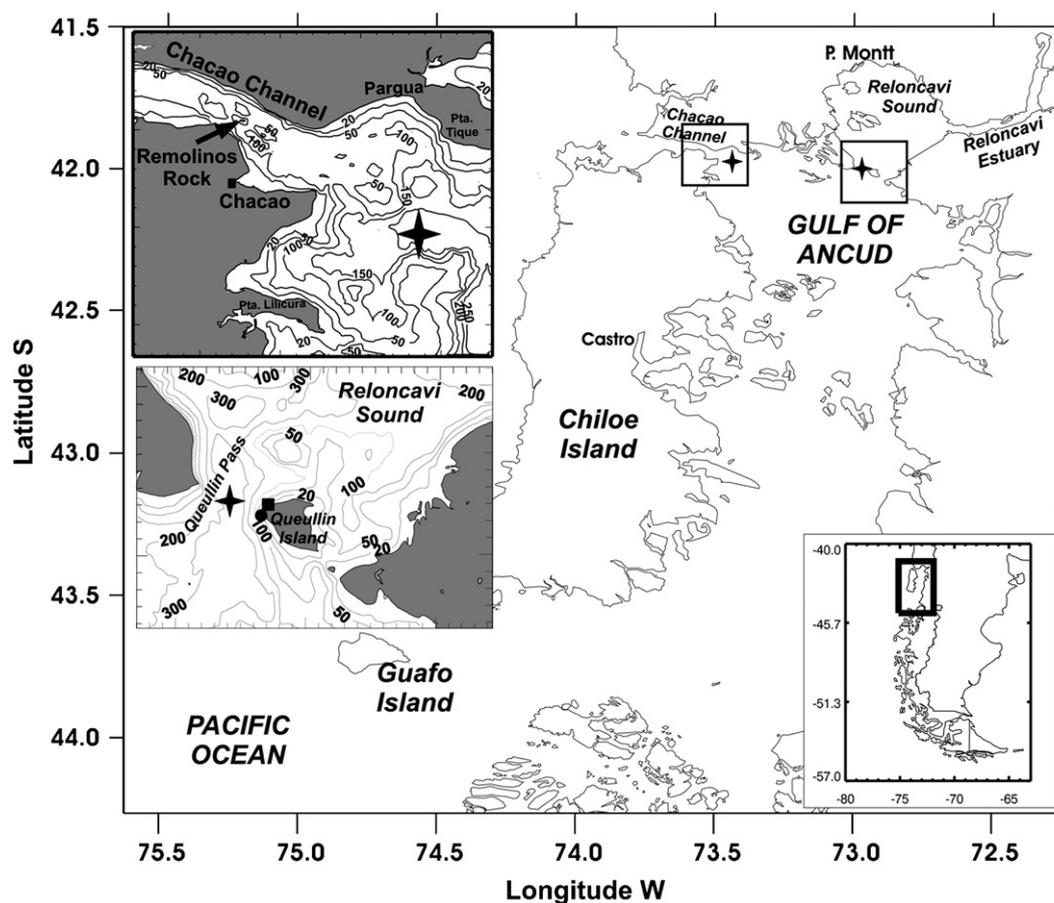


Fig. 1. Study area and position of sampling stations (depicted by stars) in Chacao Channel and Queullin Pass. The solid square off Queullin Island is the tidal gauge and the solid circle is the meteorological station.

surrounded by depths of about 100 m, as shown by Cáceres et al. (2003). Current velocities decrease east of this channel as its width increases toward Gulf of Ancud. The hydrodynamics of this gulf are dominated by stratification on the east and tidal mixing on the west; both phenomena have important consequences for the horizontal and vertical distribution of nutrients in the water column. Maximum tidal ranges during spring tides into the Gulf of Ancud are typically 5–6 m according to nautical charts published by the Servicio Hidrografico y Oceanografico of the Chilean Navy (SHOA). Typical tidal ranges in the western end of Chacao Channel are about 2–3 m, suggesting that a strong pressure gradient develops in the east-west direction in this passage, in turn yielding strong tidal currents in the channel.

Abundant larval stages of many local coastal fish and crustacean species occur in spring in the northern part of the Patagonian area along with early life stages of many species from the continental shelf, the shelf-break, or even from offshore epipelagic and mesopelagic zones adjacent to the fjords and channels (Balbontín and Bernal, 1997; Mujica and Medina, 1997).

The mechanisms of larval dispersal from the inner waters to the outer parts of the channels have been investigated on a seasonal scale for several species (Landaeta and Castro, 2006; León et al., 2008). On a shorter time scale (diurnal), the responses of diverse holoplankton and meroplankton communities to the strong tidal mixing regime and stratification in this area have not yet been assessed. This study reports changes in abundance of larvae for three fish species at two sites in the Gulf of Ancud, northern Patagonia, over two 27-h cycles. The sites are representative of mixed and stratified conditions. The species studied are two demersal fishes, *Hippoglossina macrops* (bigeye flounder) and *Merluccius australis* (southern hake), and a small coastal pelagic fish (*Normanichthys crockeri*). At one site (Chacao Channel, closer to the open sea), we also studied two crustaceans: *Rhincalanus nasutus*, a continental shelf-break holoplanktonic copepod reported to display clear diel vertical migrations (Castro et al., 1993) and the zoea stages of *Munida gregaria*, a benthic galatheid squat lobster. The study set out to assess whether the tidal regime at these two sites has a similar effect on

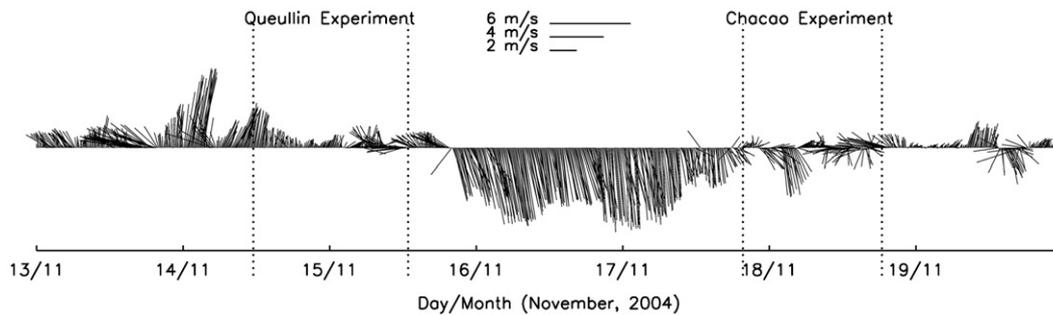


Fig. 2. Stick diagram of wind data at Queullin Island, covering periods of both experiments.

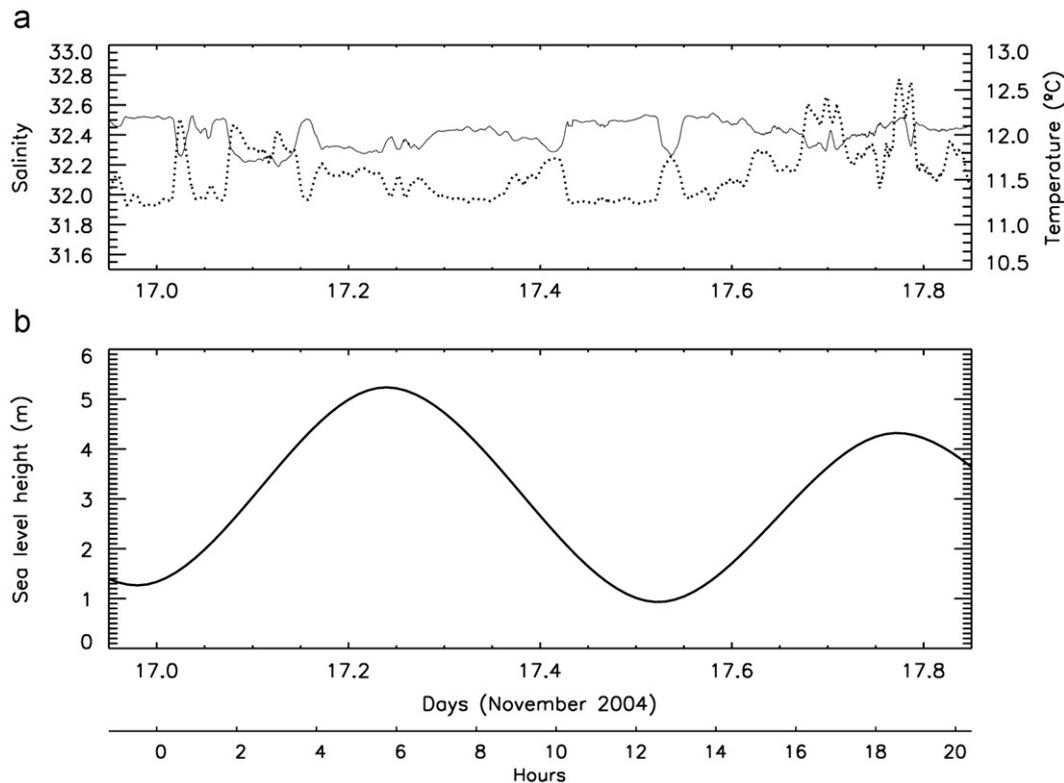


Fig. 3. (a) Running mean of surface salinity (solid line) and temperature (dotted line) data series recorded with an SBE-37 instrument in Chacao Channel. (b) Sea level height at Chacao.

the larval stages of species from different origins whose abundances are known to peak in austral spring.

## 2. Methods

### 2.1. Study sites

The study was conducted by performing two 27-h experiments (Chacao and Queullin) in the Gulf of Ancud on 14 and 17 November 2004, six and three days before neap tides, respectively, at 2 oceanographic stations located 23 nautical miles apart, depicted with stars in Fig. 1 (41.85°S 73.40°W, 220 m depth; and 42° 10'S 72° 58'W, 350 m depth). Both samplings were done during the CIMAR 10-Fiordos cruise using the oceanographic research vessel AGOR Vidal Gormaz.

### 2.2. Hydrographic and current data collection and analyses

At each station, hydrographic casts were made every 3 h down to 200 m depth using a CTD Seabird-25; seawater samples were collected from nine depths (0, 5, 10, 25, 50, 75, 100, 150, 180 m) with the aid of a 24-Niskin-bottle rosette. The salinity sensor was calibrated using water samples obtained with the rosette and analyzed with an Autosal Salinometer. Seawater samples were also used for chl-*a* and fluorometric determinations following Parsons et al. (1984) and for nutrient determinations (nitrate+nitrite, phosphate, silicic acid) with an autoanalyzer according to Atlas et al. (1971). Between CTD casts, the ship navigated slowly (at about 1 m/s) back and forth along a 2-nautical mile (nm) transect roughly oriented in the north-south direction at each station, taking biological samples with towing nets. The oceanographic stations were in the middle of the corresponding transects.

For the Chacao experiment, current profiles were obtained with a broadband 307.2 KHz RD-Instruments Acoustic Doppler Current Profiler (ADCP) mounted looking downward on a catamaran (3 m length) towed from one side of the research vessel during navigation on the 2-nm transect. Velocity profiles with a vertical resolution of 2 m and ping rates of ~1 Hz were averaged every 30 s. A Seabird probe SBE-37 was attached to the catamaran to record the surface temperature and salinity data at 10-s intervals during current measurements. Data series were filtered with a running mean weighted on intervals of 10 min. For the Queullin experiment, a mooring with current meters was installed at 100 and 200 m depth from 20 August to 15 November 2004 at Queullin Pass (star in Fig. 1). Another ADCP of 307.2 KHz was also installed at 50 m depth looking upward, but data from this device became unrecoverable and unsuitable for analysis.

In the Chacao experiment, ADCP current data were rotated 40° counter-clockwise to an along- (*v* flow) and across- (*u* flow) channel coordinate system. This angle was oriented in the direction of the greatest variability of the tidal currents and of the weakest across-channel tidal flows. In order to use representative current data for the position of the station sampling, we discarded vertical current profiles obtained during navigation on the 2-nm transect that were taken beyond a circumference with a 500-m radius centered on the station position. After that, data were interpolated onto a uniform time-depth grid of 5 min and 1 m, respectively.

Wind data for both experiments were obtained with an Aanderaa station installed on Queullin Island (Fig. 1; solid circle) from 3 August to 21 November 2004. During the Chacao experiment, sea level observations were obtained from a permanent tidal gauge of SHOA located near Chacao (Fig. 1); this showed maximum tidal ranges of 5.3 m during spring tides.

Sea level data for the Queullin experiment were obtained from a tidal gauge installed off Queullin Island (Fig. 1; solid square) from 28 September to 21 November 2004.

### 2.3. Zooplankton sampling and data analyses

While navigating the central part of the transect, oblique stratified mesozooplankton samples were collected every 3–4 h with the aid of a Tucker trawl net (1 m<sup>2</sup> mouth opening, 300 μm mesh, with a flowmeter mounted in the net frame). Strata sampled were 0–50 and 50–100 m at Chacao and 0–25, 25–50, and 50–100 m at Queullin. Zooplankton samples were preserved in formalin 10% buffered with sodium borate for later analyses in the laboratory.

All larval fishes from the samples collected at both stations were identified and the three most abundant species were classified based on their notochord flexion stage as pre-flexion (young larvae) and post-flexion (older larvae). From the samples

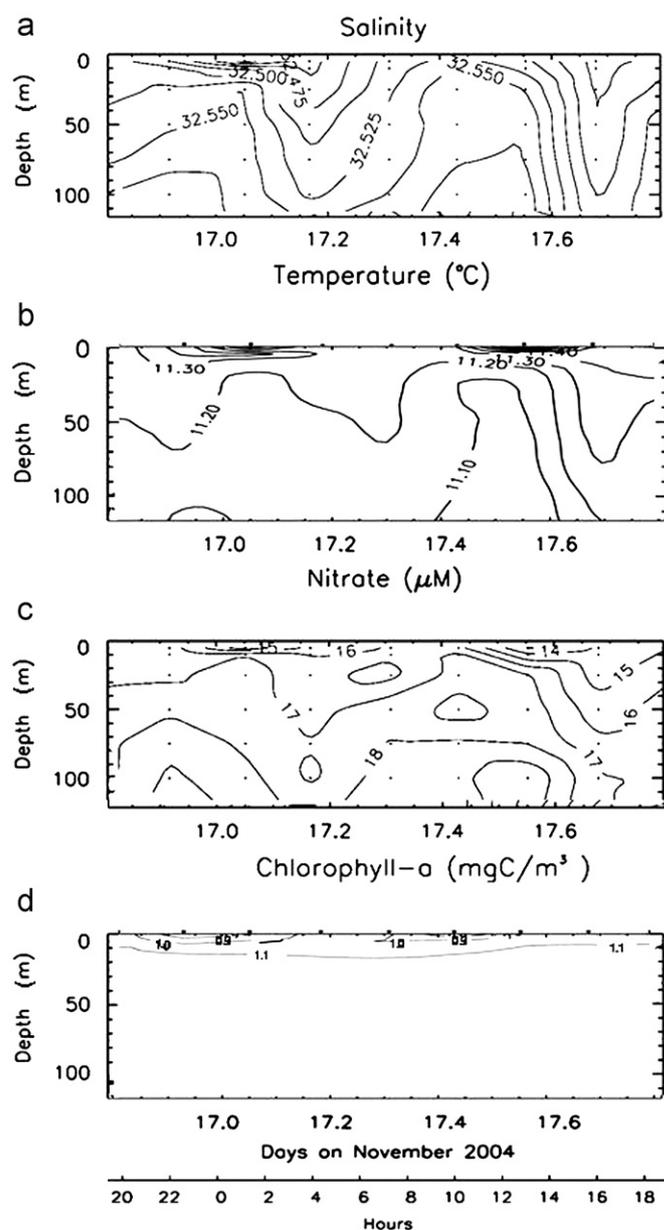


Fig. 4. Evolution over time of (a) salinity (upper panel), (b) temperature, (c) nitrate ( $\mu\text{M}$ ), and (d) chlorophyll-*a* during the sampling period in Chacao Channel.

collected in Chacao, the copepodite stages and adults of *R. nasutus* in the zooplankton samples were also identified, sorted, and counted, as were all the zoea stages of the squat lobster *M. gregaria*. Zooplankton and ichthyoplankton abundances were standardized to individuals per 1000 m<sup>3</sup> of filtered seawater. To determine whether the changes in sea level and density ( $N_{ti}$ ) of all developmental stages (copepodite+adults; all zoea, all larvae) during the sampling period were associated with the tidal regime (semi-diurnal), we used a non-linear, least-squares regression analysis to fit a sinusoidal function to the sea level data and larval density data ( $\log(N_{ti}+1)$ ) as

$$Y = M + A \cos[(2\pi t)/\lambda - \theta] + v \sin[(2\pi t)/\lambda - \theta] + \varepsilon$$

where  $Y$  is the independent variable (sea level at  $t_i$  or  $\log(N_{ti}+1)$ ),  $M$  is the mean of the independent variable,  $A$  is the amplitude of  $Y$ ,  $t$  is the hour of sampling,  $\lambda$  is the period,  $\theta$  is the acrophase angle,  $v$  is a parameter, and  $\varepsilon$  is the random error term. This and other similar approaches have been utilized recently to describe cyclic variations in plankton abundance and distributions (Yannicelli et al., 2006; Castro et al., 2007) as well as to explore periodicity in decapod crustacean settlement data (Amaral et al., 2007).

### 3. Results

#### 3.1. Temperature, salinity, nutrients, wind, and tidal regime

Wind variations during both experiments are shown in Fig. 2. Northerly winds with mean magnitudes of 2.61 m/s were dominant in Queullin, and variable directions with mean magnitudes of 2.89 m/s were observed in Chacao, suggesting that wind forcing had low relevance for the dynamics at both sites. A southerly wind event with maximum magnitudes of about 7 m/s occurred on November 16 and 17, having low effect on the experiment in Chacao. Both experiments had lower magnitudes than those typical for the season in Gulf of Ancud.

##### 3.1.1. Chacao experiment

Fig. 3 shows the sea level, surface temperature, and salinity observed during the Chacao sampling period. Temperature and

salinity varied little throughout the tidal cycle and changes in salinity were inversely correlated with changes in temperature ( $R=0.71$ ), which is typical for tidally mixed systems. The time evolution of CTD data (Fig. 4) also showed small variations of salinity with depth but, despite this, some patterns of the tidal effect were evident: minimum salinity almost matched the end of the flood tide and maximum salinity the end of the ebb tide. Nitrate concentrations were high throughout the sampling period. At the surface (i.e., =0 m), nitrate concentration fluctuated between 8.47 and 17.47  $\mu\text{M}$  and the lowest registered nitrate values ( $< 15 \mu\text{M}$ ) occurred at the surface during periods of low salinity. Phosphate and silicic acid distributions (not shown here for the sake of brevity) exhibited similar near-surface decreases. Nitrate concentrations were strongly correlated with salinity throughout the sampling period ( $R=0.81$ ).

The current data also contained evidence of vertical mixing (Fig. 5), as velocity contours of the  $u$ -component were nearly vertical throughout the whole diurnal cycle. Changes in the direction of the flow associated with the tidal cycle (Fig. 2) were evident throughout the water column. Positive values of tidal currents in Fig. 4 correspond to the flood tide and negative values to the ebb tide, being out of phase with the height level for about 1–3 h.

The distributions above revealed a pattern of slight increments in stratification due to surface salinity during high tides. This also leads to decreased nutrient availability (Fig. 4), suggesting short periods of rising phytoplankton biomass, represented here by chlorophyll concentrations, during slack waters at the end of flood currents (Fig. 5).

##### 3.1.2. Queullin experiment

Fig. 6a and b shows the variations of salinity and temperature over time in Queullin. Salinities between 27 and 32 were observed in the first 20 m, suggesting a halocline (pycnocline) at that depth (see also nitrate section). Two drops in surface salinity, spaced about 12 h apart, noticeably matched the times of higher surface temperatures (Fig. 6b) and ebb tides (Fig. 7). The sea level and currents at 100 and 200 m depth (Fig. 7) seemed to be out of phase by about 3 h. Our current data suggested internal waves of significant magnitudes (about 40 cm/s) that might promote

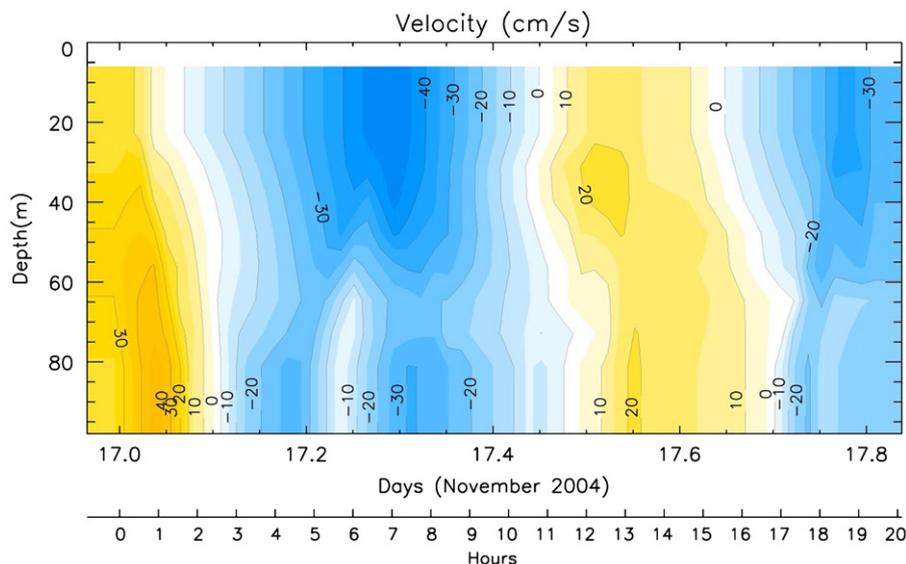
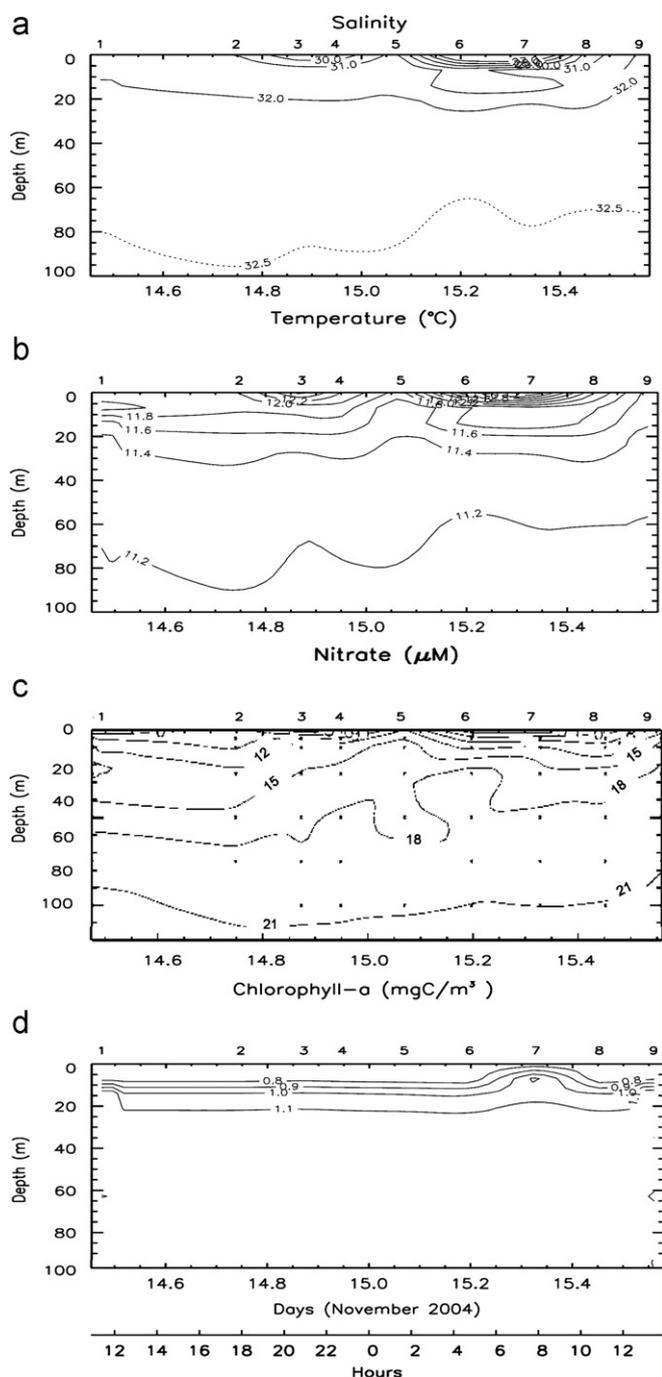


Fig. 5. Evolution over time of velocity data (east-west component, cm/s) obtained with an ADCP device during the sampling period. Positives values southeastward are flood currents and negative values northwestward are ebb currents in Chacao Channel.



**Fig. 6.** Evolution over time of (a) salinity and (b) temperature, (c) nitrate and (d) chlorophyll-*a* contours in Queullin Pass. Numbers on upper horizontal line are times of CTD stations.

entrainment to upper layers and zooplankton transport into the deeper layers (deeper than reported herein). Nitrate in Queullin was lower in the upper layer (i.e., upper 50 m) than in the Chacao area. During ebb tides (casts 3–4 and 6–7), surface nitrate (i.e., 0 m) was very low and fluctuated between 0.1 and 1.6  $\mu\text{M}$ . During flood tides (casts 1–2, 5 and 8–9), surface nitrate was higher and fluctuated between 2.8 and 10  $\mu\text{M}$ . Below the surface layer, the nitrate content was higher (approx. 4  $\mu\text{M}$ ) than in Chacao (Fig. 6).

Chlorophyll distributions (Fig. 6e) were similar to those found in Chacao, increasing at the surface at about 8 h, apparently associated with a strong decline in surface salinity (Fig. 6a).

### 3.2. Fluctuations in the abundance of larval fish and crustaceans

The vertical distribution of fish larvae in Chacao Channel was similar among species: during the day and night, most individual were located in the shallower 50 m layer (Fig. 8). In Queullin Pass, the distribution was different between day and night. Here, the three species were located in the shallower layer during the day but at night *M. australis* and *H. macrops* were located only in the deepest strata and *N. crockeri* showed similar abundance throughout the first 100 m.

The fitting of the sinusoidal function to the sea level data during the sampling period revealed that the sea level fluctuations followed a semi-diurnal pattern (Fig. 9). In Chacao Channel, the sinusoidal function accounted for 93% of the sea level variation ( $R^2=0.93$ ) and 99% of the sea level variation in Queullin Pass (Table 1). In Chacao Channel, the organism density fluctuations (0–100 m deep) also fit, albeit less closely, the sinusoidal pattern. The best larval density data fittings corresponded to the flounder *H. macrops* ( $R^2=0.67$ ), the copepod *Rhincalanus nautus* ( $R^2=0.78$ ), and the squat lobster *M. gregaria* ( $R^2=0.72$ ); all three showed higher densities during the flooding phase of the tide (Fig. 10). The fit of the data for southern hake *M. australis* ( $R^2=0.49$ ) and the small pelagic fish *N. crockeri* ( $R^2=0.53$ ) to the sinusoidal function was less clear ( $R^2 < 0.55$ ) and also out of phase with the semi-diurnal sea level height fluctuations (Table 1).

In Queullin, semi-diurnal changes in larval fish density fluctuations were clearer than in Chacao (Fig. 9). The larval density fluctuations for flounder *H. macrops* ( $R^2=0.76$ ) and southern hake *M. australis* ( $R^2=0.78$ ) were well fit to the semi-diurnal sea level fluctuations, and larval densities either peaked with the highest tides or occurred during flooding. The fitting of a semi-diurnal function to the larval density data of the small pelagic *N. crockeri* ( $R^2=0.56$ ) was less clear than for the other two species, but it was better than in Chacao, and its peak densities were also in phase with the tide or occurred just before it.

In Chacao Channel, the splitting of the crustacean data into different developmental stages and strata also revealed that the maximum densities for the different stages peaked during different flood hours of the day (Fig. 11). *R. nasutus*, for instance, switched from a maximum abundance of early copepodites in the afternoon flood to a peak abundance of adults during the night flood. *M. gregaria* larvae did not switch much between early and older stages, but showed different hours of peak abundance between the shallow (more abundant during the afternoon flood) and deeper layers (more abundant during the night flood). Again, early zoeae and postlarvae peaked during flood hours.

## 4. Discussion

The results of this study showed that changes in temperature, salinity, and nutrients coincided with changes in abundance in all larval stages of crustacean and fish species from different origins throughout the 27-h cycle. In both experiments, temperature and salinity were inversely correlated, exhibiting small variations throughout the tidal cycle in Chacao and large ones in Queullin. Interestingly, nutrient values in Chacao were permanently high throughout the column, albeit slightly lower in the surface layer (0–25 m; 1.3–1.9  $\mu\text{M}$  phosphate, 9–17  $\mu\text{M}$  nitrate, 6–16  $\mu\text{M}$  silicic acid) than in deeper layer (25–100 m; 1.8–2.2  $\mu\text{M}$  phosphate, 15–20  $\mu\text{M}$  nitrate, 10–17  $\mu\text{M}$  silicic acid). As with the salinity patterns, the nutrient concentrations differed slightly between ebb and flood tide. The picture in Queullin was very different, as salinity differences were high (about 5) between ebb and flood periods. The surface zone was thin ( $\approx 5$  m) and had low salinity

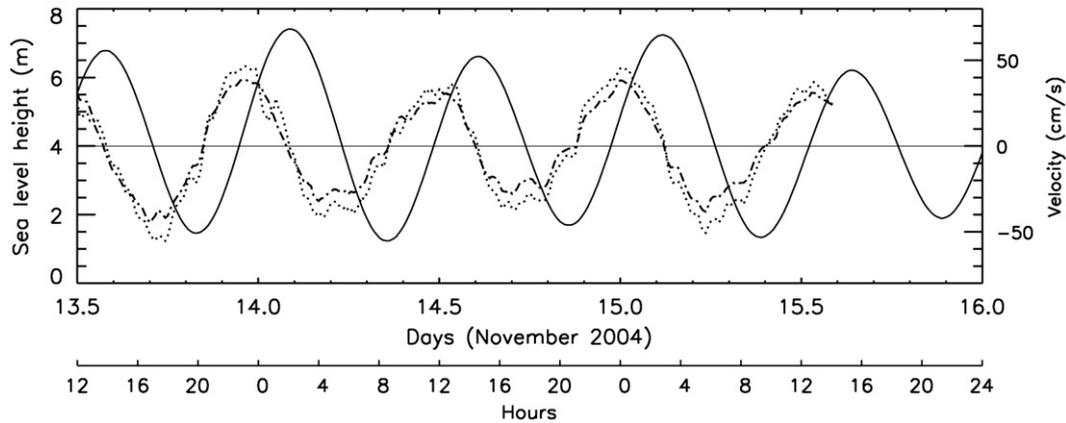


Fig. 7. Sea level heights off Queullin Island (solid line) and current velocities ( $v$ -component) from current meters at 100 m (dotted line) and 200 m (dashed line).

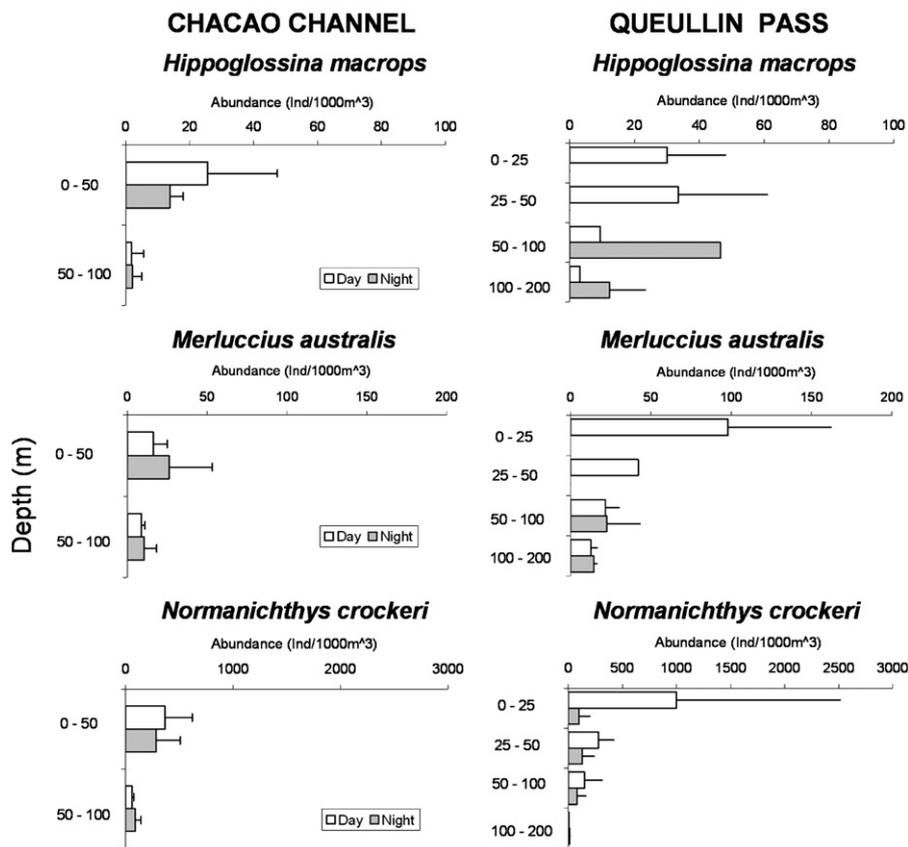
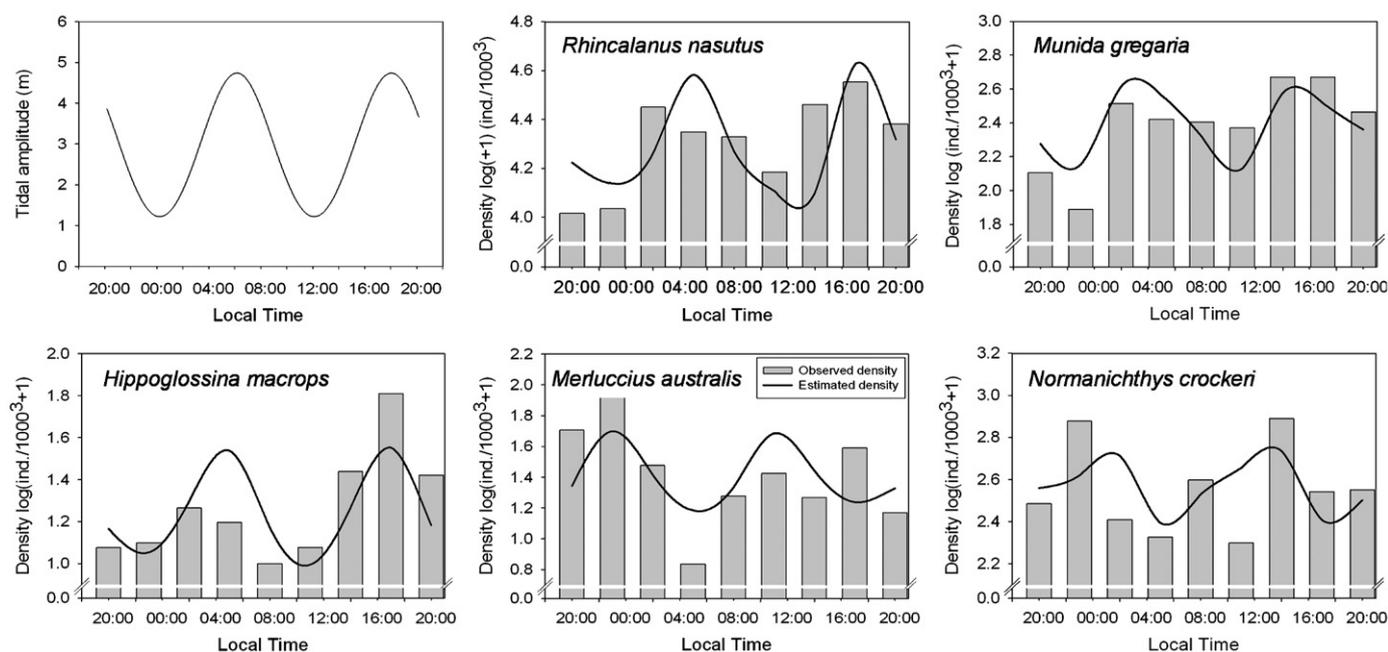


Fig. 8. Mean vertical distribution of fish larvae at the Chacao Channel and Queullin Pass during night and day hours.

and very low phosphate and nitrate contents during the ebb phase (27.3 salinity, 0.13–0.57  $\mu\text{M}$  phosphate, 0.5–1.6  $\mu\text{M}$  nitrate), whereas, during the flood phase, salinity and both nutrients increased (31.7 salinity, 0.79–1.54  $\mu\text{M}$  phosphate, 2.8–10  $\mu\text{M}$  nitrate). The behavior of silicic acid was the opposite that of nitrate and phosphate: when nitrate and phosphate increased, silicic acid decreased. Silicic acid was high (2–49  $\mu\text{M}$ ) during ebb and low (8–21  $\mu\text{M}$ ) during flood phases, reflecting contributions from rivers to the estuarine water flowing back and forth across the mouth of Reloncaví Sound. According to Silva (2008), local rivers have low nitrate and phosphate but high silicic acid contents. Therefore, Queullin Pass, which is closer to freshwater sources than Chacao, shows higher differences in salinity and nutrient contents than Chacao. Therefore, in this

region the nutrients needed for photosynthesis are provided by the phosphate–nitrate rich oceanic waters and the silicic acid rich river water. This is not the situation for other fjord or channel regions such as those of Galicia, Asturias and Cantabria Rias, where the freshwaters from local rivers are richer in phosphate–nitrate–silicic acid than the marine waters, providing high loads of nutrients to estuaries (Vergara and Prego, 1997; Prego and Vergara, 1998). Similar situations happens in some Canadian estuaries such as St. Lawrence (Greisman and Ingram, 1977). Overall, the high nutrient concentrations in the gulf area may result in no limitations for phytoplankton growth (Iriarte et al., 2007), at least during this study period, which corresponded to the season in which many fish and crustaceans reproduce in these northern inshore Patagonian areas (Balbontín and Bernal, 1997;



**Fig. 9.** Sea level variations, larval fish, copepodite, and zoea density variations (0–100 m) in Chacao Channel, and their fit to the sinusoidal model for the sea level variations. Parameters to fit data for each species are shown in Table 1a.

**Table 1**

Parameters of the sinusoidal function fitted to the sea level data and larval density data. (a) Chacao channel. (b) Queullin Pass. Species data are of total individuals (all stages considered),  $\lambda$  is the period,  $\theta$  is the acrophase angle,  $M$  is the mean value of the independent variable,  $A$  is the amplitude,  $R^2$  is determination coefficient, EV: explained variance, standard deviation are shown in parentheses, significant values ( $P < 0.05$ ) are shown in bold.

	$\lambda$ (h)	$\theta$ (h)	$M$	$A$	$R^2$	Error	EV (%)
<b>(a) CHACAO CHANNEL</b>							
Sea level	<b>11.88</b> (0.029)	–	<b>2.98</b> (0.090)	<b>1.76</b> (0.073)	0.92	26.1	86
<i>Hippoglossina macrops</i>	–	– <b>1.24</b> (0.198)	<b>0.27</b> (1.348)	<b>1.28</b> (1.603)	0.67	1.73	45
<i>Merluccius australis</i>	–	– <b>0.94</b> (0.277)	<b>0.76</b> (0.661)	<b>0.67</b> (0.743)	0.50	1.41	24
<i>Normanichthys crockeri</i>	–	– <b>1.08</b> (0.250)	<b>1.79</b> (2.025)	<b>0.86</b> (2.670)	0.53	0.72	28
<i>Rhincalanus nasutus</i>	–	– <b>1.26</b> (0.042)	<b>3.55</b> (0.929)	<b>1.10</b> (1.280)	0.78	0.11	60
<i>Munida gregaria</i>	–	– <b>1.31</b> (0.164)	<b>2.27</b> (0.287)	<b>0.37</b> (0.292)	0.72	0.25	52
<b>(b) QUEULLIN PASS</b>							
Sea level	<b>13.28</b> (0.011)	–	<b>4.32</b> (0.041)	<b>2.77</b> (0.033)	0.99	10.73	98
<i>Hippoglossina macrops</i>	–	– <b>1.98</b> (0.191)	<b>0.53</b> (0.249)	<b>0.76</b> (0.285)	0.76	1.16	60
<i>Merluccius australis</i>	–	– <b>0.204</b> (0.096)	<b>1.10</b> (0.193)	<b>0.40</b> (0.285)	0.78	1.42	61
<i>Normanichthys crockeri</i>	–	– <b>0.222</b> (0.180)	<b>1.936</b> (0.204)	<b>0.45</b> (0.313)	0.56	0.96	30

Mujica and Medina, 1997; Landaeta and Castro, 2006; Bustos et al., 2007; León et al., 2008).

In Chacao, stratification was always low and it was weaker during slack waters after the near-surface flood tidal current, coinciding with decreased surface nutrient concentrations. The ADCP data did not show any evidence of a layered system. The relatively high nitrate, phosphate, and silicic acid concentrations found in most of the water column suggested that tidal currents drive a continuous supply of nutrients from deeper layers up to the euphotic zone, allowing high phytoplankton production to continue in spring and summer. Nonetheless, the tidally induced regime exhibited low magnitudes of current data when compared with those of the Chacao Channel. Decreased velocities from Remolinos Rock (3–4 m/s) to the site of the experiment (0.4 m/s) may be attributed to the coastal geometry of Chacao Channel, which widens and deepens as it enters the Gulf of Ancud, facilitating the dissipation of tidal energy. In spite of this decrease, tidally mixed conditions were maintained throughout the tidal cycle, as shown by salinity, temperature, nutrient, and current data.

Our comparison of chlorophyll distributions also suggested a pattern of entrainment. In Chacao, pulses of chlorophyll were evident in association with tidal forcing, decreasing at the surface during ebbing (Fig. 5). But in Queullin (Fig. 6d), the isolines did not seem to respond to changes in tidal pulses, showing upward entrainment that might be attributed to a change in wind direction. When compared with other tidally mixed systems of the coastal ocean, Chacao exhibits similar patterns of continuous food supply year-round induced by coastal banks (Illes and Sinclair, 1982; Lough and Manning, 2001). Stratification induced by salinity, as observed in Queullin, is also a recognized mechanism to increase productivity in estuaries (Cloern, 1984) and fjords (Masson and Peña, 2009). Other fjordic systems exhibit a pattern of alternation between stratification and mixing during spring and winter, respectively (Simpson and Rippeth, 1993), a feature not observed in this work, where both stations are dominated for each corresponding pattern the entire year.

The vertical distribution of two of the larval fishes differed between areas. Whereas larvae of the three fish species were located in the shallower layer in Chacao Channel, in Queullin Pass,

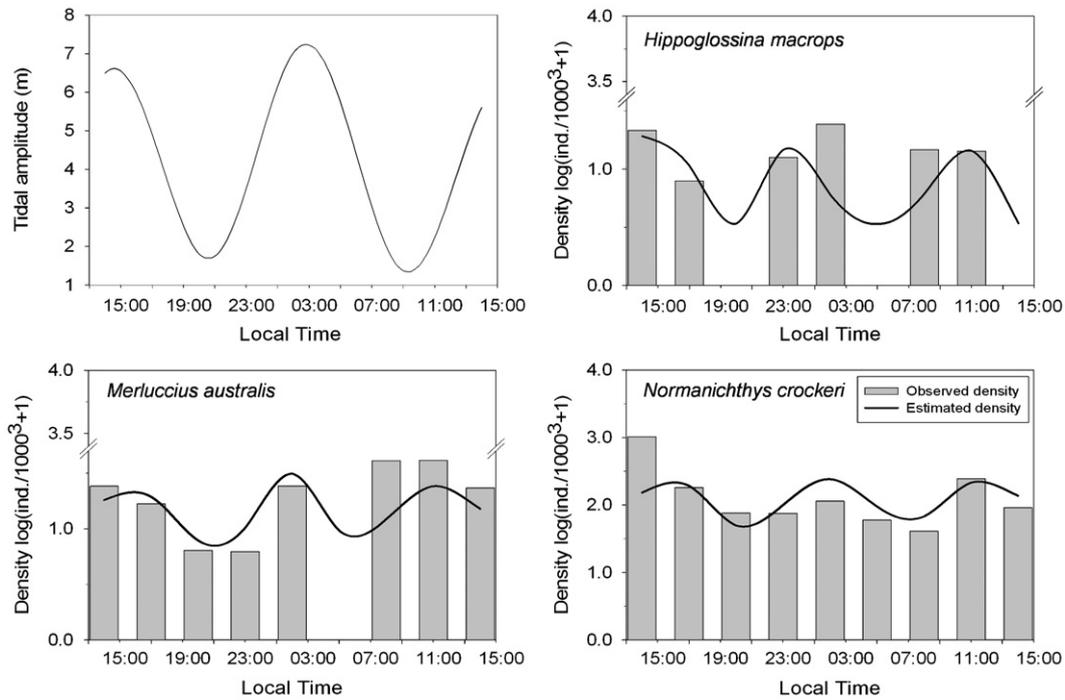


Fig. 10. Modeled tides, total larval density variations (0–100 m) of the three fish species targeted in Queullin Pass, and their respective fits to the tidal model. Data for sinusoidal functions for the fit of data on each species are shown in Table 1b.

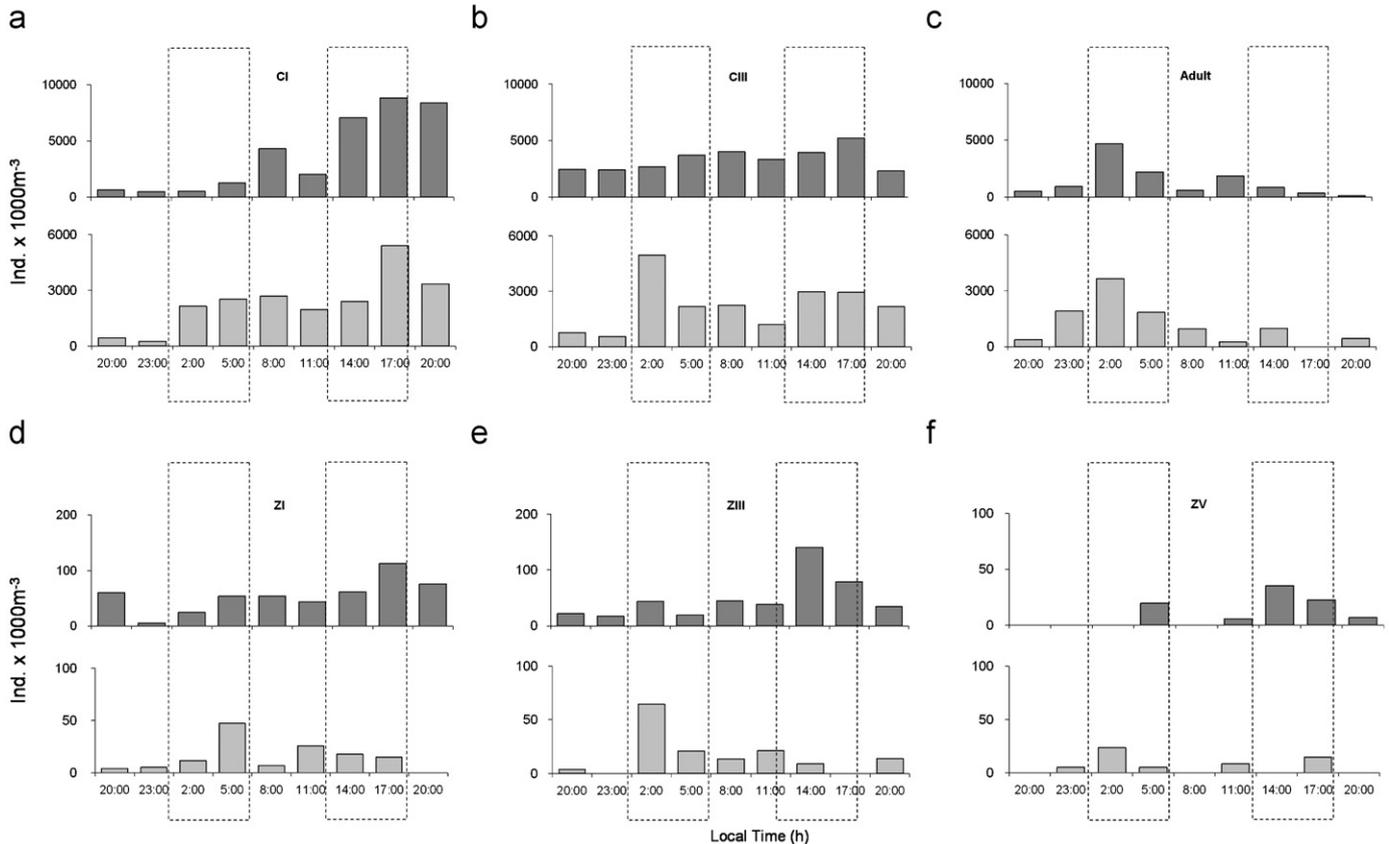


Fig. 11. Evolution of copepod and zoea densities (individuals/1000 m<sup>3</sup>) in the shallow (0–50 m, dark bars) and deeper (50–100 m, light bars) strata along the sampling period in Chacao Channel. *R. nasutus*: (a) copepodite CII, (b) copepodite CIII, and (c) adult copepod. *M. gregaria* zoea stages (d) ZI, (e) ZIII, and (f) ZV. Vertical boxes (dotted) indicate flood hours.

*M. australis* and *H. macrops* distributions were broader and their highest mean densities were also deeper. These results were unexpected because stronger vertical mixing and, hence, a more uniform vertical distribution, was expected in Chacao Channel. The shallower distribution in the latter area could be explained by the ability of the larvae to maintain a vertical positioning in the water column for some time under these turbulent conditions. Fish larvae of the size observed herein (mostly < 12 mm SL) are usually not strong enough swimmers to oppose vertical velocity shears. However, if they could adjust their buoyancy by inflating their gas bladders (Forward et al., 1999), this might favor their permanence in the shallow layers, even under turbulent conditions. Changes in vertical distributions have been observed under increased levels of turbulence induced by wind (Franks, 2001). However, on those occasions, adjustments in buoyancy have led to deeper distributions away from the source of turbulence. In our study, the adjustment of the vertical positioning of fish larvae might have occurred by displacement toward shallower layers.

The semi-diurnal variations in sea level differed in several ways (i.e., period, amplitude) between areas. Interestingly, variations in larval density for the three fish species and both crustaceans in the shallower 100 m corresponded well with semi-diurnal variations in sea level. These results, however, do not mean that all species responded synchronically to the same tidal phases; rather, some presented a time lag between the peak larval abundances and highest sea level heights. In Chacao Channel, for instance, *H. macrops*, *R. nasutus*, and *M. gregaria* varied in phase but presented a time lag between maximum sea level height and peak larval abundances, and were almost opposite in phase with *M. australis* and *N. crockeri*. In Queullin Pass, however, the three larval fish species studied followed the same phase and were nearly synchronous with tidal phases.

In Queullin, stratification by the estuarine buoyant plume in Reloncavi Sound was evident in the first 20 m, as well as tidal pulses. A pattern of internal waves in the deeper layers was observed in the current data at 200 m and might play a role as a larval transport mechanism. In our study, we focused on fish species and crustacean stages located in the shallower layers. However, a deeper zooplankton sampling scheme than ours might have detected variations in some taxa that we were not able to determine in this study. Mesopelagic fish species such as *Maurollicus parvipinnis*, whose eggs occur deep in the water column in other areas along central Chile (Landaeta and Castro, 2002), occur abundantly within the fjords and channels in Patagonia and may well be the subject of transport by internal tides, as reported herein.

In Chacao, variations in abundance during the sampling period for both crustaceans (copepod *R. nasutus* and squat lobster *M. gregaria*) corresponded well to flooding phases during the tidal cycle. The fitting of their density data to the sinusoidal model gave high regression coefficients ( $R^2$ ) despite the limitations in the length of the data set. Said results suggested the tidal component was an important feature that modulated the crustacean larval abundance. The regression coefficients ( $R^2$ ) obtained were within the range of other longer time studies on zooplankton fluctuations in coastal areas or in studies using similar approaches but focusing on changes in crustacean diel vertical distributions (Queiroga et al., 2006; Yannicelli et al., 2006; Amaral et al., 2007; Castro et al., 2007) in other areas. For these two crustaceans, thus, a second pattern emerged from the changes observed in the abundance of copepodites and zoas (see Fig. 7) in both strata: older individuals increased in abundance during flood tides at night and younger ones during flood tides in the day. Thus, older planktonic crustacean individuals, which are capable of diel vertical migrations, seemed to respond to tidally induced up-estuary

transport for nurserying; this is consistent with the hypothesis that some larvae utilize an endogenous rhythm for flood-tide transport (DeVries et al., 1994; Welch and Forward, 2001) rather than one based on salinity changes, as shown by Tankersley et al. (1995). The transport mechanism has been shown to be particularly efficient if the vertical migration period is synchronized exactly with the tidal period (Hill, 1991); this mechanism is known as selective tidal stream transport (Queiroga et al., 1997, 2006). In this case, crustacean organisms rose on successive flood tides and descended on ebbs, inducing a net transport in the flood direction. High abundances of younger individuals in daytime flood tides, alternatively, might be attributed to limitations in displacement capacities and the exploitation of abundant food during daylight. These non-migrating organisms should exhibit short displacements, as modeled by Hill (1991).

Overall, this study shows that organisms from different habitats and phylogenetic origins seem to respond to fluctuations in the tidal regime in two estuarine habitats of the northern Chilean Patagonia. Some of these organisms have been classified as either mesopelagic (i.e., *R. nasutus*) or from deeper benthic habitats (*M. gregaria*), and the adults are not expected to face strong tidal variations on a regular basis, as observed in tidally mixed shallow areas. For these crustacean species, the behavioral responses observed herein (diel vertical migrations, tidal synchronization) might provide them the benefit of transport to inshore food-rich areas. However, the tides also affected the changes in abundance of the larval fish species analyzed at both sites in this study; these fish have been reported to be spawned in fjords and channels as well as offshore waters over the shelf or shelf-break (i.e., southern hake). Semi-diurnal variations in larval abundance do not necessarily follow the tidal phases in all areas. Instead, inter- and intra-specific variations occur depending on the degree of stratification of each habitat.

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