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# Ichthyoplankton spatial distribution and its relation with water column stratification in fjords of southern Chile (46°48'–50°09'S) in austral spring 1996 and 2008

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## ABSTRACT

The occidental shore of the southern tip of South America is one of the largest estuarine ecosystems around the world. Although demersal finfish fisheries are currently in full exploitation in the area, the fjords south of 47°S have been poorly investigated. Two bio-oceanographic cruises carried out in austral spring 1996 and 2008 between 47°S and 50°09'S were utilized to investigate the spatial distribution of fish eggs and larvae. Small differences in the environmental conditions were identified in the top 200 m of the water column between years (5.3–10.5 °C and 0.7–33.9 units of salinity in October 1996; 6.3–11.5 °C and 1.2–34.2 units of salinity in November 2008). The low salinity surface layer generated a highly stable water column within the fjords (Brunt–Väisälä frequency,  $N > 0.1$  rad/s; wave period  $< 60$  s), whereas a well-mixed water column occurred in the gulfs and open channels. For both years, the ichthyoplankton analysis showed that early life stages of lightfish *Maurolicus parvipinnis* were dominant ( $> 75\%$  total eggs and  $> 70\%$  total larvae) and they were collected throughout the area, irrespective of the water column stratification. However, other components of the ichthyoplankton such as Falkland sprat *Sprattus fuegensis*, rockfish *Sebastes oculatus*, and hoki *Macruronus magellanicus* were more abundant and found in a wider range of larval sizes in less stable waters ( $N < 0.1$  rad/s). Oceanic taxa such as myctophids (*Lampanyctodes hectoris*) and gonostomatids (*Cyclothone* sp.) were collected exclusively in open waters. The October 1996 observation of *Engraulis ringens* eggs in plankton samples corresponded to the southernmost record of early stages of this fish in the Pacific Ocean. We found a significant negative relationship between the number of larval species and  $N$ , and a significant positive relationship between the number of larval species and wave period. Therefore, only some marine fish species are capable to utilize fjords systems as spawning and nursery grounds in areas having high amounts of freshwater discharges and very high vertical stratification during austral spring season.

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## 1. Introduction

In fjord systems, high levels of freshwater discharge promote stratification in the head of fjords (upper fjords), whereas strong tidal currents enhance some vertical mixing (Etherington et al., 2007; Valle-Levinson et al., 2007). On the other hand, because of the larger tidal velocities over the sills, mixing can be strong and

the stratification weaker in the mouth of a fjord (Dyer, 1997). In this sense, along a fjord system several suitable environments are available for the reproduction and nursery of marine fishes of a wide range of habitats. In coastal areas, positive relationships between larval fish abundance and stratification (Reiss et al., 2002; Bustos et al., 2008a) and between the location of larval fish in the water column and stratification have been identified (Sánchez-Velasco et al., 2007; Øresland and André, 2008).

The fjord ecosystem in southern Chile (41°20'–55°58'S, Fig. 1) is over 1600 km long and has a surface area of about 240,000 km<sup>2</sup>, with a high degree of geomorphologic and hydrographic complexity, forming one of the largest estuarine areas in the world (Palma and Silva, 2004). The water column of the area is

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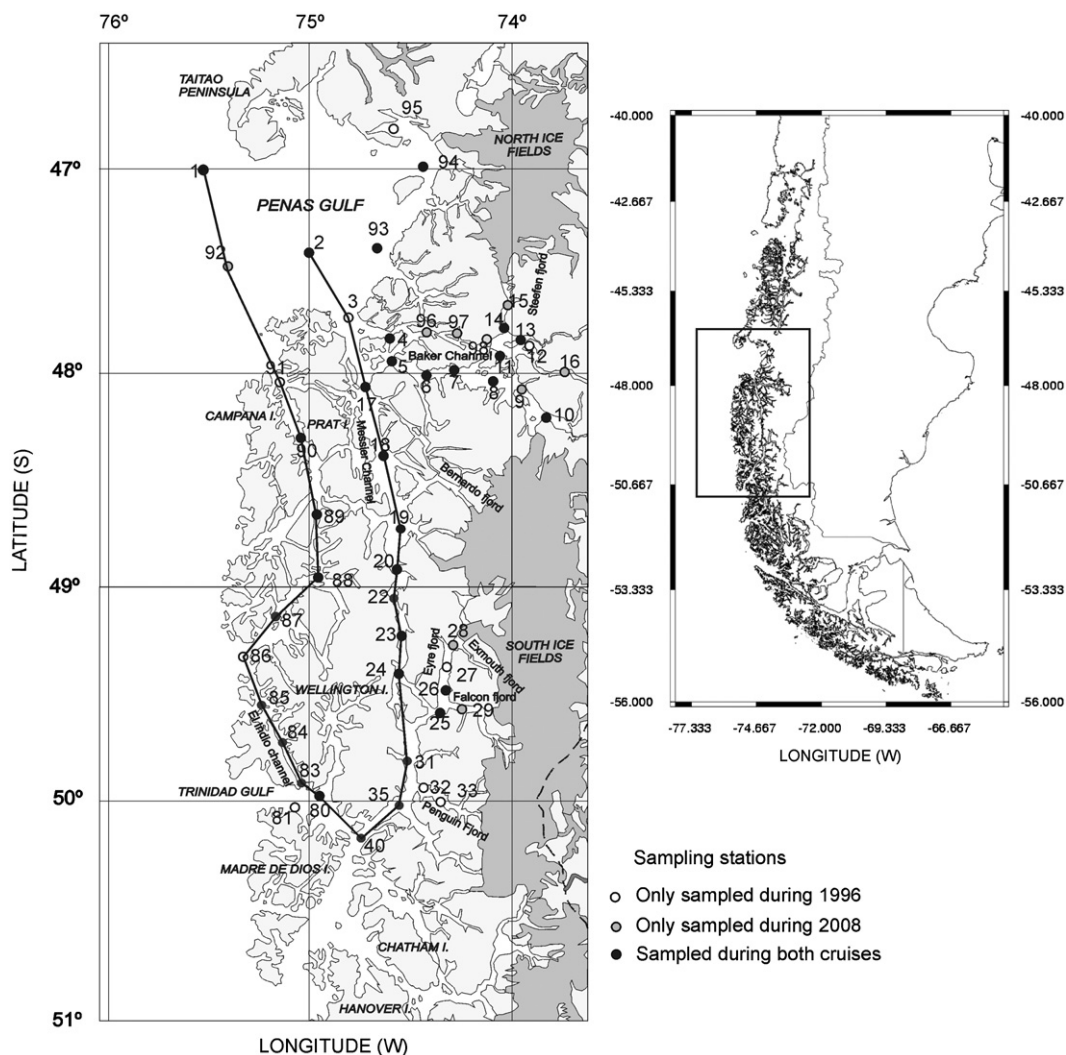


Fig. 1. Map showing the location of the stations sampled in October 1996 and November 2008. Lines correspond to transects showed in Figs. 2 and 3.

characterized by a low salinity surface layer (due to freshwater discharge, high precipitation rates, and coastal runoff) and relatively high salinity, low temperature, and high-density bottom water. A sharp vertical salinity gradient occurs between these layers at 20–30 m depth, producing a highly stratified system (Silva et al., 1995, 1998; Cáceres et al., 2006). The coastal waters follow a classical spring and autumn chlorophyll bloom cycle (Toro et al., 1999) in which primary production is co-limited by strong seasonal changes in light and nitrate (Iriarte et al., 2007). Recently, the area between 41°20'S and 46°S has been the subject of intensive marine research because it is heavily used for fisheries, aquaculture, and ecotourism (Soto and Norambuena, 2004; Buschmann et al., 2006; Aranís et al., 2007; Bustos et al., 2008a; Silva et al., 2009).

The area south of Taitao Peninsula (46°S) has been less studied. Off the coast, Subantarctic Surface Water (SASW) dominates between the surface and 150 m depth. In the channels and fjords, Surface Estuarine Water flows seaward in the upper level (0–50 m) (Sievers et al., 2002; Silva and Calvete, 2002). Compared with the adjacent coastal waters (open waters), the inner sea of the channels and fjords is characterized by higher concentrations of chlorophyll-*a*, larger amounts of suspended organic and inorganic particulate matter (Pizarro et al., 2000) which produces a milky water. In relation to zooplankton, higher densities of gelatinous zooplankton (siphonophores *Lensia conoidea*; Palma

and Silva, 2004), and reduced densities of micronecton (*Euphausia vallentini*; Palma and Silva, 2004) and some taxa of larval decapod crustaceans (such as Porcellanidae and *Neotrypaea uncinata*; Mujica and Medina, 2000) have been detected. Over the continental shelf of the adjacent coastal waters, dense aggregations of adult southern blue whiting *Micromesistius australis*, southern hake *Merluccius australis*, hoki *Macruronus magellanicus*, and warehou *Seriola caerulea* are currently captured by industrial fisheries (Saavedra et al., 2007). Fjords located between 41°20'S and 46°S in southern Chile are used as spawning and nursery grounds by a series of marine organisms such as mollusks (Molinet et al., 2005, 2006, 2008), decapod crustaceans (Gebauer et al., 2007; León et al., 2008), and fishes (Balbontín and Bernal, 1997; Bernal and Balbontín, 1999; Balbontín and Bernal, 2005; Córdova and Balbontín, 2006; Landaeta and Castro, 2006; Bustos et al., 2007, 2008a, b; Landaeta et al., 2008). Moreover, dense aggregations of demersal fishes occur nearby (Saavedra et al., 2007). Therefore, it is expected that areas south to Taitao Peninsula also act as spawning and nursery grounds for several groups of marine fishes. In the area, Baker river and the melting of North and South Ice Fields (Fig. 1) add cold freshwater in the upper fjords, which produce strong gradients on stratification and stability of the water column along fjords and channels. Because egg and larval marine fishes from southern Chile require different environmental conditions for its development, it is also expected

that only some fish species may utilize areas of low water temperature and salinity (and very high vertical stability) as spawning grounds. We formulate the hypothesis that a relationship exists between stratification of the water column and the composition and abundance of early life stages of marine fishes during austral spring conditions. The main goal of this research was to identify the ichthyoplankton from southern fjords located between 46°48'S and 50°09'S during austral spring 1996 and 2008, and relate them to the environmental conditions of the water column, utilizing the vertical density gradients as measure of stratification. Also, we will compare the composition and abundance of ichthyoplankton between years to observe if changes have occurred in a time lapse of 12 years in the area, in the context of the global climate change.

## 2. Methods

### 2.1. Field work

Two bio-oceanographic cruises were carried out in austral spring onboard the R/V Vidal Gormaz between 46°48'S and 50°09'S (Fig. 1). The first cruise, conducted between 16 October and 7 November 1996, sampled 37 stations whereas the second, carried out between 1 and 18 November 2008, comprised 42 stations. At each station, environmental data of the water column (temperature, salinity, density) were collected from the surface to 800 m depth or 10 m above the bottom with a Seabird SBE-19 CTD profiler. Plankton samples were collected from 200 m depth or 10 m above the bottom to the surface through oblique tows with a Bongo net (66 cm diameter, 300  $\mu$ m mesh size) with a TSK flowmeter mounted in the frame of the net to estimate the volume of seawater filtered. Towing speed was  $\sim$ 2–3 knots. The volume filtered in each tow (October 1996: range=39.5–398.3 m<sup>3</sup>/tow, mean  $\pm$  standard deviation=171.8  $\pm$  87.8 m<sup>3</sup>/tow; November 2008: range=101.9–881.6 m<sup>3</sup>/tow, mean  $\pm$  standard deviation=419.9  $\pm$  151.1 m<sup>3</sup>/tow) was calculated from flowmeter counts. Once over the vessel, the nets were washed and one sample was fixed in 5% formalin buffered with sodium borate for the identification of ichthyoplankton and morphologic measurements and the other was preserved with 90% ethanol for studies on larval growth (not shown in this work).

### 2.2. Laboratory work and data analyses

All eggs and larval fish were separated from all zooplankton samples collected during both cruises and they were counted and identified to the lowest taxonomic level possible. Identification was carried out following Moser (1995), Balbontín et al. (2004), Bustos and Landaeta (2005), Uribe and Balbontín (2005), and Landaeta et al. (2008). Larvae were classified according to the developmental stage as pre- or postflexion (inflexion larvae were included in postflexion). All undamaged larvae ( $n=535$ ) were measured to the nearest 0.1 mm (notochord length, NL, from the tip of the snout to the tip of the notochord, or standard length, SL, from the tip of the snout to the base of the hypurals). No attempt was made to correct lengths for the effects of preservation. Egg and larval counts were standardized to individuals  $\times 10^{-2}$  in the water column for each sampling station.

With the information from the CTD, we calculated at each oceanographic station the Brunt-Väisälä frequency ( $N=[(g/\rho) \times (\partial\rho/\partial z)]^{1/2}$ ), where  $g$  is the gravity (9.8 m/s<sup>2</sup>),  $\rho$  the density of sea water, and  $z$  the depth, which is the frequency at which a vertically displaced parcel will oscillate within a statically stable environment. We also calculated the period of the wave ( $\tau$ )

following Mann and Lazier (2006), utilizing  $\tau=2\pi/N$  for the maximum value of  $N$  estimated in the water column at each station. Finally, stations were classified considering the highest value of  $N$  estimated in the water column at highly stable ( $> 0.1$  rad/s) or less stable ( $< 0.1$  rad/s) sampling stations.

Comparisons were carried out on larval size distributions of selected fish species collected from highly ( $> 0.1$  rad/s) or less stable ( $< 0.1$  rad/s) sampling stations. Also, mean larval size of each species was compared between cruises (1996 versus 2008). Non-parametric statistics were utilized, i.e., Mann-Whitney  $U$  tests, to compare larval sizes, after homogeneity of variances was rejected (Levene's test,  $p < 0.001$  for all cases).

Least square linear regressions were computed between the number of larval species ( $S$ ) and  $N$ , and between  $S$  and the period of the waves at each station for each sampling year.

## 3. Results

### 3.1. Physical setting

Two latitudinal sections (inner and outer transects) were constructed to show the stratification of the water column in temperature and salinity along channels of southern Chile. They were selected in order to show the wide range of environments in the study area: open oceans, channels, and areas influenced by river discharge and ice melting. In October 1996 (Fig. 2), physical conditions ranged from 5.3 to 10.5 °C and 0.7 to 33.9 units of salinity. The highest temperatures were found in the surface waters of Penas Gulf (10.5 °C). On the outer transect, tongues of warmer surface waters ( $\sim$ 25 m depth) were identified along Fallos and Ladrilleros channels (Fig. 2). All along the surface waters of transects thermal gradients were detected. Slightly warmer subsurface waters were found along Picton Channel and Trinidad Gulf (Fig. 2). Water column salinity was strongly stratified in the upper 15 m depth. Salinity was lower ( $< 25$ ) along Fallos Channel and Trinidad Gulf (Fig. 2). Salinity values higher than 33 were detected below 75 m depth in Penas Gulf. Saltier waters were found deeper ( $> 110$  m) inside latitudinal channels (Fig. 2). In the inner transect, the Angostura Inglesa Constriction (AIC) divided water parcels, where a thermal front also occurred. Messier Channel, which is connected with Penas Gulf through its northern side (Fig. 1), showed relatively warmer subsurface waters than Wide Channel. In the latter channel, a thermal inversion was noticeable (Fig. 2) because of the entrance of glacier melt water from some fjords (Eire, Falcon, and Penguin) and the Southern Ice Fields (Fig. 1) advected into the channels through the fjord system. Vertical salinity stratification was also observed in the upper 15 m depth (Fig. 2).

Similar trends in the water column structure were observed in November 2008 in the channels of southern Chile (Fig. 3). Temperature and salinity were 6.3–11.5 °C and 1.2–34.2 units of salinity, respectively. Again, warmer and saltier waters were found in Penas Gulf and a vertical thermal inversion was detected in Wide Channel south of AIC; a core of cold ( $< 7$  °C) and salty (34.5) water was denoted below 140 m depth (Fig. 3). In the outer and inner transects, surface waters showed a latitudinal temperature gradient ranging from 10.68 °C in Penas Gulf to 7.77 °C in Trinidad Gulf in the top 10 m depth (Fig. 3). Salinity was lower in the top 15 m depth and the lowest values ( $< 27$ ) were associated with Fallos and Wide channels and Trinidad Gulf (Fig. 3). North of AIC, the water column was less vertically stratified in temperature and salinity.

Vertical profiles of the Brunt-Väisälä frequency ( $N$ ) showed spatial rather than temporal variability (Fig. 4). Stations located in areas directly influenced by the open ocean (waters from Penas

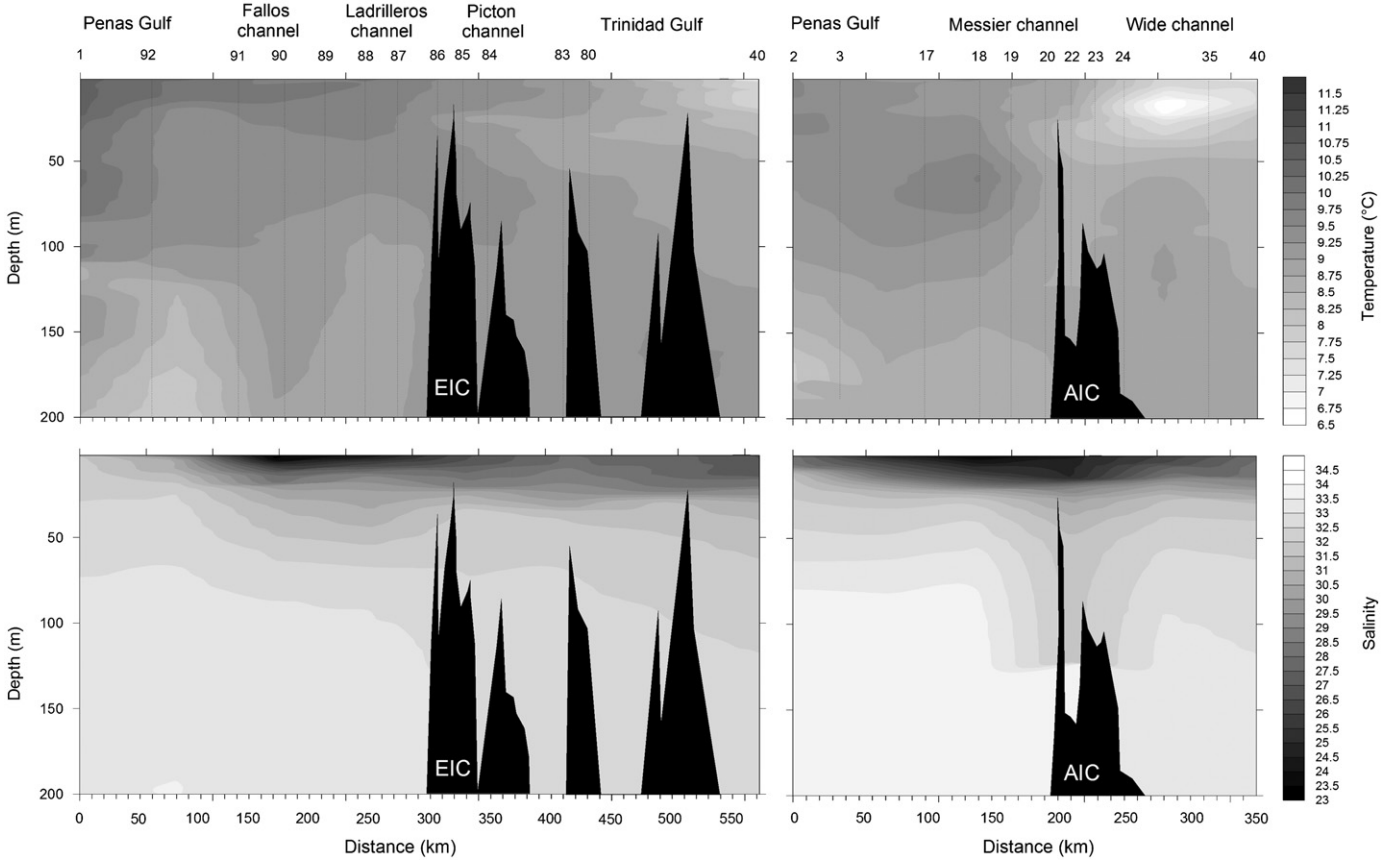


Fig. 2. Vertical sections of temperature (°C) and salinity in October 1996. See number of stations in Fig. 1 for details. EIC=El Indio Constriction; AIC=Angostura Inglesa Constriction.

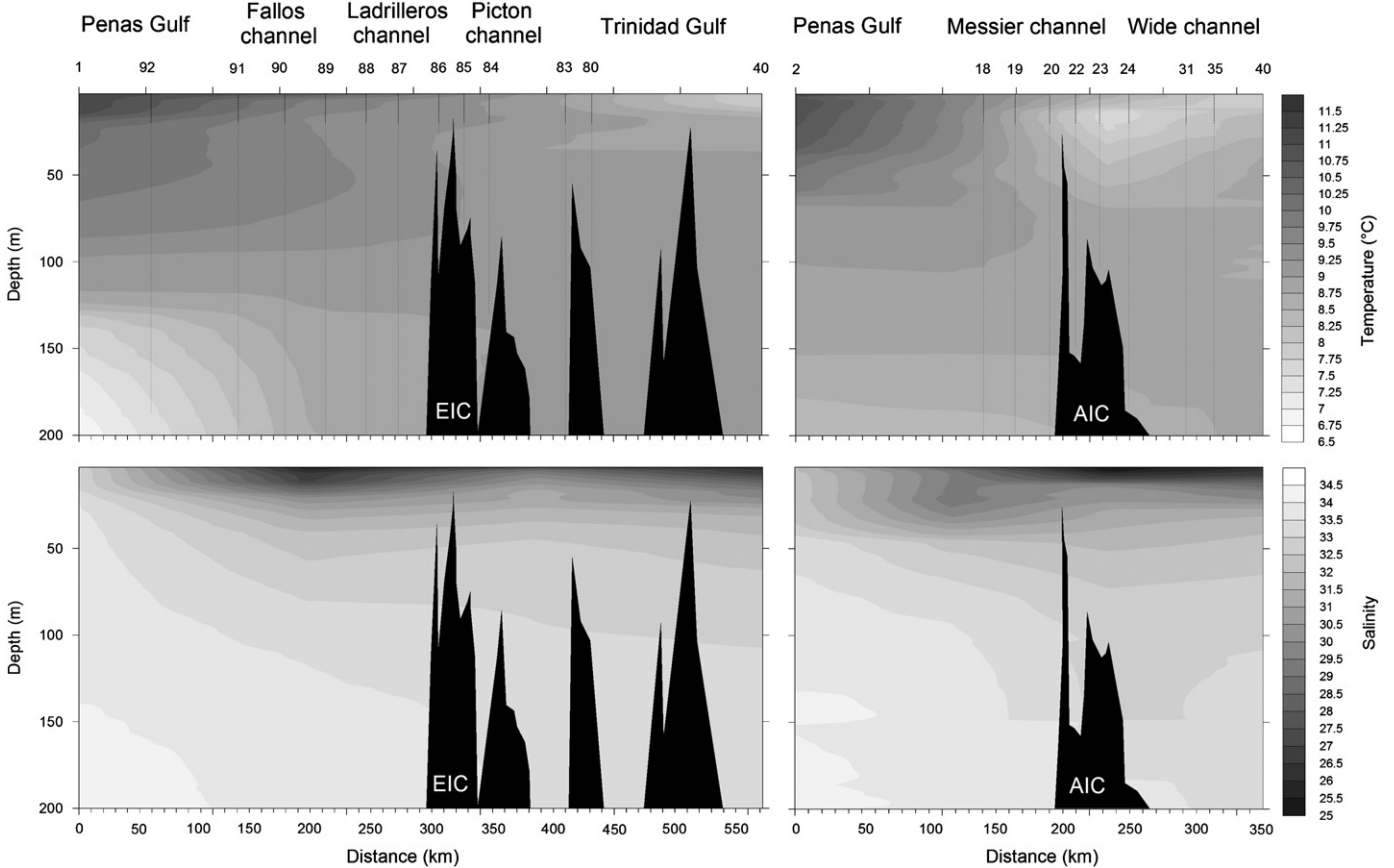
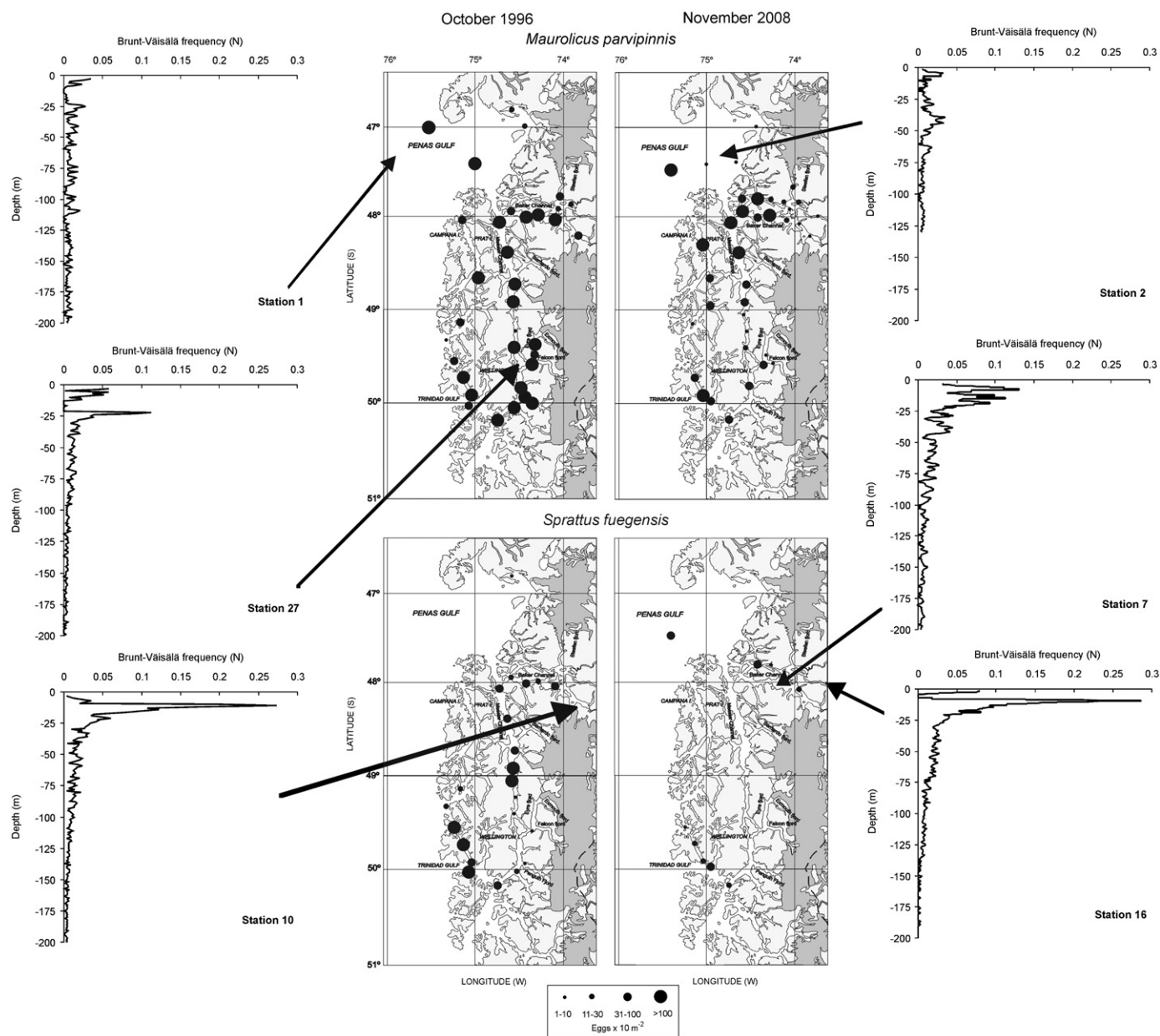


Fig. 3. Vertical sections of temperature (°C) and salinity in November 2008. See number of stations in Fig. 1 for details. EIC=El Indio Constriction; AIC=Angostura Inglesa Constriction.



**Fig. 4.** Vertical distribution of Brunt-Väisälä frequency ( $N$ ) in October 1996 and November 2008 and horizontal distribution of fish eggs in October 1996 and November 2008. Abundance is given in individuals  $\times 10^{-2}$ .

Gulf) were less stable (i.e.,  $N < 0.05$  rad/s) than those located in the channels and fjords (maximum value of  $N \sim 0.1$  rad/s) and at the heads of fjords and near Baker River, where the maximum  $N$  reached  $\sim 0.25$  rad/s (Fig. 4). In October 1996, maxima estimated values of stability ranged between 0.013 and 0.296 rad/s, occurring at 3–34 m depth. In November 2008, the maxima  $N$  were 0.034–0.286 rad/s; these were located between 2 and 40 m depth. Therefore, in this study  $N$  not only indicated water column stability, but also showed spatial variability (location) because all well-mixed stations were located close to the open ocean (Penas Gulf and adjacent coastal waters) and all stratified stations were located inside fjords and channels.

### 3.2. Biological data

During the cruise carried out in October 1996, a total of 1396 fish eggs and 415 larvae (353 preflexion and 62 postflexion) were

separated from zooplankton samples; these were identified as belonging to 11 (egg) and 18 (larva) taxa (Tables 1 and 2). In November 2008, 575 fish eggs and 242 larvae (154 preflexion and 88 postflexion) were separated from the zooplankton samples; these belonged to 9 (egg) and 20 (larva) taxa (Tables 1 and 2). Interestingly, in October 1996, eggs of the anchoveta *Engraulis ringens* appeared in plankton samples from four stations (Table 1), probably corresponding to incidental spawning of this species in the area. This is the southernmost record of early stages of this species in the Pacific Ocean to date. During the cruises, the dominant (> 75%) and most frequently collected egg type over the entire area was that of the lightfish *Maurolicus parvipinnis*, although densities declined between years 1996 and 2008 (Fig. 4, Table 1). Eggs of the Falkland sprat *Sprattus fuegensis* and southern hake *Merluccius australis* were also collected, showing mean abundances ( $\pm 1$  standard deviation, SD) around  $22.9 \pm 13.9$  and  $26.2 \pm 43.4$  eggs  $\times 10^{-2}$  m $^{-2}$ , respectively (Table 1). Strong differences were noticeable in the spatial distribution of *S. fuegensis* eggs between

**Table 1**  
Summary of basic statistics for fish egg abundance (eggs  $\times 10\text{ m}^{-2}$ ). SD=one standard deviation. Dominance corresponds to the percentage of the abundance of a given taxon in relation to total abundance. Occurrence corresponds to the percentage of oceanographic stations where a given taxon was positively collected.

	October 1996					November 2008				
	Mean	SD	Median	Dominance	Occurrence	Mean	SD	Median	Dominance	Occurrence
Eggs				(%)	(%)				(%)	(%)
<i>Congiopodus peruvianus</i>	9.07	–	9.07	0.09	2.70	–	–	–	–	–
<i>Engraulis ringens</i>	14.95	8.26	13.29	0.60	10.81	–	–	–	–	–
<i>Lampanyctodes hectoris</i>	–	–	–	–	–	6.09	4.66	6.09	0.50	4.76
<i>Genypterus</i> sp.	17.19	–	17.19	0.17	2.70	3.54	0.38	3.54	0.29	4.76
<i>Hippoglossina mystacium</i>	7.90	3.54	7.68	0.24	8.11	5.47	–	5.47	0.23	2.38
Macrouridae	16.89	12.68	14.19	0.85	13.51	3.01	–	3.01	0.12	2.38
<i>Macruronus magellanicus</i>	16.89	–	16.89	0.17	2.70	–	–	–	–	–
<i>Maurolucus parvipinnis</i>	220.94	225.86	117.07	75.59	91.89	51.95	52.38	31.40	81.75	90.48
<i>Merluccius australis</i>	16.71	13.85	10.86	1.68	27.03	26.16	43.41	4.89	5.42	11.90
<i>Normanichthys crockeri</i>	54.28	83.25	8.45	1.64	8.11	12.18	–	12.18	0.50	2.38
Pinguipedidae	42.24	6.85	45.33	1.27	8.11	–	–	–	–	–
<i>Sprattus fuegensis</i>	66.13	84.97	35.39	14.64	59.46	22.92	13.95	23.50	8.54	21.43
<i>Scomberesox saurus</i>	–	–	–	–	–	3.81	–	3.81	0.16	2.38
Unidentified taxa	25.29	28.66	12.87	3.05	32.43	6.67	3.75	5.59	2.49	21.43

**Table 2**  
Summary of basic statistics for larval fish abundance (individuals  $\times 10\text{ m}^{-2}$ ). SD=one standard deviation. Dominance corresponds to the percentage of the abundance of a given taxon in relation to total abundance. Occurrence corresponds to the percentage of oceanographic stations where a given taxon was positively collected.

	October 1996						November 2008					
	Mean	SD	Median	Dominance (%)	Occurrence (%)	Size range (mm)	Mean	SD	Median	Dominance (%)	Occurrence (%)	Size range (mm)
<b>Epipelagic taxa</b>												
<i>Normanichthys crockeri</i>	–	–	–	–	–	–	4.06	–	4.06	0.40	2.38	4.9
<i>Sprattus fuegensis</i>	271.29	446.88	98.00	70.10	75.68	5.2–22.9	10.42	17.94	5.67	16.24	38.10	4.8–23.2
<i>Serirolella caerulea</i>	7.68	–	7.68	0.07	2.70	6.5	–	–	–	–	–	–
<i>Stromateus stellatus</i>	17.72	10.52	14.19	0.82	13.51	4.8–7.0	–	–	–	–	–	–
<b>Mesopelagic taxa</b>												
<i>Bathylagichthys parini</i>	19.81	20.44	12.06	1.83	27.03	7.8–12.9	14.04	14.59	8.92	6.84	11.90	5.8–8.0
<i>Cyclothone</i> sp.	4.47	–	4.47	0.04	2.70	–	9.68	9.32	6.10	3.77	9.52	4.9–9.1
<i>Lampanyctodes hectoris</i>	9.74	3.79	9.97	0.27	8.11	6.9–14.5	18.09	17.85	18.09	3.52	4.76	3.8–18.0
<i>Maurolucus parvipinnis</i>	38.23	38.39	25.34	10.23	78.38	3.5–13.3	11.09	9.85	7.18	35.64	78.57	3.7–15.2
<i>Protomyctophum crockeri</i>	7.49	4.27	7.49	0.14	5.41	6.7	5.23	1.98	5.23	1.02	4.76	3.6–8.6
<i>Protomyctophum</i> sp.	–	–	–	–	–	–	3.60	–	3.60	0.35	2.38	–
<i>Symbolophorus</i> sp.	–	–	–	–	–	–	2.79	–	2.79	0.27	2.38	8.7
<b>Demersal taxa</b>												
<i>Echiodon cryomargarites</i>	14.19	–	14.19	0.13	2.70	7.9	2.79	–	2.79	0.27	2.38	11.1
<i>Genypterus blacodes</i>	–	–	–	–	–	–	2.79	–	2.79	0.27	2.38	4.8
<i>Hippoglossina mystacium</i>	23.71	29.56	15.38	4.16	51.35	3.3–12.1	7.56	–	7.56	0.74	2.38	11.1–15.7
<i>Macruronus magellanicus</i>	14.46	13.93	10.51	2.54	51.35	4.2–35.7	4.06	–	4.06	0.40	2.38	6.6
<i>Merluccius australis</i>	21.38	32.03	8.66	1.97	27.03	4.1–6.4	4.18	1.23	3.99	1.22	7.14	3.1–9.5
<i>Micromesistius australis</i>	4.47	–	4.47	0.04	2.70	11.1	–	–	–	–	–	–
Moridae	15.35	–	15.35	0.14	2.70	4.9	3.88	1.15	3.88	0.76	4.76	4.9–11.3
Ophichthyidae	–	–	–	–	–	–	3.01	–	3.01	0.29	2.38	20.2
<b>Subtidal/Intertidal taxa</b>												
<i>Agonopsis chiloensis</i>	–	–	–	–	–	–	6.24	–	6.24	0.61	2.38	19.5
<i>Bovictus chilensis</i>	4.47	–	4.47	0.04	2.70	–	–	–	–	–	–	–
<i>Helcogrammoides cunninghammi</i>	13.50	8.23	13.50	0.25	5.41	3.2–6.9	4.43	2.02	3.85	1.72	9.52	4.0–5.0
Nototheniidae	5.72	1.72	5.00	0.16	8.11	–	4.89	–	4.89	0.48	2.38	6.5
<i>Prolatilus jugularis</i>	12.51	6.80	14.10	0.58	13.51	3.2–7.2	–	–	–	–	–	–
<i>Sebastes oculatus</i>	31.42	22.93	28.20	6.09	56.76	3.3–10.7	10.70	8.08	7.62	23.96	54.76	3.1–7.8
Unidentified taxa	7.34	2.61	7.35	0.41	16.22	–	6.35	4.29	6.35	1.24	4.76	–

years. In October 1996, eggs of this species were distributed along the Baker, Messier, and Picton channels, and standardized abundances were as high as 760 eggs  $\times 10\text{ m}^{-2}$  (Fig. 4). However, in November 2008, mean egg density was reduced three times

(Table 1) and the spatial distribution was restricted to some channels and one positive station in Penas Gulf (Fig. 4).

For larval fish, *M. parvipinnis* was collected throughout the sampled area during both cruises, but densities were higher in

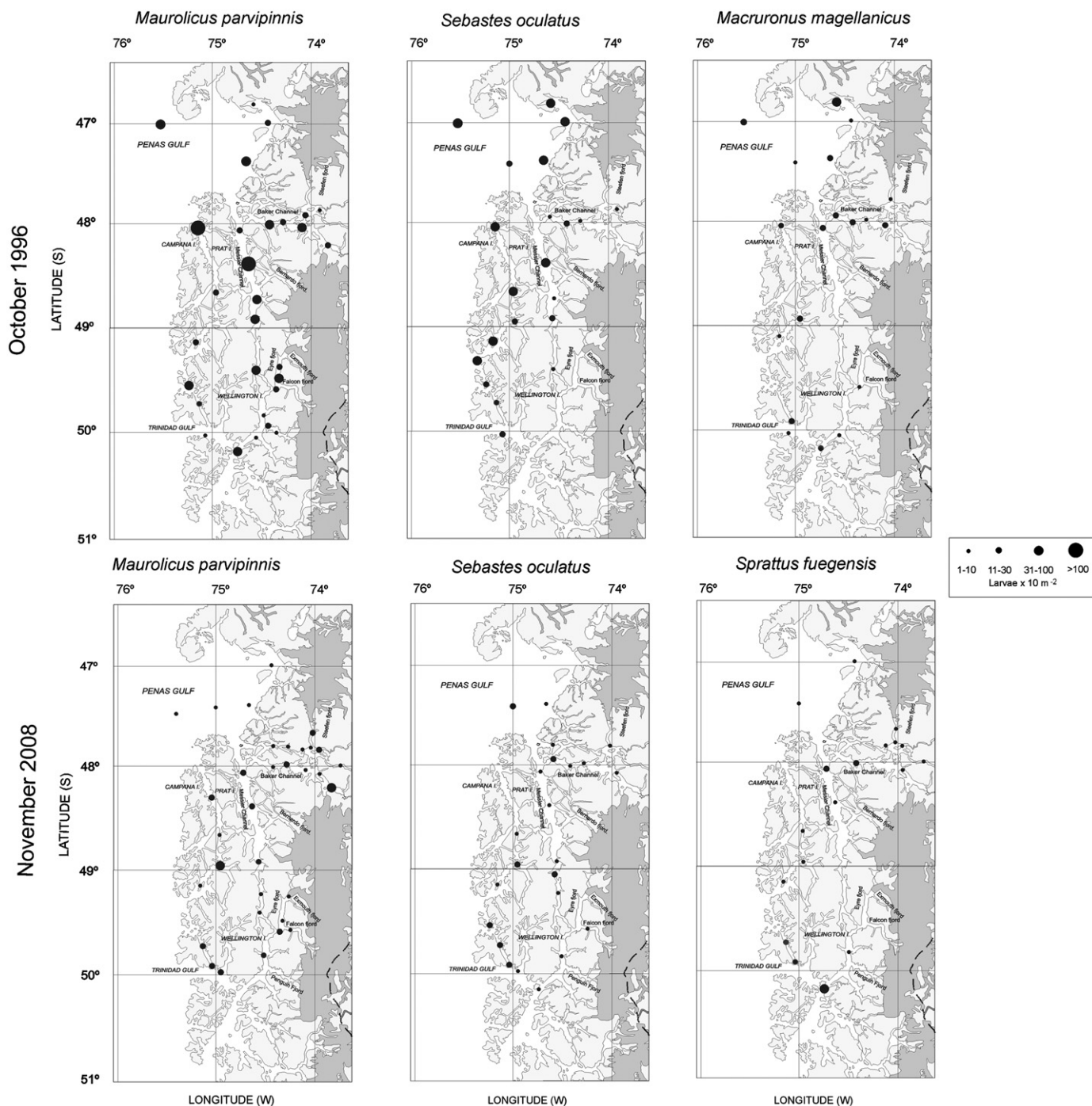
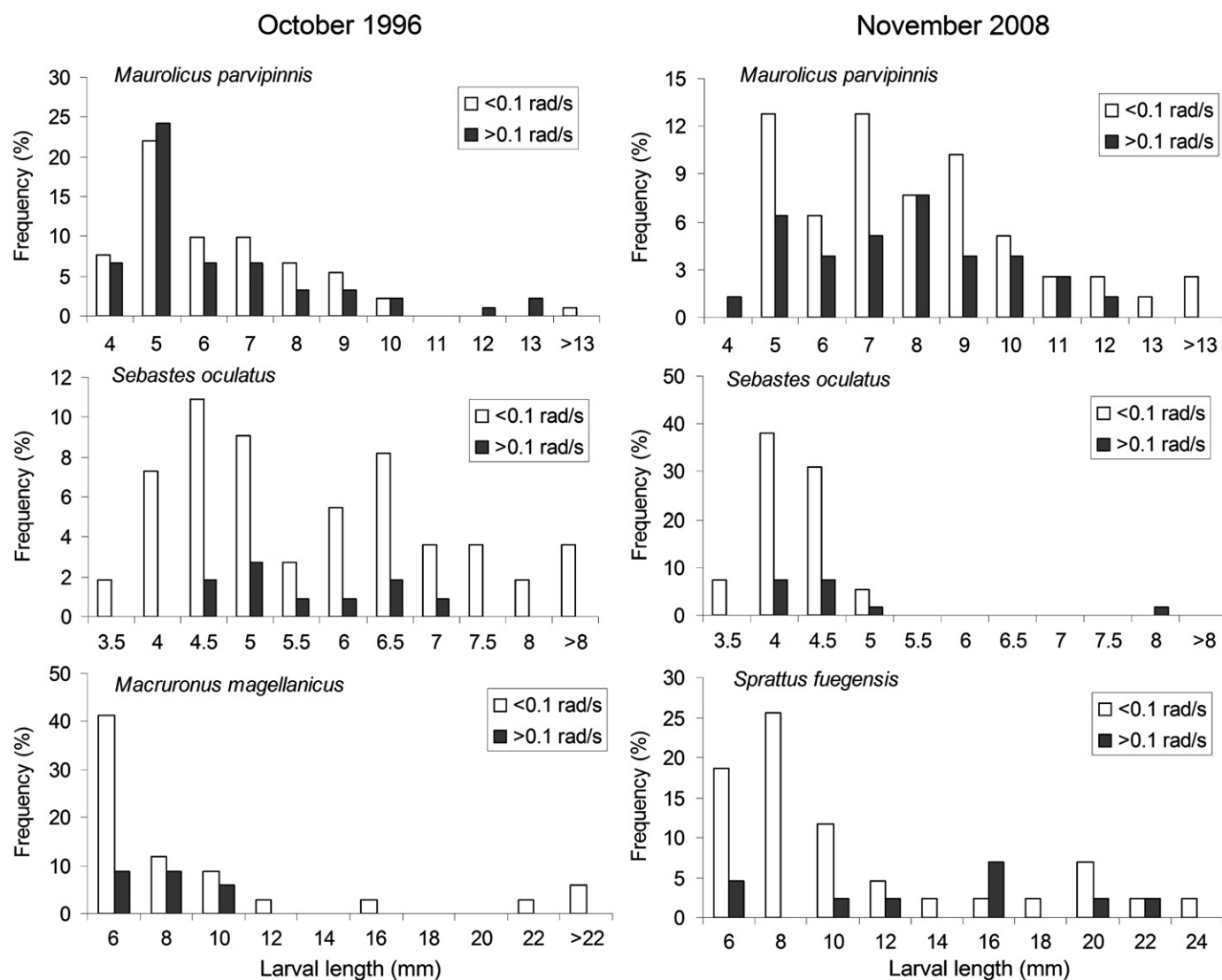


Fig. 5. Horizontal distribution of larval fish in October 1996 and November 2008. Abundance is given in individuals  $\times 10 \text{ m}^{-2}$ .

October 1996 ( $5.5\text{--}121.3 \text{ larvae} \times 10 \text{ m}^{-2}$ ) than November 2008 ( $2.2\text{--}39.8 \text{ larvae} \times 10 \text{ m}^{-2}$ , Fig. 5). A similar pattern was detected for larval rockfish *Sebastes oculatus* ( $4.2\text{--}90.9$  vs.  $2.9\text{--}27.9 \text{ larvae} \times 10 \text{ m}^{-2}$  in 1996 and 2008, respectively). Larval hoki *M. magellanicus* and sprat *S. fuegensis* were collected along the Baker and Ladrillos channels and in Trinidad Gulf (Fig. 5), showing reduced larval densities (*M. magellanicus*,  $2.5\text{--}61.4 \text{ larvae} \times 10 \text{ m}^{-2}$ , *S. fuegensis*,  $3.4\text{--}77.1 \text{ larvae} \times 10 \text{ m}^{-2}$ , Table 2). In general, several egg and larval taxa were less abundant (mean and median values) in 2008 than in 1996 (Tables 1, 2).

Mean larval size was not statistically different in highly ( $> 0.1 \text{ rad/s}$ ) and less stable waters ( $< 0.1 \text{ rad/s}$ ) for *M. parvipinnis*

during both cruises (October 1996:  $U=1464$ ,  $p=0.679$ ; November 2008:  $U=707$ ,  $p=0.943$ ). No significant differences were detected in the mean larval size in relation to stratification in several taxa (October 1996: *S. oculatus*,  $U=312$ ,  $p=0.905$ ; *M. magellanicus*,  $U=101$ ,  $p=0.919$ ; November 2008: *S. oculatus*,  $U=175$ ,  $p=0.208$ ; *S. fuegensis*,  $U=108$ ,  $p=0.429$ ), however they were more frequently captured at sites with less stratified waters (Fig. 6). Comparing larval size between cruises (1996 versus 2008), larval *M. parvipinnis* collected in November 2008 were significantly larger (mean  $\pm$  SD =  $7.46 \pm 2.54 \text{ mm}$ ) than larvae found in October 1996 ( $5.79 \pm 1.97 \text{ mm}$ ;  $U=2462$ ,  $p<0.001$ , Fig. 6), and is apparently associated with lower stability values. Larval rockfish



**Fig. 6.** Size distribution of selected larval fish collected in October 1996 and November 2008 in highly stable ( $N > 0.1$  rad/s) and less stable ( $N < 0.1$  rad/s) stations of southern Chile.

*S. oculatus* collected in November 2008 ( $4.02 \pm 0.62$  mm) were significantly smaller than those caught in October 1996 ( $5.44 \pm 1.47$  mm;  $U = 108$ ,  $p < 0.001$ ).

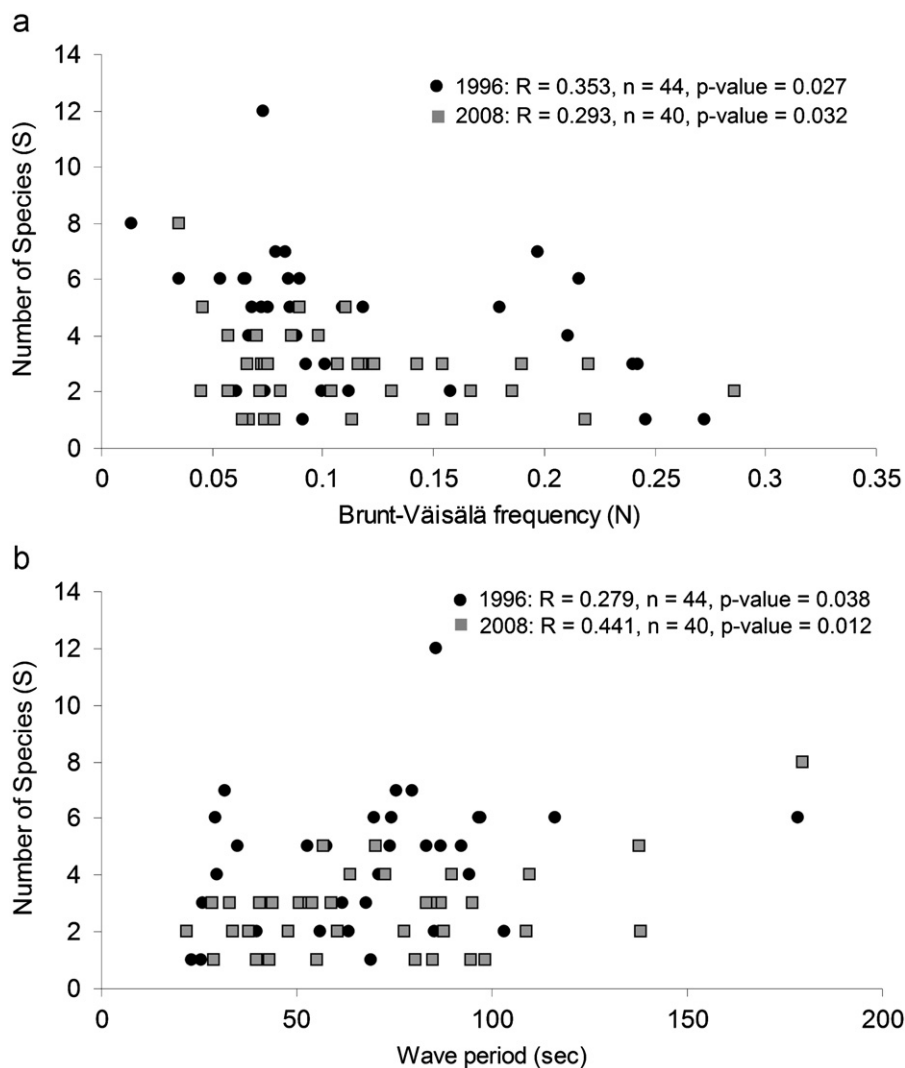
Significant ( $p < 0.05$ ) relationships were detected between numbers of larval species and the Brunt-Väisälä frequency for both cruises; however, the explained variance of the linear model was low for both sampling years ( $r$  between 0.293 and 0.353). The trend showed that as  $N$  decreased as a measure of water column stability, the number of taxa of collected fish larvae in the plankton samples augmented (Fig. 7a). For example, at the stations located in Penas Gulf, where  $N$  was low (Fig. 4), several taxa of oceanic fishes such as gonostomatids (*Cyclothone* sp.) and myctophids (*Lampanyctodes hectoris*, *Protomyctophum crockeri*, *Symbolophorus* sp.) were collected that were absent within the fjords and channels. However, when  $N$  increased beyond 0.25 rad/s, only one to three fish species were collected, the ubiquitous *M. parvipinnis*, *S. fuegensis*, and *S. oculatus*. Similarly, significant positive trends were identified between species number and wave period of the vertical fluctuation of the stratification for both cruises (October 1996 and November 2008) (Fig. 7b), although, again,  $r$  was low (0.279 and 0.441 for 1996 and 2008, respectively).

#### 4. Discussion

Spatial and temporal variability in ichthyoplankton abundance and distribution were detected in austral spring 1996 and 2008 in the fjords and channels of southern Chile located between  $46^{\circ}48'S$  and  $50^{\circ}09'S$ . On a spatial scale, ichthyoplankton was more diverse (in terms of species number) in areas where vertical stratification of the water column was lower, e.g., when water masses were more mixed. At the species level, higher abundances and broader ranges of larval sizes were found in deep, open channels compared with stations inside the fjords, although mean larval size were similar between locations. On a temporal scale, the taxonomic composition of the ichthyoplankton, i.e., the fish species that actually spawned in the area was similar; however, for several fish taxa a decrease in egg and larval abundance occurred between spring 1996 and 2008. Particularly, differences in mean larval sizes were detected for two species: rockfish *S. oculatus* and lightfish *M. parvipinnis*.

Fish eggs and larvae from a wide range of taxa, including epipelagic, mesopelagic, demersal, and intertidal species, were collected in southern Chile during austral spring. Some physical mechanisms may partially explain this occurrence. According to





**Fig. 7.** Relationship between (a) Brunt-Väisälä frequency (N) and number of larval species and (b) wave period and number of larval species for October 1996 (black dots) and November 2008 (grey squares).

Dávila et al. (2002), in austral spring-summer, southward wind stress induces eastward Ekman water transport, piling up freshwater near the coast. The onshore transport of coastal waters may also advect early stages of oceanic taxa such as gonostomatids and myctophids located in the surface waters. On the other hand, freshwater input from the Baker (47.81°S, 73.63°W) and Serrano (48°6'S, 73.07°W) rivers and ice melting from the Northern and Southern Ice Fields may increase offshore advection of surface waters (Dávila et al., 2002) and the transport of zooplankton, intertidal and subtidal fish larvae, and postlarval hake (Basedow et al., 2004; Bustos et al., 2007). Landaeta and Castro (2006) and León et al. (2008) suggested such a pattern to explain the off-channel transport of larval rockfish *S. capensis* (= *S. oculatus*) and early zoeae of *Munida gregaria* in austral spring from 44° to 46°S.

The presence of oceanic taxa, particularly myctophids and gonostomatids larvae at upper fjords was probably limited by topographic features (constrictions) rather than physiological constraints by low salinity waters. For example, in glacial fjords of North America, Abookire et al. (2002) collected juveniles and adults of northern lampfish *Stenobrachius leucopsarus* (Myctophidae) and northern smoothtongue *Leuroglossus schmidti* (Bathylagidae) between 10 and 20 m depth. In Chilean fjords, Uribe and Balbontín (2005) found larval *Bathylagichthys parini* (Bathylagidae), probably because this is where the species

reproduces. Larval size distributions of the species indicate the presence of recently hatched larvae (*S. oculatus*, *S. fuegensis*) as well as postlarval stages of several marine fish taxa (e.g., *M. parvipinnis*, *M. magellanicus*, *S. fuegensis*) in channels. Large hoki larvae (15.2–35.7 mm) were collected exclusively in less stratified waters; however, the large variance of the data precluded the identification of significant differences in mean larval sizes. Differences in larval sizes inside and outside the fjords have been found for hake larvae in southern Chile (Bustos et al., 2007) and cod in Sweden. Studying cod larvae inside and outside Gullmar Fjord, Øresland and André (2008) found that fjord larvae were more common in surface waters, were shorter, had unimodal length and hatch date distributions, and differed in their genetic composition when compared to the larvae collected outside the fjord. In the present case, fish larvae of similar size in and out fjords may indicate that reproduction may have been occurring all over the place, and differences in size range may be explained by differences in larval growth and survival between colder, turbid areas (upper fjords) and warmer, saltier and more mixed zones (open waters and channels).

If fjords around the world are utilized by several marine and estuarine taxa as spawning and nursery zones (Asplin et al., 1999; Halliday et al., 2001; Bustos et al., 2007), and if positive relationships have been found between N and fish egg and larval

abundances (Reiss et al., 2002; Bustos et al., 2008a, b), why were so few larval species collected in the highly stratified areas of the upper fjords? In our case, both temperature and salinity were low ( $\sim 6^{\circ}\text{C}$ ,  $< 15$ ) within the fjords from  $46^{\circ}48'$  to  $50^{\circ}09'S$ . Also, the optical density of organic and inorganic particulate material was two to four times higher than at oceanic stations (Pizarro et al., 2000) because of the erosive action of runoff and precipitation. This is provoked mainly by Baker river, the largest Chilean river in terms of volume of water, and melting of North and South Ice Fields, the largest continuous mass of ice outside of the polar regions, which produce high amounts of freshwater (Fig. 1). Although chlorophyll-*a* concentrations were higher inside fjords ( $< 1\text{--}17.5\text{ mg/m}^3$ ) than in adjacent waters ( $0.2\text{--}3.7\text{ mg/m}^3$ ) in spring 1996 (Pizarro et al., 2000), the physical characteristics of the water column could be detrimental to the efficient energy transfer to fish larvae (Coombs et al., 1994). Therefore, only few fish taxa may be capable for utilizing this very cold, fresh and turbid environment as a nursery ground.

The exception was *M. parvipinnis*. This small, mesopelagic fish species shows high plasticity in its reproductive tactics and early life dynamics. Eggs and larvae of this species have been collected in upwelling ecosystems (Landaeta and Castro, 2002), oceanic islands (Landaeta and Castro, 2004), and the inner seas and fjords of the Pacific Ocean (Balbontín and Bernal, 1997; Bernal and Balbontín, 1999; Córdova and Balbontín, 2006; Bustos et al., 2008b). In October 1996 and November 2008, *M. parvipinnis* eggs and larvae were collected throughout the study area irrespective of water column stratification. Previously, Bustos et al. (2008b) reported that early stages of this species were collected in greater abundance in the fjords of the inner sea of Chiloé, southern Chile ( $41^{\circ}30'\text{--}44^{\circ}5'$ ) where stratification was strongest, similar to that described by Lopes (1979) and Halliday et al. (2001) for *M. muelleri* eggs and larvae in Norwegian fjords. The similarity in the frequency of larval size distribution among sites with different stratification in the study area seems to indicate that advection off fjords is negligible for this species. Retention within the fjords may be increased by a combination of deep-water spawning (Lopes, 1979; Landaeta and Castro, 2002) and differences in vertical distribution (Halliday et al., 2001) and/or vertical migrations of larger larvae on diel (Landaeta and Castro, 2002) and/or tidal time scales (Landaeta et al., 2010).

A decrease in standardized abundance (mean and median values) was evident for several taxa, both in egg and larval stages, together with a slight increase in seawater temperature between October 1996 and November 2008, although the sampling effort (measured as filtered seawater) was two times higher in 2008 (see Section 2.2). The slight increase in water temperature in November 2008 may have triggered earlier spawning of some taxa (e.g., *M. parvipinnis*), partially explaining the lower abundance of eggs, larvae, and differences in larval sizes. Methodological problems were probably negligible because the same gear and ship were used for both cruises. Therefore, differences may have been caused by variations in the timing of spawning, adult biomass, and other aspects. One of the most striking variations was observed in abundance of early stages of hoki *M. magellanicus*: in October 1996, hoki larvae were found at half the stations, comprising 2.54% of the total collected larvae yet, by November 2008, only one specimen (a preflexion larva) was collected in the area. A drastic decrease in the abundance of this species was also observed from ichthyoplankton collected in October 1995 and November 2005 in the Inner Sea of Chiloé, southern Chile ( $41^{\circ}20'\text{--}44^{\circ}5'$ ; Bustos et al., 2008b). Then, can this may be an ecological response to recent climate change? Differences in seawater temperature probably are caused by changes in ice melting, triggering variations in phenology of marine fishes and alterations in assemblages of species (Walther et al. 2002).

However, this item should be investigated by continuous monitoring of the area to understand the temporal fluctuations of fish communities of fjord systems.

In conclusion, only some marine fish species are capable to utilize fjords systems as spawning and nursery grounds in areas having high amounts of freshwater discharges and very high vertical stratification during austral spring season. Majority of fish taxa are using relatively warmer, saltier and less stable seawater in adjacent open coastal waters during early development between  $46^{\circ}48'S$  and  $50^{\circ}09'S$ . Further studies are necessary to elucidate the role of seawater stability and mixing in feeding success and larval growth in this highly stratified zone.

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## References

- Abokire, A.A., Piatt, J.F., Speckman, S.G., 2002. A nearsurface, daytime occurrence of two mesopelagic fish species (*Stenobrachius leucopsarus* and *Leuroglossus schmidti*) in a glacial fjord. *Fish. Bull.* 100, 376–380.
- Aranis, A., Melendez, R., Pequeño, G., Cerna, F., 2007. *Sprattus fuegensis* in the inland waters of Chiloe, Chile (Osteichthyes: Clupeiformes: Clupeidae). *Gayana* 71, 102–113.
- Asplin, L., Salvanes, A.G.V., Kristoffersen, J.B., 1999. Nonlocal wind-driven fjord-coast advection and its potential effect on plankton and fish recruitment. *Fish. Oceanogr.* 8 (4), 255–263.
- Balbontín, F., Bernal, R., 1997. Distribución y abundancia del ictioplancton en la zona austral de Chile. *Cienc.Tecnol. Mar.* 20, 155–163.
- Balbontín, F., Bernal, R., 2005. Seasonal changes in the composition and abundance of the ichthyoplankton of the austral channels from Corcovado Gulf to Elefantes Gulf. Chile. *Cienc. Tecnol. Mar.* 28, 99–111.
- Balbontín, F., Uribe, F., Bernal, R., Braun, M., 2004. Descriptions of larvae of *Merluccius australis*, *Macruronus magellanicus*, and observations on a larva of *Micromesistius australis* from southern Chile (Pisces: Gadiformes). *N.Z. J. Mar. Freshwater Res.* 38, 609–619.
- Basedow, S.L., Eiane, K., Tverberg, V., Spindler, M., 2004. Advection of zooplankton in an Arctic fjord (Kongsfjorden, Svalbard). *Estuar. Coast. Shelf Sci.* 60, 113–124.
- Bernal, R., Balbontín, F., 1999. Ictioplancton de los fiordos entre el Golfo de Penas y Estrecho de Magallanes y factores ambientales asociados. *Cienc. Tecnol. Mar.* 22, 143–154.
- Buschmann, A.H., Riquelme, V.A., Hernández-González, M.C., Varela, D., Jiménez, J.E., Henríquez, L.A., Vergara, P.A., Guíñez, R., Filún, L., 2006. A review of the impacts of salmonid farming on marine coastal ecosystems in the south-eastern Pacific. *ICES J. Mar. Sci.* 63, 1338–1345.
- Bustos, C.A., Landaeta, M.F., 2005. Desarrollo de huevos y larvas tempranas de la merluza del sur, *Merluccius australis*, cultivados bajo condiciones de laboratorio. *Gayana* 69, 402–408.
- Bustos, C.A., Balbontín, F., Landaeta, M.F., 2007. Spawning of the southern hake *Merluccius australis* (Pisces: Merluccidae) in Chilean fjords. *Fish. Res.* 83, 23–32.
- Bustos, C.A., Landaeta, M.F., Balbontín, F., 2008a. Spawning and early nursery areas of anchoveta *Engraulis ringens* Jenyns, 1842 in fjords of southern Chile. *Rev. Biol. Mar. Oceanogr.* 43, 381–389.
- Bustos, C.A., Landaeta, M.F., Balbontín, F., 2008b. Efectos ambientales sobre la variabilidad espacial del ictioplancton de Chile austral durante noviembre de 2005. *Rev. Chil. Hist. Nat.* 81, 205–219.
- Cáceres, M., Valle-Levinson, A., Molinet, C., Castillo, M., Bello, M., Moreno, C., 2006. Lateral variability of flow over a sill in a channel of southern Chile. *Ocean Dynamics* 56, 352–359.

- Coombs, S.H., Robins, D.B., Conway, D.B.P., Halliday, N.C., Pomroy, A.J., 1994. Suspended particulates in the Irish Sea and feeding conditions for fish larvae. *Mar. Biol.* 118 (1), 7–15.
- Córdova, G., Balbontín, F., 2006. Distribución espacial de la abundancia y de la talla de ocho tipos de larvas de peces entre la Boca del Guafo y Bahía Anna Pink, zona austral de Chile. *Cienc. Tecnol. Mar.* 29, 153–161.
- Dávila, P.M., Figueroa, D., Müller, E., 2002. Freshwater input into the coastal ocean and its relation with the salinity distribution off austral Chile (35°–55°S). *Cont. Shelf Res.* 22, 521–534.
- Dyer, K.R., 1997. *Estuaries. A physical introduction* 2nd edition Wiley, Chichester, England 195p.
- Etherington, L.L., Hooge, P.N., Hooge, E.R., Hill, D.F., 2007. Oceanography of Glacier Bay, Alaska: implications for biological patterns in a glacial fjord estuary. *Estuar. Coasts* 30 (6), 927–944.
- Gebauer, P., Paschke, K., Moreno, C.A., 2007. Reproductive biology and population parameters of *Petrolisthes laevigatus* (Anomura: Porcellanidae) in southern Chile: consequences on recruitment. *J. Mar. Biol. Ass. UK* 87, 729–734.
- Halliday, N.C., Coombs, S.H., Smith, C., 2001. A comparison of LHPR and OPC data from vertical distribution sampling of zooplankton in a Norwegian fjord. *Sarsia* 86, 87–99.
- Iriarte, J.L., González, H.E., Liu, K.K., Rivas, C., Valenzuela, C., 2007. Spatial and temporal variability of chlorophyll and primary productivity in surface waters of southern Chile (41.5–43°S). *Estuar. Coastal Shelf Sci.* 74, 471–480.
- Landaeta, M.F., Castro, L.R., 2002. Spring spawning and early nursery area zone of the mesopelagic fish *Maurolicus parvipinnis* at the coastal upwelling zone off Talcahuano, central Chile. *Mar. Ecol. Prog. Ser.* 226, 179–191.
- Landaeta, M.F., Castro, L.R., 2004. Zonas de concentración de ictioplancton en el Archipiélago de Juan Fernández. Chile. *Cienc. Tecnol. Mar.* 27 (2), 43–53.
- Landaeta, M.F., Castro, L.R., 2006. Larval distribution and growth of the rockfish, *Sebastes capensis* (Sebastes, Pisces), in the fjords of southern Chile. *ICES J. Mar. Sci.* 63, 714–724.
- Landaeta, M.F., Balbontín, F., Herrera, G.A., 2008. Larval development of the Patagonian brotula *Cataetys messieri* (Pisces, Bythitidae) from fjords of southern Chile. *J. Fish Biol.* 73, 302–310.
- Landaeta, M.F., Muñoz, M.I., Castro, L.R., 2010. Variabilidad estacional y a pequeña escala en la distribución vertical del ictioplancton en un fiordo estratificado del sur de Chile. *Cienc. Tecnol. Mar.* 32 (2), 27–42.
- León, R., Castro, L.R., Cáceres, M., 2008. Dispersal of *Munida gregaria* (Decapoda: Galatheididae) larvae in Patagonian channels of southern Chile. *ICES J. Mar. Sci.* 65, 1131–1143.
- Lopes, P.C., 1979. Eggs and larvae of *Maurolicus muelleri* (Gonostomatidae) and other fish eggs and larvae from two fjords in western Norway. *Sarsia* 64, 199–210.
- Mann, K.H., Lazier, J.N.R., 2006. *Dynamics of marine ecosystems: Biological-physical interactions in the oceans*. Wiley Blackwell, Oxford, UK 496p.
- Molinet, C., Arévalo, A., González, M.T., Moreno, C.A., Arata, J., Niklitschek, E., 2005. Patterns of larval distribution and settlement of *Concholepas concholepas* (Bruguiera, 1789) (Gastropoda, Muricidae) in fjords and channels of southern Chile. *Rev. Chil. Hist. Nat.* 78, 409–423.
- Molinet, C., Niklitschek, E., Moreno, C.A., Arévalo, A., 2008. Vertical distribution of early and competent larvae of *Concholepas concholepas* in two systems of Chilean inland seas. *Mar. Biol.* 153, 779–788.
- Molinet, C., Valle-Levinson, A., Moreno, C.A., Cáceres, M., Bello, M., Castillo, M., 2006. Effect of sill processes on the distribution of epineustonic competent larvae in a stratified system of Southern Chile. *Mar. Ecol. Prog. Ser.* 324, 95–104.
- Moser, H.G., 1995. The early stages of fishes in the California Current Region. CalCOFI Atlas No. 33, Allen Press Inc., Lawrence, Kansas, USA 1505p.
- Mujica, A., Medina, M., 2000. Larvae decapod crustacean, distribution and abundance in austral channel area. *Cienc. Tecnol. Mar.* 23, 49–68.
- Øresland, V., André, C., 2008. Larval group differentiation in Atlantic cod (*Gadus morhua*) inside and outside the Gullmar Fjord. *Fish. Res.* 90, 9–16.
- Palma, S., Silva, N., 2004. Distribution of siphonophores, chaetognaths, euphausiids and oceanographic conditions in the fjords and channels of southern Chile. *Deep-Sea Res. II* 51, 513–535.
- Pizarro, G., Iriarte, J.L., Montecino, V., Blanco, J.L., Guzmán, L., 2000. Distribution of phytoplankton biomass and maximum primary productivity of southern fjords and channels (47°–50°S) in October 1996. *Cienc. Tecnol. Mar.* 23, 25–48.
- Reiss, C.S., Anis, A., Taggart, C.T., Dower, J.F., Ruddick, B., 2002. Relationships among vertically structured *in situ* measures of turbulence, larval fish abundance and feeding success and copepods on Western Bank, Scotian Shelf. *Fish. Oceanogr.* 11 (3), 156–174.
- Saavedra, A., Correa, V., Céspedes, R., Ojeda, V., Adasme, L., Díaz, E., Oliva, J., Rojas, P., 2007. Evaluación hidroacústica del stock parental de merluza de tres aletas en su unidad de pesquería, año 2005. Final report Project FIP 2005–06 203p.
- Sánchez-Velasco, L., Jiménez-Rosemberg, P.A., Lavín, M.F., 2007. Vertical distribution of fish larvae and its relation to water column structure in the Southwestern Gulf of California. *Pacific Sci.* 61 (4), 533–548.
- Sievers, H.A., Calvete, C., Silva, N., 2002. Distribution of physical characteristics, water masses and general circulation patterns of some southern Chilean inlets between Gulf of Penas and Strait of Magellan (CIMAR-Fiordo 2 cruise). *Cienc. Tecnol. Mar.* 25 (2), 17–43.
- Silva, N., Calvete, C., Sievers, H., 1998. Physical and chemical oceanographic features of southern Chilean inlets between Penas Gulf and Magellan strait (CIMAR-Fiordo 2 cruise). *Cienc. Tecnol. Mar.* 25 (1), 23–88.
- Silva, N., Calvete, C., Sievers, H., 1998. Masas de agua y circulación general para algunos canales australes entre Puerto Montt y Laguna San Rafael, Chile (Crucero Cimarr-Fiordo 1). *Cienc. Tecnol. Mar.* 21, 17–48.
- Silva, N., Haro, J., Prego, R., 2009. Metals background and enrichment in the Chiloé Interior Sea sediments (Chile). Is there any segregation between fjords, channels and sounds? *Estuar. Coast. Shelf Sci.* 82, 469–476.
- Silva, N., Sievers, H., Prado, R., 1995. Oceanographic features and a proposal for the circulation of some southern Chile inlets between 41°20'S and 46°40'S. *Rev. Biol. Mar.* 30, 207–254.
- Soto, D., Norambuena, F., 2004. Evaluation of salmon farming effects on marine systems in the inner seas of southern Chile: a large-scale mensurative experiment. *J. Appl. Ichthyol.* 20, 493–501.
- Toro, J.E., Paredes, P.I., Villagra, D.J., Senn, C.M., 1999. Seasonal variation in the phytoplanktonic community, seston and environmental variables during a 2-year period and oyster growth at two mariculture sites, southern Chile. *Mar. Ecol. Prog. Ser.* 20, 63–89.
- Uribe, F., Balbontín, F., 2005. First description of larvae of *Bathylagichthys parini* (Pisces, Bathylagidae) from the southeastern Pacific. *Bull. Mar. Sci.* 77, 201–208.
- Valle-Levinson, A., Sarkar, N., Sanay, R., Soto, D., León, J., 2007. Spatial structure of hydrography and flow in a Chilean fjord, Estuario Reloncaví. *Estuar. Coasts* 30 (1), 113–126.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395.