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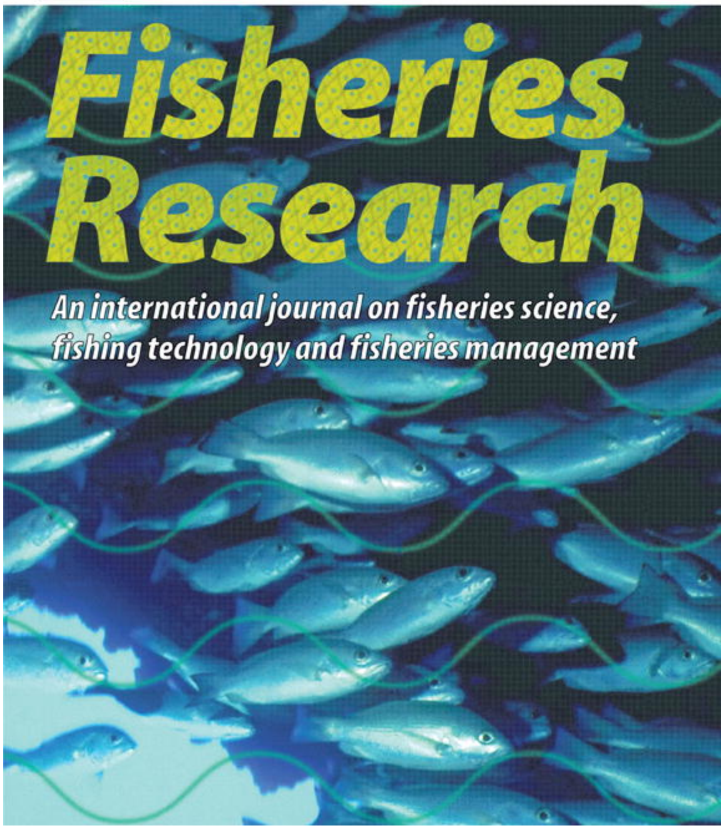
Volume 83, issue 1, January 2007
ISSN 0165-7836



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Spawning of the southern hake *Merluccius australis* (Pisces: Merlucciidae) in Chilean fjords

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Received 29 March 2006; received in revised form 10 August 2006; accepted 18 August 2006

Abstract

The southern hake *Merluccius australis* constitutes an important fishery in southern Chile, but its reproductive biology is scarcely known, and until now the Chilean fjords have not been considered as potential spawning zones. Oceanographic surveys carried out during austral spring and summer of 1995–2002 in the Chilean fjords (43°30′S–47°S), are used to describe for first time the spawning of *M. australis* in the inland sea of southern Chile. Large patches of eggs with undeveloped embryos (<4 days old, >150 eggs per 10 m^2), eggs in late development and abundant southern hake larvae (up to 385 larvae per 10 m^2) were observed inside Chilean fjords during austral spring season. Eggs and preflexion larvae (<9 mm) were scarcely detected in open ocean-influenced waters (<30 ind per 10 m^2). This pattern of horizontal distribution may be determined by spawning events of inland resident stocks and/or by inshore migration of adult hakes during austral spring. The higher frequency of small larvae inside fjord waters, and the presence of postflexion larvae outside fjords are indicative that fjords are used also as nursery areas for early stages of southern hake. Finally, inter-annual variability in egg size (i.e., diameter) was detected, despite the relatively constant seawater temperature (10–11 °C). Further investigations are needed to determine the maintenance and the health of this spawning and early nursery area in a zone highly disturbed by salmon culture activity.

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Keywords: Ichthyoplankton; Spawning; Nursery zone; Chilean fjords

1. Introduction

The austral zone of Chile comprises one of the largest estuarine ecosystems with a length over 1600 km, a surface area of about 240,000 km^2, and a high degree of geomorphologic and hydrographical complexity (Palma and Silva, 2004). Topography is characterized by the presence of deep fjords and basins generated during the past glaciation, and a coastal zone with numerous small islands and channels, resulting in a high variety of habitats. Rainfall (2.5 m $year^{-1}$, Strub et al., 1998) and freshwater input from rivers draining from the Andes generate a surface layer of low salinity (<10–30) of ~20 m depth, producing a strong halocline and high stratification (Silva et al., 1995, 1997, 1998; Bastén and Clement, 1999). Below the surface layer in the inland sea, the water column is nearly homogeneous, with characteristics of subantarctic water. Additionally, the dominant semidiurnal tidal forcing range from approximately 1.5–8.0 m, produces strong tidal currents in the channels (up to 4 m s^{-1}, Cáceres et al., 2003). The phytoplankton community is characterised by high biomass values durind austral spring and summer (Toro et al., 1999) and a diverse assemblage of calanoid copepods (Marín and Antezana, 1985), particularly abundant in the inland sea (Landaeta and Castro, 2006a).

The Chilean fjord region is an important zone of trawl and longline (industrial and artisan) fishery based on gadiform fish such as southern hake *Merluccius australis* (Hutton, 1872) and Patagonian grenadier *Macrucronus magellanicus*. Southern hake supports annual catches of 30,000 t in the past decade in Chilean waters (Payá and Ehrhardt, 2005). This demersal fish species is distributed from 40°S (off Chiloe Island, South Pacific), southward around the southern tip of South America, to the Argentinian waters (38°S in the Atlantic), between 60 and 800 m depth (Arkhipkin et al., 2003). Some overlap exist with the distribution of the common hake *M. gayi* (around 40–41°S);

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doi:10.1016/j.fishres.2006.08.010

however, this does not affect the species composition of the catches because the fleets operate in areas far from this area (Payá and Ehrhardt, 2005). There is another exploited population of *M. australis* in New Zealand, where adults aggregate over Chatam Rise (Bull et al., 2001). In the southeast Pacific, gonadic analysis suggest a reproductive activity during austral winter and early spring (July–September) (Balbontín and Bravo, 1993) when adults concentrate in large schools over the shelf-break between Guafo and Guamblín Islands (43°30′S–45°S). In this offshore area eggs and larvae have been collected in abundances lower than 100 individuals per 10 m^2 during austral winter near Guafo island (Lillo et al., unpublished). Like other hake species, spawning occurs below surface waters (Coombs and Mitchell, 1982; Moser et al., 1997; Vargas and Castro, 2001) and it has been hypothesized that eggs and larvae are transported through subsurface waters by estuarine circulation to the nursery areas located at the inland sea where recruitment occurs (Payá and Ehrhardt, 2005).

The fjords are used as spawning and nursery areas for marine fish species with different adult habitat in the North Hemisphere (Lopes, 1979; Stenevik et al., 1996; Smedbol and Wroblewski, 1997) and off southern Chile by the rockfish *Sebastes capensis* (Landaeta and Castro, 2006a). Similarly, isolated populations of *Merluccius productus* utilize fjord-like environment of Puget Sound, Strait of Georgia and Dabob Bay (Bailey and Yen, 1983; Gustafson et al., 2000; Fulmer and Bollens, 2005) as spawning and nursery grounds. Using ichthyoplankton samples collected between 42°S and 47°S during 1995, Balbontín and Bernal (1997) and Bernal and Balbontín (1999) have described the presence of larvae of *M. australis* in the fjord area of Chile; no information of the distribution of the eggs was presented. Also, juveniles and recruits (21–65 cm total length) have been recently collected near the mouth of fjords in the inland sea of southern Chile (Lillo et al., unpublished). However, the connectivity and/or the isolation of the inshore (fjord) and offshore populations are unknown so far.

Through a series of oceanographic surveys carried out between austral spring and summer 1995 and 2002 along the Chilean fjord region, we describe the inshore spawning zones of the southern hake *M. australis* and the potential utilization of this area as a larval retention zone.

2. Methods

Oceanographic cruises were carried out in the Chilean fjord region between 1995 and 2002 onboard the vessel Vidal Gormaz, as part of the CIMAR projects to study remote areas of Chile (Fig. 1 and Table 1). Between 18 October and 15 November 1995, a total of 99 oceanographic stations were sampled between 41°30′S and 46°30′S (CIMAR-FIORDOS 1). Between 37 and 44 oceanographic stations located between 43°30′S and 46°30′S were sampled during September–October 1998 (CIMAR-FIORDOS 4-1), February–March 1999 (CIMAR-FIORDOS 4-2) and November 2002 (CIMAR-FIORDOS 8). At each station, temperature and salinity profiles were recorded from surface to 300 m depth or near bottom in shallower waters with a Seabird SBE-19 CTD. As a measure of water stratifi-

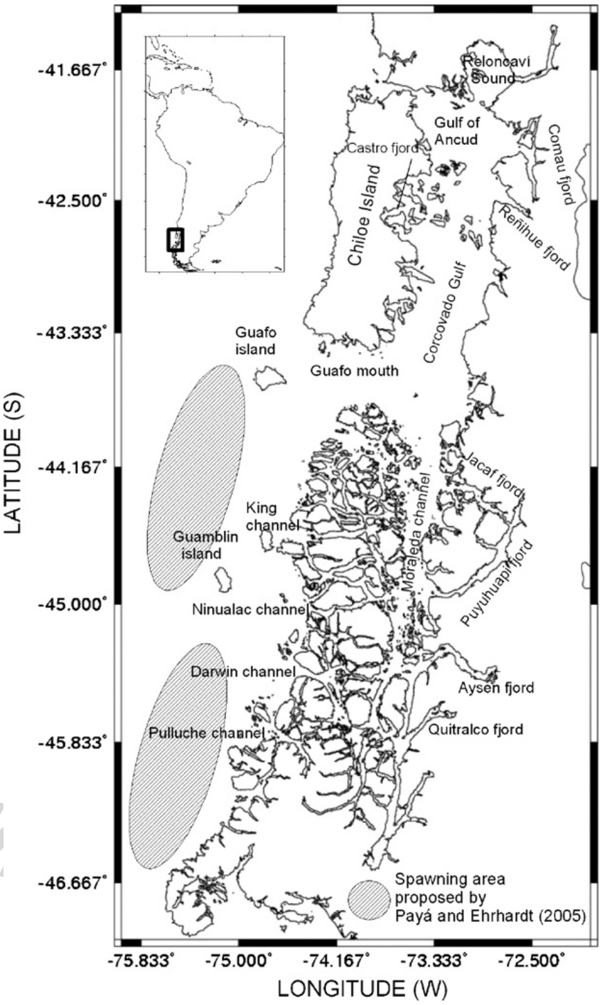

Fig. 1. Surveyed area during CIMAR cruises carried out in October and November 1995, September–October 1998, February–March 1999, and November 2002 in the Patagonian fjords of Chile. Dashed circles indicate spawning area proposed by Payá and Ehrhardt (2005).

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Table 1
Summary of the main characteristics of the surveys carried out

Cruise	Survey dates	Latitude range	Gear	Samples
CMAR-FIORDOS 1	18–25 October 1995	41°30′S–43°30′S	BONGO	30
CMAR-FIORDOS 1	26 October–11 November 1995	43°30′S–47°S	BONGO	69
CMAR-FIORDOS 4–1	26 September–9 October 1998	43°30′S–46°30′S	BONGO	40
CMAR-FIORDOS 4–2	25 February–8 March 1999	43°30′S–46°30′S	BONGO	37
CMAR-FIORDOS 8	15–28 November 2002	43°30′S–46°S	BONGO	44

cation, the Brunt-Väisäla frequency ($N^2 = g/\rho\ (\partial\rho/\partial z)$, where g is the gravity ($9.8\,\mathrm{m\,s^{-1}}$) and ρ the water density) was calculated.

Oblique ichthyoplankton samples were collected from 200 m deep to surface using a standard Bongo net (0.6 m diameter, 300 μm mesh size) equipped with a TSK flowmeter to estimate filtered water volume. Towing speed was ca. 2–3 knots. All samples were preserved on board in 4% buffered formalin solution. In the laboratory, total fish eggs and larvae were sorted from all samples, and early stages of southern hake, *M. australis*, were identified and counted ($n = 802$) following Balbontín et al. (2004) and Bustos and Landaeta (2005). Eggs were measured (i.e., diameter) and classified according to the developmental stage: stage 1 (undeveloped embryo), stage 2 (early embryo) and stage 3 (prehatching). Larvae ($n = 236$) were classified as pre and postflexion according to the bending of the notochord, and measured from the tip of the snout to the tip of the notochord (notochord length (NL) in preflexion larvae) and to the posterior margin of the hypurals (standard length (SL) in postflexion larvae). All measurements were made to the nearest 0.1 mm by using a dissecting microscope fitted with an eyepiece micrometer. No correction was made for shrinkage due to fixation procedures. Total egg and larval abundances were standardised to individuals per $10\,\mathrm{m}^2$ and mapped. Statistical analyses were performed using STATISTICA software package.

3. Results

3.1. Horizontal distribution of early stages

Eggs and larvae of southern hake were concentrated in high abundance (>100 individuals per $10\,\mathrm{m}^2$) in fjords of the inland sea of southern Chile during almost all surveys. The exception occurred during February–March 1999, when no early life stages of *M. australis* were detected throughout the sampled area. During October 1995 (CIMAR-FIORDOS 1), a high amount of recently spawned eggs (stage 1, 347 eggs per $10\,\mathrm{m}^2$), eggs in late development (stages 2 and 3) and larvae (385 larvae per $10\,\mathrm{m}^2$) were collected inside Reloncaví Sound (Fig. 2). Interestingly, southern hake eggs and larvae were also collected in lower abundance (31–100 individuals per $10\,\mathrm{m}^2$) in the head and mouth of the Comau, Reñihué and Castro fjords, and inside Gulf of Ancud. Eggs and larvae were not observed in the ocean-influenced waters of the Corcovado Gulf (Fig. 2).

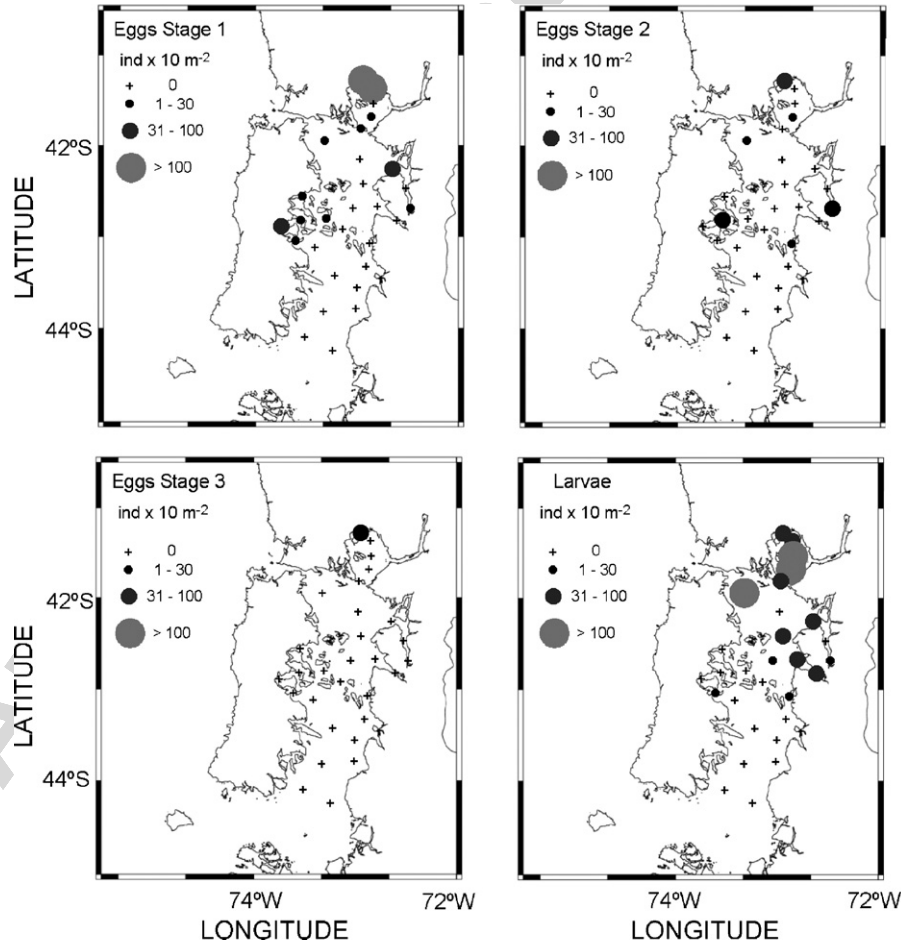

Fig. 2. Egg and larval abundance (individuals per $10\,\mathrm{m}^2$) of southern hake *Merluccius australis* during October 1995 (CIMAR–FIORDOS 1). Symbol ‘+’ indicates location of sampling stations.

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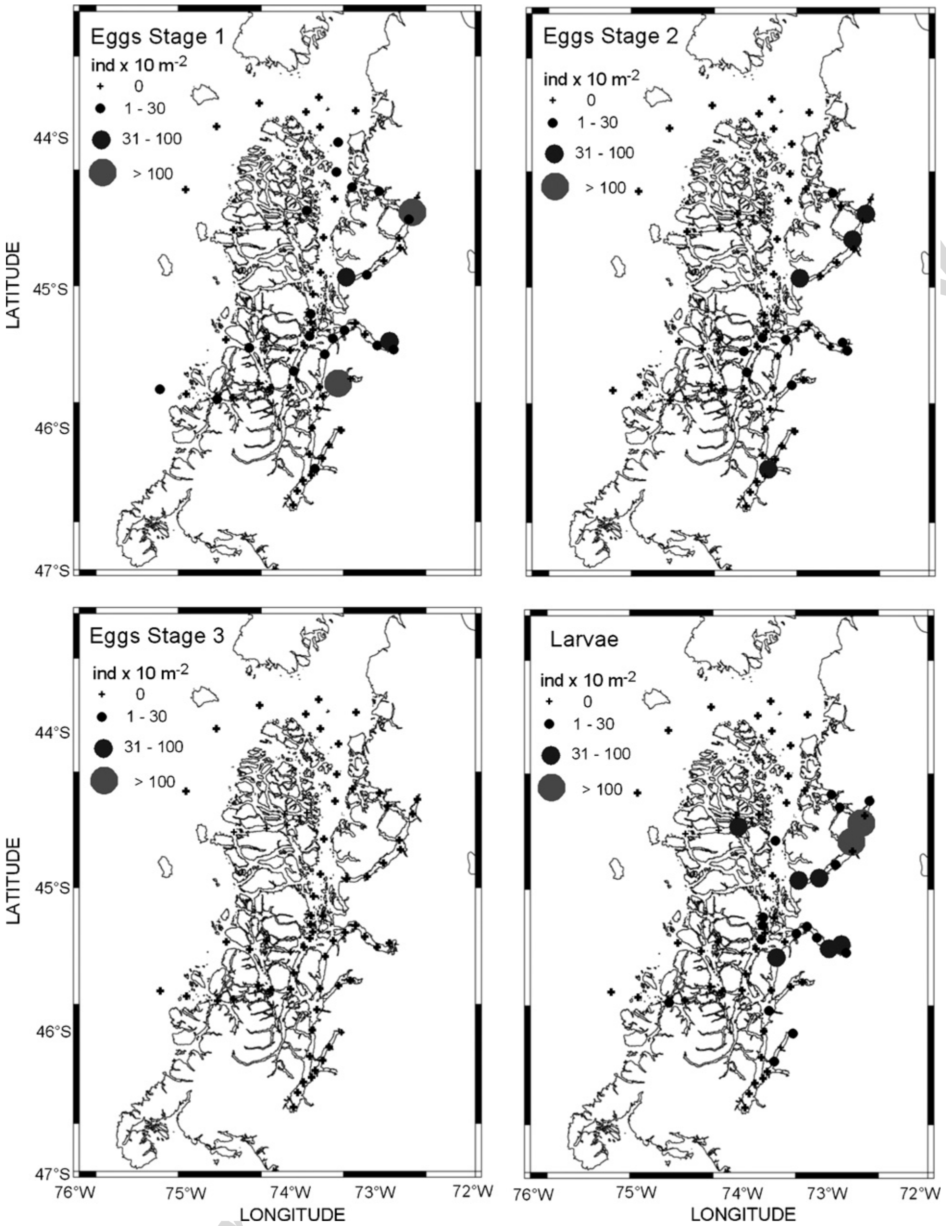

Fig. 3. Distribution of southern hake eggs and larvae sampled during November 1995. Abundance given in individuals per 10 m^2. Symbol '+' indicates location of sampling stations.

Reproductive events also were detected in the inland sea between 44°S and 46°30′S during November 1995 (Fig. 3). High abundance of eggs occurred (up to 150 eggs per 10 m^2) in heads and mouths of several fjords (Jacaf, Puyuhuapi, Aysen and Quitralco fjords); eggs were collected in lower density in the deep Moraleda channel, and the transversal King, Darwin and Pulluche channels; no eggs with late embryo (stage 3) were collected during this survey. Southern hake larvae occurred in high abundance (up to 162 larvae per 10 m^2) inside Puyuhuapi and Aysen fjords (Fig. 3). Eggs and larvae were not collected in areas connected with the ocean, i.e., near Guafo Island or Guafo mouth (Fig. 3). Additionally, no significant differences in the spawning (i.e., total egg abundance) and larval abundance were detected between zones during October and November 1995 (eggs: Mann–Whitney test, $U = 112$, $p = 0.09$; larvae: Mann–Whitney test, $U = 109$, $p = 0.053$).

During September–October 1998 (CIMAR-FIORDOS 4–1) eggs in all developmental stages and larvae were collected mainly near the mouth of the Aysen fjord (Fig. 4). In this fjord egg abundance ranged between 21 and 466 eggs per 10 m^2; hake larval abundance ranged between 9 and 54 larvae per 10 m^2. Eggs and larvae occurred in low abundance near Guafo Island and Guafo mouth (<30 individuals per 10 m^2).

During November 2002 (CIMAR-FIORDOS 8), fjords were not sampled, excepting for a single station in the Aysen fjord. Low abundance (<80 individuals per 10 m^2) of recently spawned and early embryo eggs were detected in the aus-

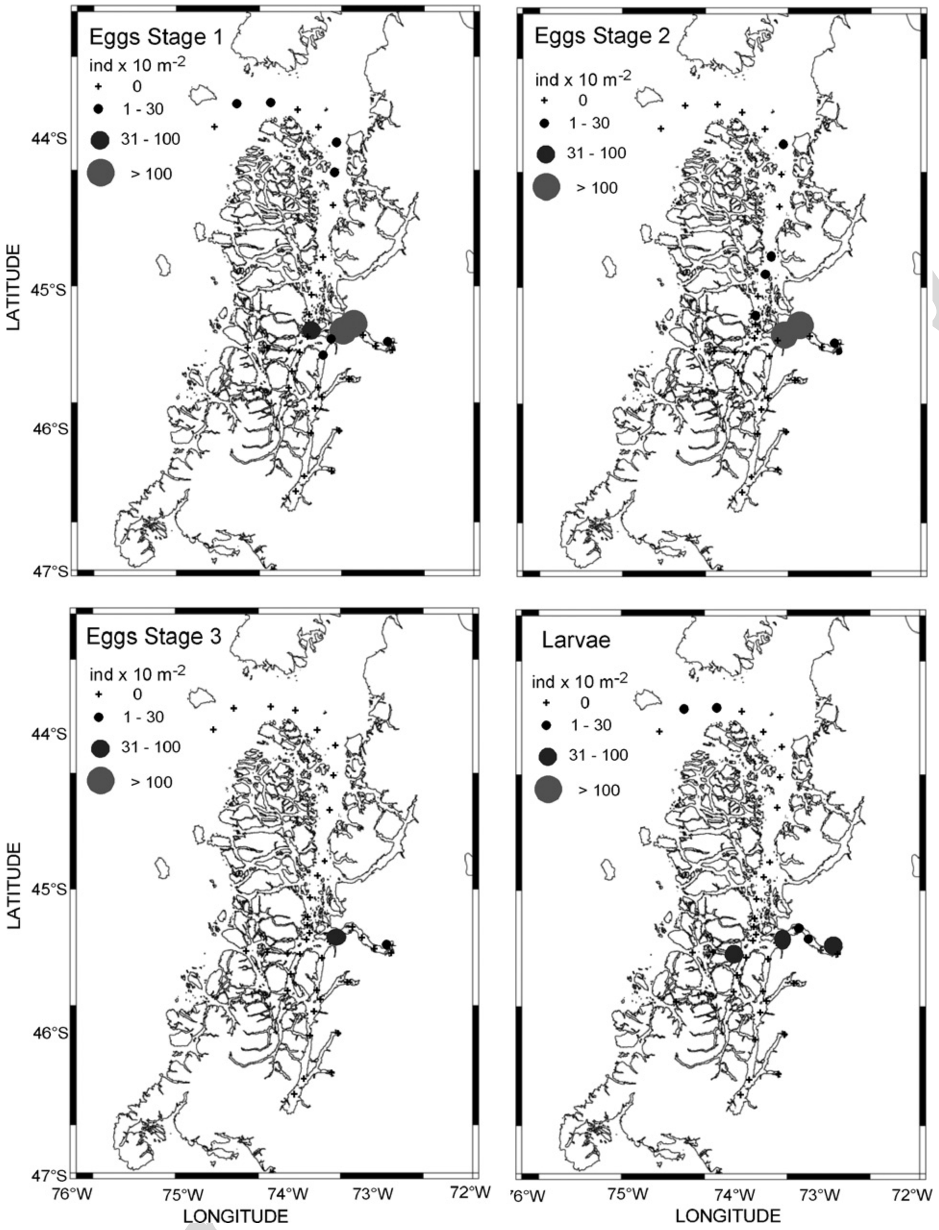

Fig. 4. Distribution of southern hake eggs and larvae sampled during September–October 1998. Abundance given in individuals per 10 m^2. Symbol ‘+’ indicates location of sampling stations.

tral channels, mainly along Moraleda channel and along Darwin and Pulluche channels (<17 eggs per 10 m^2) (Fig. 5). No eggs appeared in offshore waters. Larval hake were abundant in the inner part of the King channel (103 larvae per 10 m^2) and inside Aysen fjord, Ninualac and Moraleda channels (<95 larvae per 10 m^2). Additionally, pre and postflexion larvae were collected in low abundance (<12 larvae per 10 m^2) in the Guafo mouth and off Darwin and Pulluche channel. No significant differences in egg and larval abundance among years (1995, 1998 and 2002) were detected in the area (log-transformed egg abundance, one-way ANOVA, $F = 0.22$, $p = 0.80$; Levene’s test for homogeneity of variances, $p = 0.47$; larvae: one-way ANOVA, $F = 0.24$, $p = 0.79$, Levene’s test, $p = 0.33$).

3.2. Egg and larval size distribution

Southern hake eggs collected during October 1995 (at 42°S) ranged in size between 0.93 and 1.17 mm in diameter, with a mean size of 1.05 ± 0.06 mm (Fig. 6). A significant increment in size was noticed in eggs captured in fjords south 44°S during November 1995 (t-test, $p < 0.001$; Levene’s test $p = 0.119$), with eggs from 0.93 to 1.28 mm (mean ± 1 S.D.: 1.14 ± 0.07 mm) (Fig. 6). Southern hake eggs collected during September–October 1998 ranged between 1.09 and 1.28 mm (1.18 ± 0.05 mm) and between 1.09 and 1.30 mm (1.17 ± 0.04 mm) for the November 2002 survey. Inter-annual differences in the egg size were detected (Kruskal–Wallis ANOVA, $H = 17.78$, $p = 0.001$), egg collected during Novem-

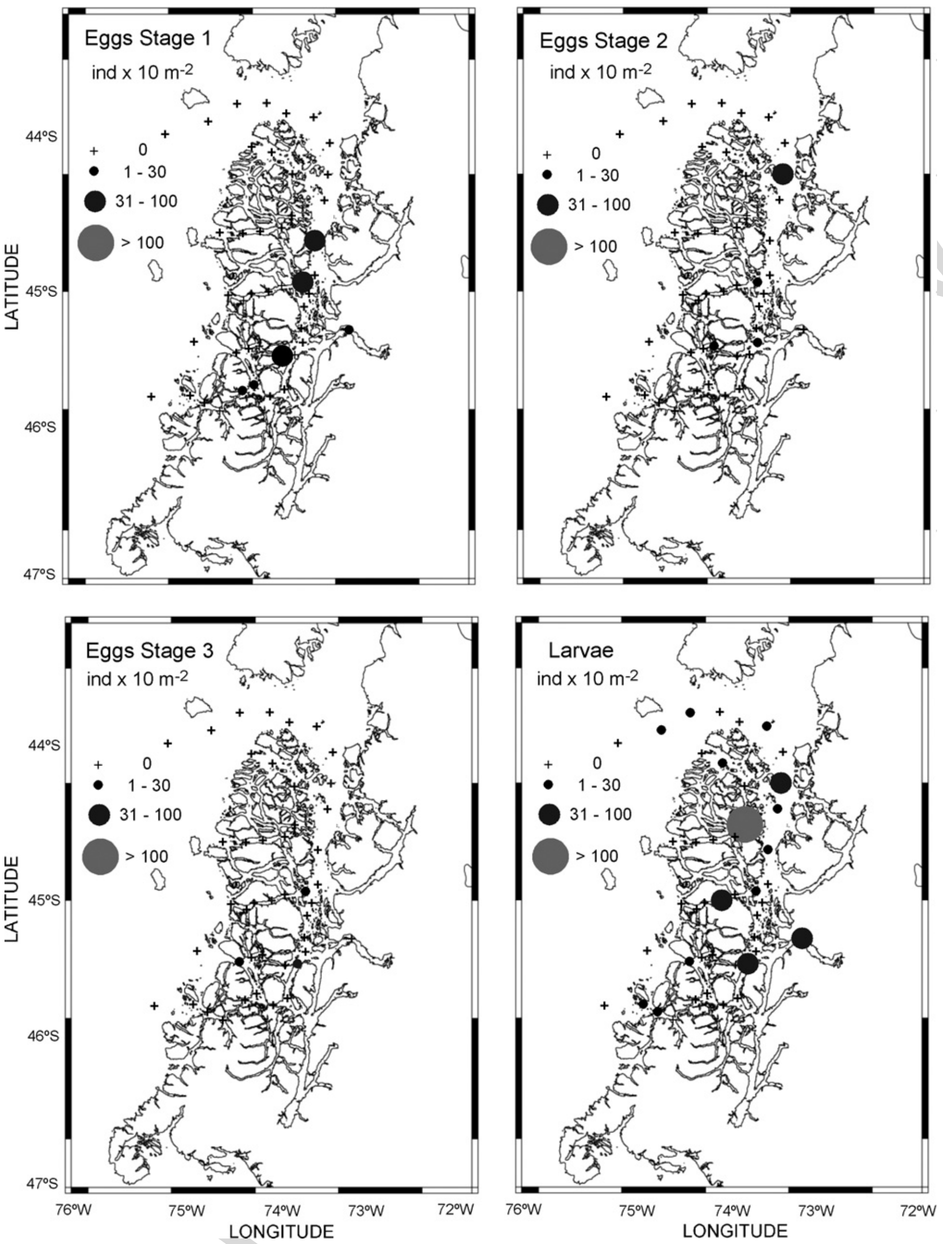

Fig. 5. Distribution of southern hake eggs and larvae sampled during November 2002. Abundance given in individuals per 10 m^2. Symbol '+' indicates location of sampling stations.

ber 1995 being significantly smaller than eggs captured during October 1998 (Mann–Whitney test, $U = 2198$, $p < 0.001$). Additionally, all eggs collected south 43°30′S were larger than captured in the northern area during October 1995 (Kruskal–Wallis ANOVA, $H = 98.35$, $p < 0.001$).

Small, preflexion larvae of *M. australis* were frequently collected in sounds and fjords of southern Chile, and they were significantly smaller in size than southern hake larvae collected off fjords and open areas (mean larval size ± 1 S.D., inside fjords = 6.22 ± 2.59 mm NL; outside fjords = 8.79 ± 3.38 mm SL; *t*-test, $p < 0.001$) (Fig. 7). Significant differences in hake larval size were detected also among years (Kruskal–Wallis ANOVA, $H = 22.78$, $p < 0.0001$), (October 1995: 5.30 ± 1.37 mm NL; November 1995: 6.78 ± 1.55 mm NL; September–October 1998: 6.05 ± 1.69 mm NL; November 2002: 9.16 ± 4.53 mm SL) due to presence of larger *M. australis* larvae captured during the 2002 survey in channels and external waters of southern Chile (Kolmogorov–Smirnov test, $p < 0.005$).

Individuals larger than 9 mm SL (postflexion larvae) were also collected in Reloncaví Sound, Comau, Puyuhuapi and Aysen fjords during October and November 1995, and along King, Ninualac and Darwin channels and Aysen fjord during November 2002. Postflexion larvae were also captured in areas connected to open ocean, like off Pulluche channel during November 1995, over the Guafo mouth in October 1998, and southern Guafo island during November 2002 (Fig. 7).

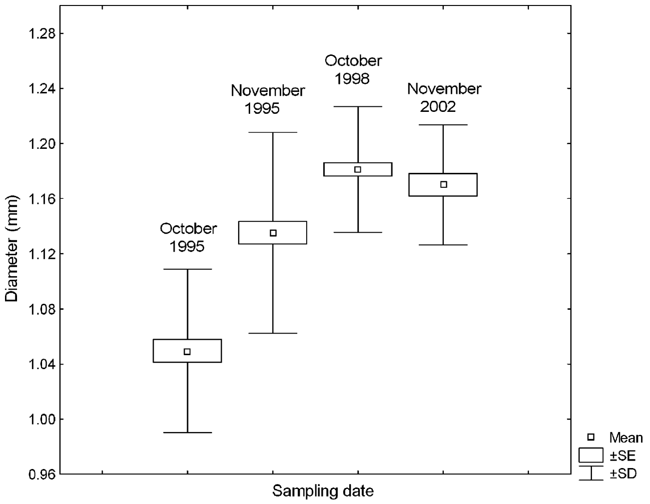

Fig. 6. Size variability in egg diameter (mm) of southern hake among surveys. S.D. and S.E. correspond to standard deviation and standard error, respectively.

3.3. Hydrographic conditions during austral spring

Physical data have been previously described elsewhere (Silva et al., 1997, 1998; Landaeta and Castro, 2006a). As a summary, the vertical physical structure of the water column inside fjords, such as Reloncaví sound during October 1995 (Fig. 8), showed a shallow mixed layer (<25 m) with strong thermocline and halocline characterized by warm surface waters (>11 °C), low surface salinity (<28) and high water stratification (i.e., high Brunt-Väisala number, ~0.0075 cycles/s). Sheltered areas (Moraleda Channel, Fig. 8) showed also a strong halocline and high stratification in surface waters ($N^2 < 2 \times 10^{-3}$ cycles/s). Instead, in areas exposed to the ocean (Corcovado Gulf and off Darwin Channel, Fig. 8), the mixed layer was deep (>100 m) with homogeneous values of temperature (~10.5 °C) and salinity (31–32) throughout the water column, and lower stratification ($N^2 < 5 \times 10^{-5}$ cycles/s) (Fig. 8).

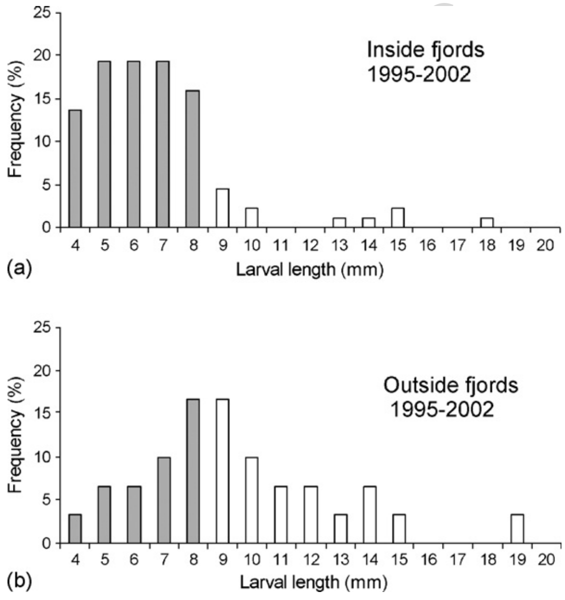

Fig. 7. Larval size distribution (mm) of southern hake in the inland sea inside and outside fjord areas. Gray bars indicate preflexion larvae and white bars shows postflexion larvae.

In the Aysen fjord during all cruises, surface water was between 10 and 11 °C, with a slight decrease in depth up to 9.5 °C. Surface salinity decreased from 12 in the oceanographic stations located in the mouth of the fjord to nearly 0 in the vicinity of the head, with a homogeneous deep layer with salinity values of 30 typical of Modified Subantarctic Waters.

4. Discussion

Hake of the genus *Merluccius* show several reproductive strategies depending of topography and circulation patterns of the area where they inhabit. In upwelling areas, hakes (i.e., *M. capensis*, *M. gayi*, *M. senegalensis*) spawn mainly in subsurface waters (50–100 m deep) in the vicinity of the continental shelf break during late winter and early spring, with a subsequent onshore transport of larvae (Olivar et al., 1988, 2003; Vargas et al., 1997; Sundby et al., 2001; Vargas and Castro, 2001). Additionally, some species display a displacement of spawners to nearshore waters as the reproductive season progresses (Alvarez et al., 2004; Landaeta and Castro, 2006b). The large coastal stock of the Pacific hake *M. productus* spawns at the slope off California region during January–February when wind-induced upwelling is of lower intensity (Bailey, 1981). However, some populations of the Pacific hake that inhabit fjord-like environments of deep Georgia Basin, spawn in locations proximate to major sources of freshwater inflow (Bailey and Yen, 1983; Bollens et al., 1992; Gustafson et al., 2000).

The spawning of *M. australis* occurs during austral winter and spring (July–September in Chilean waters, July–August off New Zealand) when adults concentrate in offshore waters off southern Chile and over Chatam Rise, respectively (Cohen et al., 1990; Balbontín and Bravo, 1993). During this season also occurs a reproductive migration of the Argentinean population southward toward the Magellan Strait (Arkhipkin et al., 2003; Payá and Ehrhardt, 2005). In our study, the highly abundant early eggs (stage 1, >150 eggs per 10 m^2) found inside fjords during 1995–2002 (Figs. 2–5), were similar in density to those found in offshore waters during August 1996 (<100 ind per 10 m^2, Lillo et al., unpublished), and probably are the product of recent reproductive events of a resident stock and/or by inshore migrating adult hakes. Egg development of *M. australis* last 7 days at 11.5 °C in the laboratory, and stage 1 eggs have less than 4 days old (Bustos and Landaeta, 2005). Since water temperature was ~10 °C in deep waters inside fjords (Fig. 8), stage 1 eggs may have been spawned no longer than 6 days ago (Bustos and Landaeta, 2005). Considering the high residence times of fjord waters, the most plausible explanation is that spawning of local populations of southern hake occurs inside fjords during spring.

The selection of spawning grounds in the inland sea associated with fjords and coves may be an adaptive behaviour of adult southern hake to increase retention times of their early life stages in highly stable surface waters (Fig. 8), rich in larval food items during austral spring (Toro et al., 1999; Landaeta and Castro,

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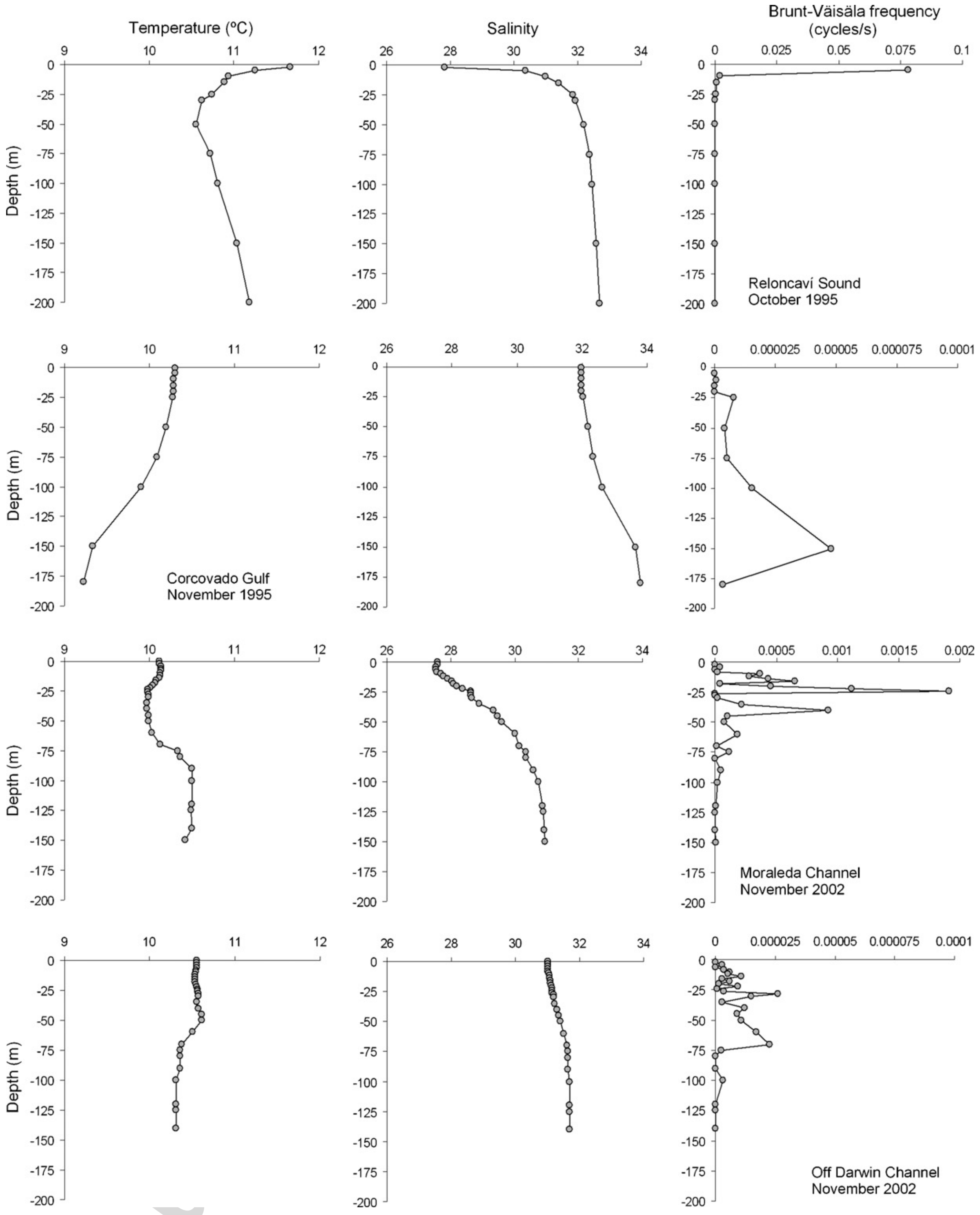

Fig. 8. Vertical profiles of temperature (°C), salinity and the Brunt-Väisäla frequency (cycles/s) as a measure of water stratification during spring season, inside fjords (Reloncaví Sound), shelterd areas (Moraleda Channel), and over exposed areas (Corcovado Gulf and off Darwin Channel).

2006a). During austral spring in southern Chile there is a reduction in the cloud cover (i.e., increase of sunlight) and diatom bloom occurs with a concomitant increment in the chlorophyll *a* concentration and primary production (Toro et al., 1999; Acha et al., 2004). These processes sustain a diverse community of epipelagic herbivorous copepods (Marín and Antezana, 1985). Copepod eggs, nauplii and copepodites represent the most important prey items for larval hake, and together with water temperature (>11 °C) and higher stratification of the surface water column (i.e., higher N^2 values) inside fjords compared with those calculated outside fjords (Fig. 8), may promote larval feeding success on copepods and faster larval growth rates (Sumida and Moser, 1980; Cass-Calay, 1997, 2003; Reiss et al., 2002, 2005).

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Also, wind stress and tidal currents may reverse the classical mean velocity profile in estuarine systems, increasing the residence time of the inner waters. In southern Chile, during spring–summer the wind regime is dominated by southerly and southwesterly winds that favour wind-driven, up-fjord surface circulation at the mouth and in the outer half of the fjords, which would decelerate the surface low salinity layer mean outflow (Cáceres et al., 2002, Fig. 8). The presence of convergence zones and internal waves off the mouth of fjords (Cáceres, 2004) may reduce off-fjord advection and explain the maintenance of eggs throughout development and the high frequency of small hake larvae (Fig. 7). Then, interaction of reproductive outputs with the oceanographic features may increase the retention of zoo and ichthyoplankton in fjords with shallow sills (Basedow et al., 2004). Larger larvae (>9 mm SL) were collected mainly in off-fjord waters of both sheltered (Gulf of Ancud) and exposed zones (Corcovado Gulf and near Guafo Island). Similarly, larger and older (>8 mm SL, up to 66 days old) larval rockfish *S. capensis* were also collected during November 2002 mainly over the continental shelf off channels (Landaeta and Castro, 2006a). Interestingly, southern hake juveniles and prerecruits (21–65 cm TL) were collected in the Gulf of Ancud and Moraleda Channel during hydroacoustic surveys carried out in the inland sea of southern Chile (Lillo et al., unpublished).

We found a slight but significant increase in the egg size (i.e., diameter) at higher latitudes and among years (Fig. 6). Seawater temperature does not show considerable variability both in depth and latitudinal range (from 9 to 11 °C) enough to explain egg size variability. Although egg size may also reflect intrinsic differences between stocks, further investigations on the reproductive biology of this commercially important species are needed to clarify this topic.

Finally, it is important to establish the persistence of the spawning and nursery areas of the southern hake and the recent health of Chilean fjords, considering the potential impact of the salmon farming industry which generates high amounts of particulate organic matter through fish faeces and pellets.

Acknowledgements

Authors want to thank comments and reviews of Beatriz Yannicelli, Samuel Hormazábal and Enrique Bay-Schmidt (Universidad de Concepción). This research was funded by the National Oceanographic Committee of Chile (CONA) grants. During the writing of this manuscript, C.A. Bustos was supported by a scholarship of CONA and Fondecyt 1040618. M.F. Landaeta was supported by a Doctoral scholarship (CONICYT, BECA AT-4040126). Two anonymous reviewers contributed to improve an early version of this manuscript.

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