

# Larval distribution and growth of the rockfish, *Sebastes capensis* (Sebastidae, Pisces), in the fjords of southern Chile

Mauricio F. Landaeta and Leonardo R. Castro

Landaeta, M. F., and Castro, L. R. 2006. Larval distribution and growth of the rockfish, *Sebastes capensis* (Sebastidae, Pisces), in the fjords of southern Chile. — ICES Journal of Marine Science, 63: 714–724.

The distribution and the growth of larval rockfish *Sebastes capensis* were studied during two oceanographic cruises carried out in a sector of the Chilean fjords (43°30'S–46°S) during spring 2002 (November) and winter 2003 (August). Abundance (up to 600 per 10 m<sup>2</sup>) of pre- and post-flexion larvae was higher during the austral spring than in winter (20 per 10 m<sup>2</sup>). Larvae were smaller principally above the halocline in the first 50 m of the water column throughout the channels and fjords; in contrast, post-flexion larvae were more abundant seawards and were totally absent in the freshest waters. Analysis of the otoliths indicated that larvae between 3.3 and 12.2-mm standard length collected during November grew 0.15 mm d<sup>-1</sup>. Additionally, it showed that older larvae from the outer part of the channels and over the shelf laid down wider otolith increments than larvae found in the interior waters, coinciding with the area of greatest abundance of larger calanoid copepods. Ontogenetic differences in distributions suggest that different habitats are utilized during the early life stages of *S. capensis*, and that they seem to be shared with several other *Sebastes* species. However, the mechanisms for transport in different areas vary widely, making the question of the evolutionary forces driving these ontogenetic changes in distribution even more intriguing.

© 2006 International Council for the Exploration of the Sea. Published by Elsevier Ltd. All rights reserved.

Keywords: larval growth, otolith, Patagonian fjords, rockfish, *Sebastes capensis*, southern Chile.

Received 8 April 2005; accepted 23 January 2006.

M. F. Landaeta and L. R. Castro: Laboratorio de Oceanografía Pesquera y Ecología Larval (LOPEL), Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Correo 3, Concepción, Chile. Correspondence to M. F. Landaeta: tel: +56 041 207029; fax: +56 041 256571; e-mail: [mlandaeta@udec.cl](mailto:mlandaeta@udec.cl).

## Introduction

The rockfish, *Sebastes* spp., are highly diversified, viviparous fish with about 72 species that are mostly endemic to the North Pacific (Nelson, 1994), where they sustain fisheries that constituted nearly 20% of the total commercial groundfish fishery in 2000 (Laidig *et al.*, 2004). In the South Pacific Ocean, there are considerably fewer *Sebastes* species. Along the Chilean coast, for instance, only one species has been recorded (Kong, 1985): *Sebastes capensis* (Gmelin 1788). It supports a small artisanal fishery, 171 t being caught in 1999, but just 45 t during 2002 (SERNAPESCA, 2002).

*Sebastes capensis* is a bottom-dwelling fish that inhabits shallow and rocky areas between 5 and 15 m deep. Females retain the eggs until maturation, when embryos are extruded throughout most of the year (Sabatés and Olivar, 1990). Pelagic larvae have been collected in coastal waters all along the Chilean coast (Loeb and Rojas, 1988; Castro *et al.*, 2000; Rodríguez-Graña and Castro, 2003), and are

particularly abundant at the southern tip of South America (Balbontín and Bernal, 1997; Bernal and Balbontín, 1999), where fjords and channels dominate the coastline.

The Chilean fjord zone (41°S–55°S) is a highly heterogeneous system consisting of several microbasins (*sensu* Antezana, 1999), forming one of the largest estuarine areas in the world. The ecosystem is more than 1600 km long and covers an area of about 240 000 km<sup>2</sup> (Palma and Silva, 2004). Surface forcing is dominated by strong poleward winds, heavy precipitation (2.5 m year<sup>-1</sup>; Strub *et al.*, 1998), freshwater run-off, and river discharge (Guzmán and Silva, 2002). The complex fjord coastline is sheltered and increases the influence of the tidal forcing (amplitudes from 1.5 to 8.0 m; Strub *et al.*, 1998; Valle-Levinson *et al.*, 2001). Two-layer estuarine circulation patterns are found in many of the fjords (Strub *et al.*, 1998). Although larvae of *S. capensis* are among the most abundant taxa in ichthyoplankton samples throughout the area (Balbontín and Bernal, 1997), there is no information on its ecology in southern Chile.

This study examines the early life history of the rockfish *Sebastes capensis* in the Patagonian fjord waters of southern Chile. Based on data from two oceanographic cruises (winter and spring), our objectives were (i) to obtain information on adult reproductive locations and seasonality (winter and spring) by examining potential differences in larval distribution and abundance, (ii) to identify potential ontogenetic changes in larval distribution within and between seasons, and (iii) to determine if differences existed in environmental characteristics between the inner and outer (seaward) zones of the channels during the main reproductive season that could be related to the changes

observed in larval distribution and back-calculated birth-dates estimated from otoliths.

## Methods

Two oceanographic cruises were conducted during 16–27 November 2002 and 9–22 August 2003 in the austral zone of Chile (Figure 1) on board the “Vidal Gormaz”. The cruise track was similar during each cruise and consisted of sampling one channel orientated in a north–south direction (Moraleda Channel) and two transverse channels orientated in an east–west direction (Ninualac and

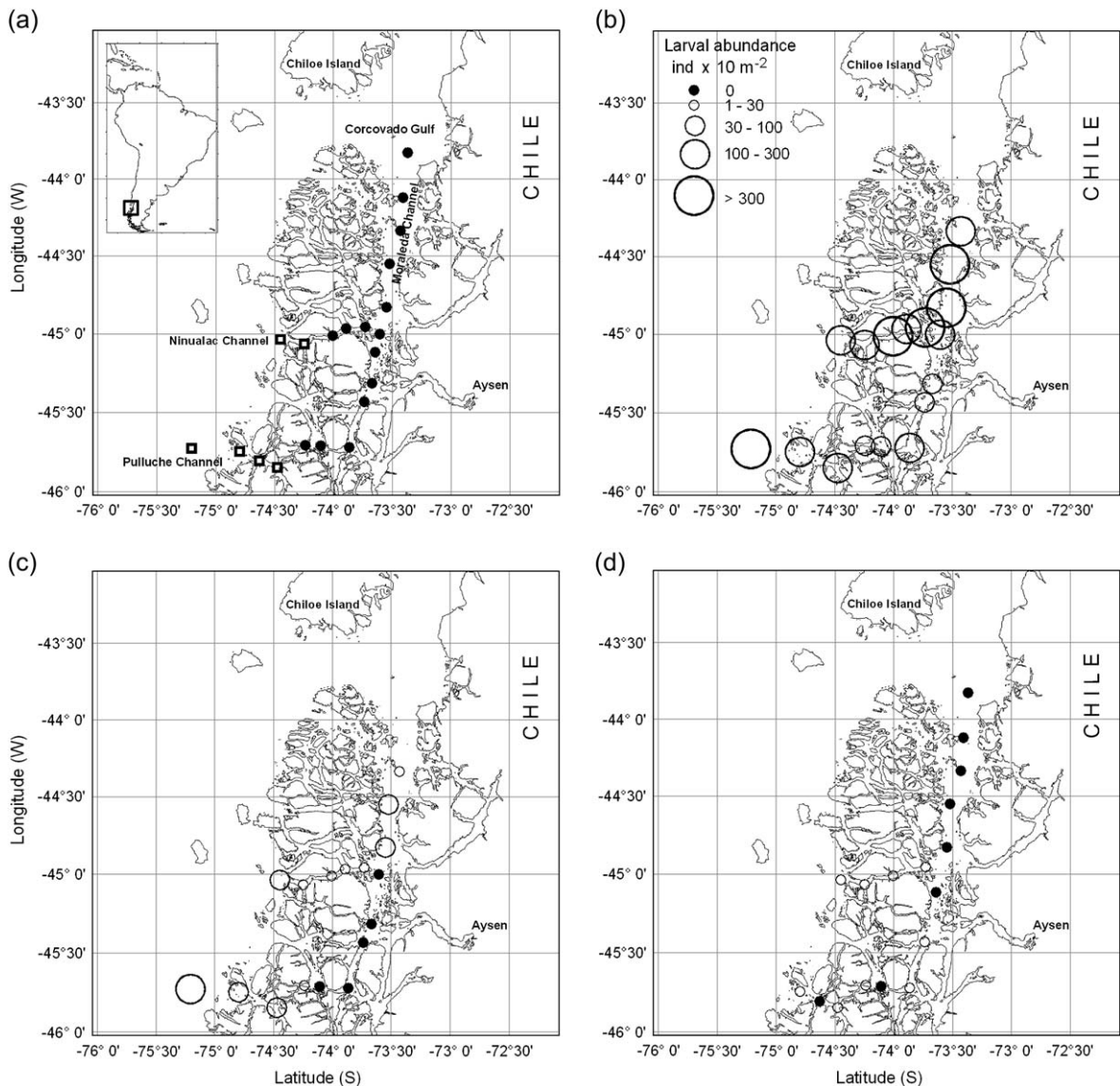


Figure 1. (a) Study area in southern Chile, indicating the oceanographic station locations inside (black dots) and outside (squares) the channels; integrated larval abundance (number per 10 m<sup>2</sup>) of (b) pre-flexion, and (c) post-flexion larval *S. capensis* during austral spring (November 2002) in southern Chile; (d) integrated larval abundance (number per 10 m<sup>2</sup>) of *S. capensis* during austral winter (August 2003) in southern Chile.

Pulluche Channels). During November 2002, the two northernmost stations were not sampled; in August 2003, a middle station in the Ninualac Channel and the outer station of the Pulluche Channel were not sampled. At each oceanographic station, hydrographic casts were performed to 300 m with a Seabird SB-19 CTD (Conductivity—Temperature—Depth) profiler. Ichthyoplankton sampling was carried out using an opening—closing 1-m<sup>2</sup>-mouth Tucker trawl, equipped with three 300- $\mu$ m mesh nets and a flowmeter mounted in the frame. The net was deployed obliquely to a maximum depth of 100 m or to near the seabed, and two or three strata were sampled (0–20, 20–50, and 50–100-m depth), depending on bottom depth. After recovery, the nets were rinsed and the ichthyoplankton samples preserved in 4% buffered formaldehyde (strata) and 95% ethanol (integrated samples).

All fish larvae were removed from each sample and identified to the lowest possible taxon; larval rockfish were identified following Sabatés and Olivar (1990). Larvae were classified according to their developmental stage as pre- or post-flexion (inflexion larvae were included in post-flexion). All undamaged larvae were measured to the nearest 0.1 mm (notochord length, NL, or standard length, SL). No attempt was made to correct lengths for the effects of preservation. Larval rockfish counts were converted to density (number 1000 m<sup>-3</sup>) for each stratum, and the integrated abundance of rockfish larvae in the water column (number 10 m<sup>-2</sup>) was estimated for each sampling station.

Otolith analysis was only performed for rockfish larvae collected during November 2002. The limited number collected in August 2003, as well as their narrow size range, prevented any analysis. Otoliths were removed from 102 larvae (3.3–12.2 mm SL), and ages were determined following the procedures given in Laidig *et al.* (1991). Otoliths were embedded in epoxy resin on a glass slide. Growth increments of sagittal otoliths were counted and measured under a light microscope at a magnification of  $\times 1000$  using an oil immersion lens. Otolith radius, distance of the extrusion check from the primordium, and otolith area were measured using a Sony CCD-IRIS video camera attached to a microscope connected to a PC with Optimas<sup>®</sup> 6.1 software.

Counting and measurement of growth increments began with the conspicuous dark mark (extrusion check), which has also been observed in otoliths of other larval *Sebastes* (Penney and Evans, 1985; Kokita and Omori, 1998; Laidig and Sakuma, 1998; Plaza *et al.*, 2003; Laidig *et al.*, 2004). Although we did not attempt to validate the daily periodicity of growth increments in *S. capensis*, other authors have confirmed the daily nature of growth increments in *S. melanops* (Yoklavich and Boehlert, 1987), *S. jordani* (Laidig *et al.*, 1991), *S. thompsoni* (Kokita and Omori, 1998), *S. paucispinis*, *S. goodie*, *S. entomelas*, and *S. flavidus* (Woodbury and Ralston, 1991).

The birthdate composition of all larvae was estimated as follows. First, a larval length-at-age key was obtained for the entire period of sampling. The length frequency distribution of larvae at each station was then converted to an

age—frequency distribution using the length-at-age key, from which the birthdate composition was back-calculated. The birthdate distribution for each sampling day was weighted according to the standardized abundance of the catch per station, then summed to obtain the distribution in the population.

Hydrographic cross-sections were generated from CTD profiles using contouring functions in Surfer 8. In order to detect potential effects of depth (above and below 50 m), time of day (day/night samples), and salinity (above or below 30) on the abundance of pre- and post-flexion *S. capensis* larvae during the austral spring cruise of November 2002, a three-way ANOVA was performed on log-transformed larval density data from the positive stations. The analysis was performed separately for pre- and post-flexion rockfish. Factors were fixed, except salinity (above or below 30), which was a random factor. The salinity value represented the average for the depth strata. Vertical migration of larvae was examined through an interaction term for the effects of depth and day/night stations in the ANOVA analysis (Table 1).

To assess whether differences existed in the potential food environment of *S. capensis* larvae in the upper 50 m between the inner and the seaward ends of the two transverse channels (Pulluche and Ninualac) during the month of maximum abundance (November, see Results), we quantified the abundance of two size fractions (300–500  $\mu$ m and >500  $\mu$ m total body length) of calanoid and cyclopoid copepods, and of metanauplii of *Rhincalanus nasutus*, a calanoid copepod with large (>300  $\mu$ m) naupliar stages. The size ranges considered may be somewhat larger than that required for first-feeding larvae. However, the aim was to observe whether a coincidence may have occurred between larval size and the size of potential food particles

Table 1. Three-way ANOVA results for abundance of pre and post-flexion larvae of *Sebastes capensis* during November 2002.

	MS effect	F	p-value
Pre-flexion larvae			
Depth	17.53	229.83	<b>0.042</b>
Day/night	0.36	0.51	0.605
Salinity	0.11	0.08	0.772
Depth $\times$ day/night	0.13	0.87	0.523
Depth $\times$ salinity	0.08	0.06	0.809
Day/night $\times$ salinity	0.70	0.54	0.466
Depth $\times$ day/night $\times$ salinity	0.15	0.12	0.733
Post-flexion larvae			
Depth	12.80	94.17	0.065
Day/night	0.29	2.17	0.380
Salinity	42.70	12.35	<b>0.001</b>
Depth $\times$ day/night	0.04	0.08	0.827
Depth $\times$ salinity	0.14	0.04	0.844
Day/night $\times$ salinity	0.13	0.04	0.845
Depth $\times$ day/night $\times$ salinity	0.50	0.15	0.705

Bold values indicate significant differences.

we would expect the larvae to eat as they grow. Finally, under the assumption that smaller larvae might benefit from developing in a food-rich and more stable environment, we calculated and compared the Brünt–Väisälä frequency ( $N = \sqrt{(g/\rho) \times (\partial\rho/\partial z)}$ , where  $g$  = gravity ( $9.8 \text{ m s}^{-2}$ )) as a measure of water stability at the innermost and the outermost (seaward) stations of both channels.

## Results

### Seasonal changes in abundance and distribution

During the austral spring (November 2002), 1505 *S. capensis* larvae were collected (1327 pre- and 178 post-flexion). Standardized integrated abundance among stations ranged between 35.8 and 664.2 per  $10 \text{ m}^2$  (Figure 1b). Pre-flexion larvae were collected at all stations sampled, although abundance was greatest in the northern part of the Moraleda Channel, high throughout the Ninualac Channel, and high also towards the outer end of the Pulluche Channel (Figure 1b). Post-flexion larvae were absent in the southern part of the Moraleda Channel and inside the Pulluche

Channel. Towards the outside of the Ninualac and Pulluche Channels and in the north of the Moraleda Channel near the Corcovado Gulf, densities of post-flexion larvae were highest (Figure 1c).

In August 2003 just 172 larvae were caught, all of them pre-flexion, with densities ranging from 0.9 to 19.9 per  $10 \text{ m}^2$ . At that time, pre-flexion larvae were found only in the Ninualac Channel, in the southern part of the Moraleda Channel, and off the Pulluche Channel (Figure 1d). Abundance was therefore significantly less in winter than in spring (Mann–Whitney  $U$ -test,  $p < 0.001$ ).

### Vertical distribution of larvae

The vertical distributions of pre- and post-flexion *Sebastes capensis* larvae differed during November 2002. Pre-flexion larvae were encountered in all strata sampled in all channels (Figure 2a–c), and their abundance was significantly greater in the upper 50 m (ANOVA,  $F = 229.83$ ,  $p < 0.05$ ) in the Pulluche and Moraleda Channels. In the Ninualac Channel (Figure 2b), pre-flexion larvae were

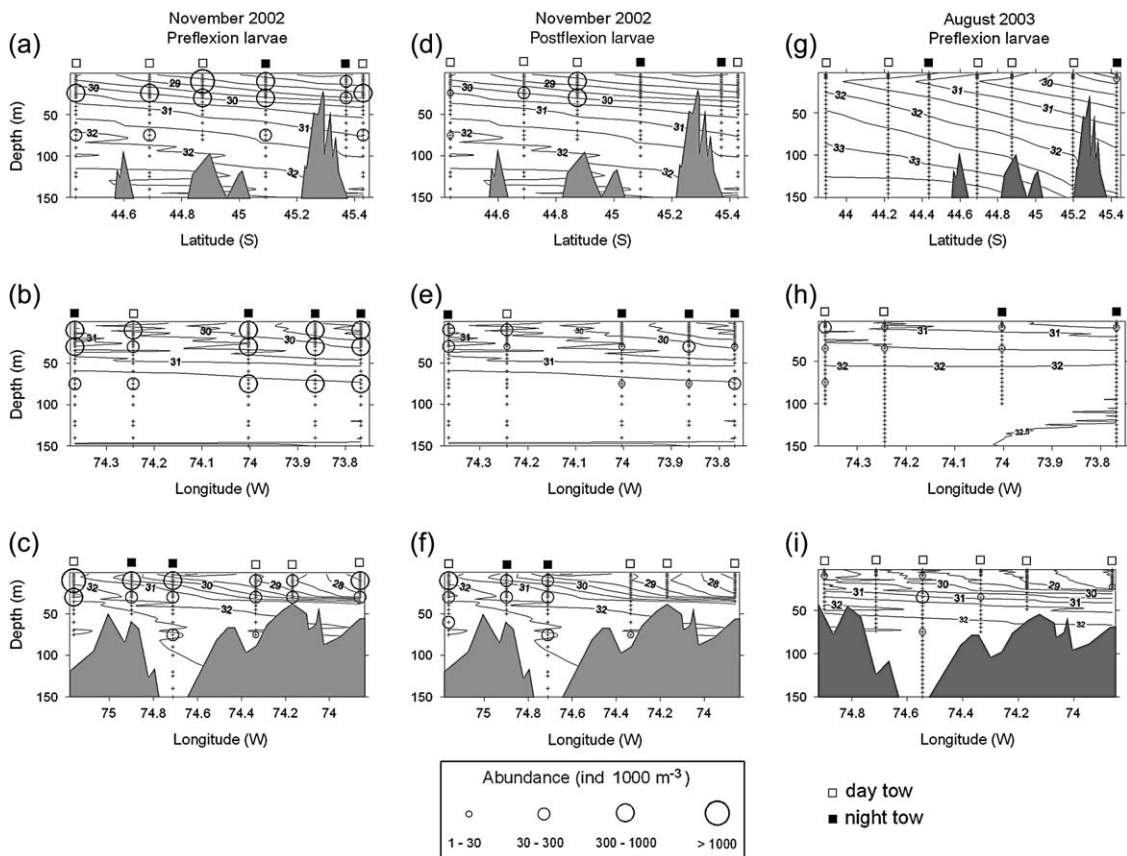


Figure 2. Vertical distribution of pre- and post-flexion larval *S. capensis* (number per  $1000 \text{ m}^3$ ) during austral spring (November 2002) and winter (August 2003) in the Moraleda Channel (a, d, and g), the Ninualac Channel (b, e, and h), and the Pulluche Channel (c, f, and i). Crosses (+) indicate salinity data used from the CTD profiler. Also shown are day (white square) and night (black square) tows. Salinity isolines are superimposed.

evenly distributed throughout the water column only inshore. No differences associated with diel vertical migration or salinity were detected in pre-flexion larvae (Table 1). Post-flexion larvae collected in November had a different vertical distribution: most were in the upper (<50 m) layer to seawards, and there was a significant reduction in abundance in surface water where the salinity was <30 (ANOVA,  $F = 12.35$ ,  $p < 0.01$ ; Table 1). This distribution was particularly evident in the inner part of the channels (Figure 2d–f), where post-flexion larvae were collected mainly in deeper, more saline water.

In August 2003, when only a few pre-flexion larvae were collected, there was no distinct pattern in vertical distribution. Only a slight broadening in the vertical distribution range was noted from the inner to the outer areas of the Ninualac and Pulluche Channels (Figure 2g–i).

### Age and growth of larvae

The larval size distribution was broader during spring 2002 (2.9–13.4 mm SL) than in winter 2003 (3.9–5.8 mm SL). Consequently, larvae collected in spring were in the pre- and post-flexion stages (smaller and larger than 7 mm SL, respectively), but those collected in winter were only pre-flexion (Figure 3). A  $t$ -test for independent samples

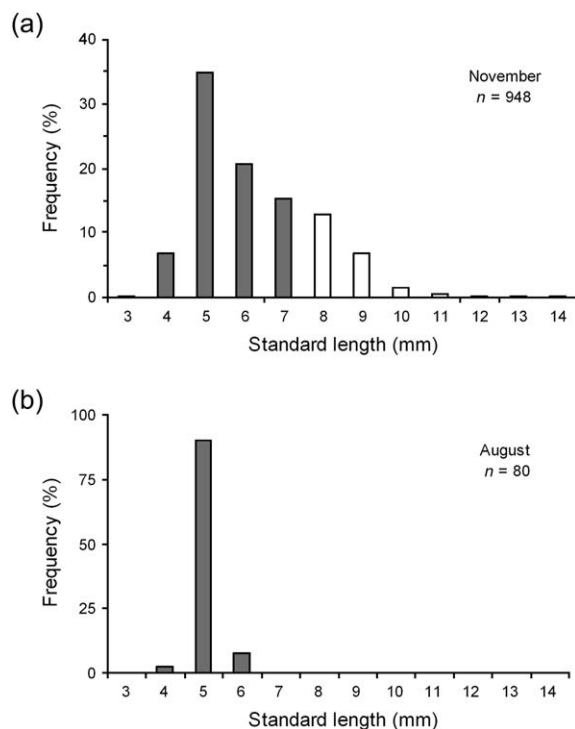


Figure 3. Length frequency of *S. capensis* larvae collected during (a) November 2002, and (b) August 2003 in southern Chile. Shaded bars are pre-flexion larvae.

( $p < 0.0001$ ) confirmed that the mean larval size was larger during November 2002.

The extrusion check observed in otoliths of larval *Sebastes capensis* collected in November ranged from 10.2 to 16.8  $\mu\text{m}$  (mean  $\pm$  s.d.:  $12.5 \pm 1.5 \mu\text{m}$ ;  $n = 67$ ). Larval growth rate was estimated by a linear model of least squares fitted to the relationship between SL and age (coefficient of determination  $r^2 = 0.92$ ,  $n = 102$ ; Figure 4a). This model estimated a growth rate of  $0.15 \text{ mm d}^{-1}$  and a larval extrusion length of 3.78 mm. Otolith radius and standard length were related linearly (Figure 4b), and otolith area was related exponentially with *Sebastes* larvae SL (Figure 4c).

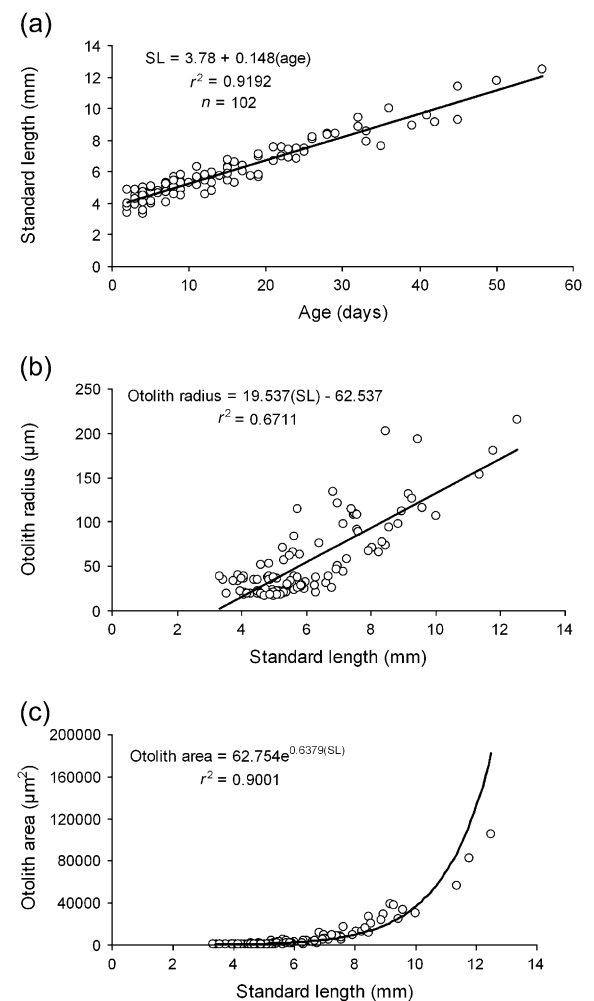


Figure 4. (a) Plot of the standard length and age of rockfish, *S. capensis* ( $n = 102$ ) collected during November 2002. The solid line indicates the predicted values from a linear model. (b) Plot of otolith radius against standard length. The solid line indicates the predicted values from a linear model. (c) Plot of otolith area against standard length. The solid line indicates the predicted values from an exponential model.

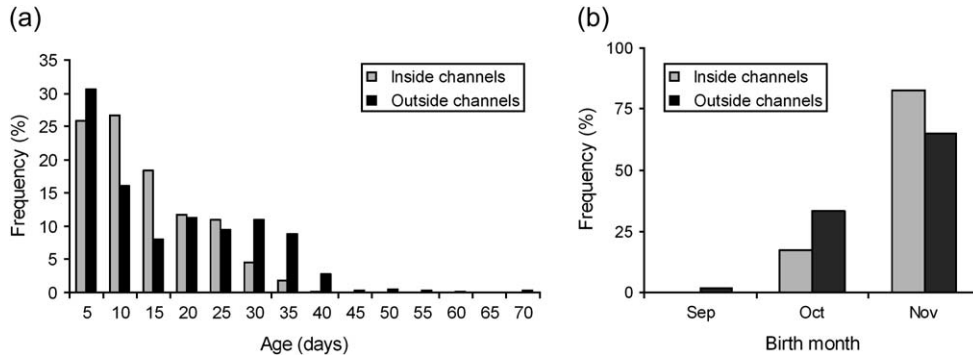


Figure 5. (a) Age—frequency and (b) back-calculated birth month of larval *S. capensis* during November 2002, captured at stations located inside (grey bars) and outside (black bars) the southern Chilean channels.

In November 2002, larvae collected in the seaward part of the channels were significantly older (up to 66 days old) than larvae from the inner areas (<40 days old; Kolmogorov–Smirnov test,  $p < 0.001$ ; Figure 5a). Back-calculated birthdates for larvae collected in November 2002 indicated that they had been extruded from September through November of the same year. Interestingly, those larvae born early in the season (September) were caught only at the seaward stations (Figure 5b).

There was no significant difference between the mean increment width of otoliths (in  $\mu\text{m}$ ) of pre- and post-flexion larvae collected inside and outside the channels (Kolmogorov–Smirnov test,  $p > 0.05$ ) during the first 20 days of larval life. However, older than 20 days, the otolith increments in larvae captured outside the channels were wider than those of larvae collected in the inner part of the channels (Kolmogorov–Smirnov test,  $p < 0.05$ ; Figure 6).

### Hydrography

In November, seawater temperature ranged from 10 to 11°C throughout the channels and throughout the water column down to 150 m (Figure 7a–c). Temperatures were

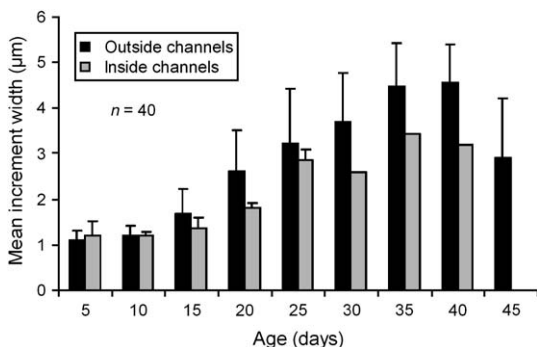


Figure 6. Temporal changes in mean otolith increment width estimated for every five-increment interval for larvae captured inside (grey bars) and outside the channels (black bars;  $n = 40$ ).

lower in the deepest strata right along the channels, including their innermost parts. Among channels, Moraleda was the coldest, with temperatures below 10.5°C immediately below the surface layer (down to 25 m), followed by Ninualac (<10.5°C below 50 m), and Pulluche (<10.5°C below 60–70 m). Strong salinity gradients were observed along all the three channels (Figure 2a–c). Salinity was at its minimum (<28) at the head of the channel head (its inner end), showing the influence of the large freshwater input from rainfall and ice melting in the mountains, as well as from the rivers located east of the channels, and the San Rafael Lake and Glacier (46°40'S 74°W) that drains at the head of the Moraleda Channel. Maximum salinity (>33) was at the outer part (seawards) of the Ninualac and Pulluche Channels, and at the Moraleda Channel mouth.

In winter (August), the overall temperature range (9.5–10.1°C) was lower than that in November, and temperature was generally inverted throughout the area (Figure 7d–f). Temperatures were lowest in the inner parts of the channels but, in contrast with the situation in November, maximum temperatures were at mid-depth (Moraleda Channel) or deeper (Ninualac and Pulluche Channels). Similar to the spring conditions (November), strong salinity gradients were observed along all three channels in winter, with minimum values (<29) in the inner part of the channels and maximum values (>33) deeper and to seaward (Figure 2g–i).

### Potential larval feeding environment in the Ninualac and Pulluche Channels

Copepod abundance (number  $\text{m}^{-3}$ ) along the Ninualac Channel (Figure 8a, b) varied between both size fractions. While smaller copepods were abundant throughout the Pulluche Channel, larger copepods and metanauplii were more abundant towards the outer side of this channel (Figure 8b). Smaller calanoid copepods, although variable in abundance throughout the channel, also tended to be more abundant towards the channel's seaward end. Cyclopoid copepods were scarce throughout.

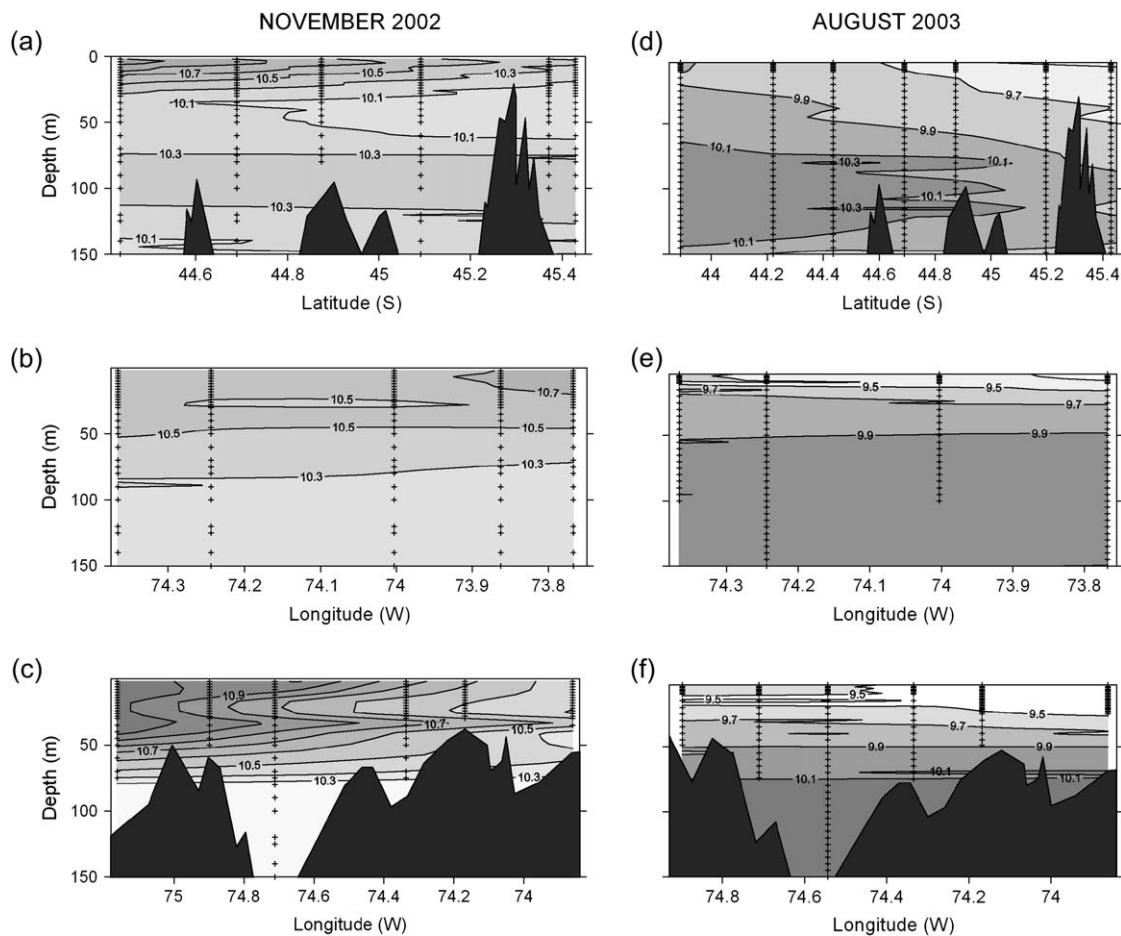


Figure 7. Water temperature during November 2002 (left panel) and August 2003 (right panel). (a and d) Moraleda Channel, (b and e) Ninualac Channel, and (c and f) Pulluche Channel.

In the Pulluche Channel (Figure 8c, d) there was an increase in abundance of small copepods towards the channel's head, particularly smaller calanoid copepods and cyclopoids, the latter occurring only close to this channel's head. Metanauplii were more abundant to seaward.

High values ( $>0.02$ ) of the Brünt–Väisälä frequency,  $N$ , denoting greater stratification, were observed in the upper layer (0–40 m) at the innermost and outermost stations of the Pulluche Channel (Figure 9a). Lower values ( $<0.01$ ) were deeper in the water column in the outer channel. In the Ninualac Channel's inner zone, high (but more variable) Brünt–Väisälä frequency,  $N$ , values were found in shallow water (0–60 m), and lower values (0.01 or less) were observed throughout the water column to seaward (Figure 9b).

The inner and seaward stations along the Ninualac Channel had similar total numbers of smaller copepods, high stratification levels, and large numbers of pre-flexion *S. capensis* larvae. Alternatively, to seaward in this channel, the greater abundance of larger copepods and the older, post-flexion larval stages coincided. In contrast, in the Pulluche

Channel, although smaller copepods were more abundant in the high stability areas (at the inner part of the channel), smaller *S. capensis* larvae were distributed throughout the channel. However, most of the older, post-flexion larvae were to seaward, where copepods were larger and the waters were more stable.

## Discussion

Fjord and channel systems in Scandinavia, Iceland, Greenland, British Columbia, Alaska, and Chile form some of the largest estuarine areas in the world (Cameron and Pritchard, 1963). These systems are utilized for spawning, nursery, and recruitment by many marine fish with contrasting life histories, varying from mesopelagic (Lopes, 1979) and pelagic (Brown, 2002) to demersal fish (Marteinsdottir *et al.*, 2000; Boje, 2002). The fjords of southern Chile are less well studied, but reports on ichthyoplankton indicate that fish eggs and larvae of small pelagic fish such as

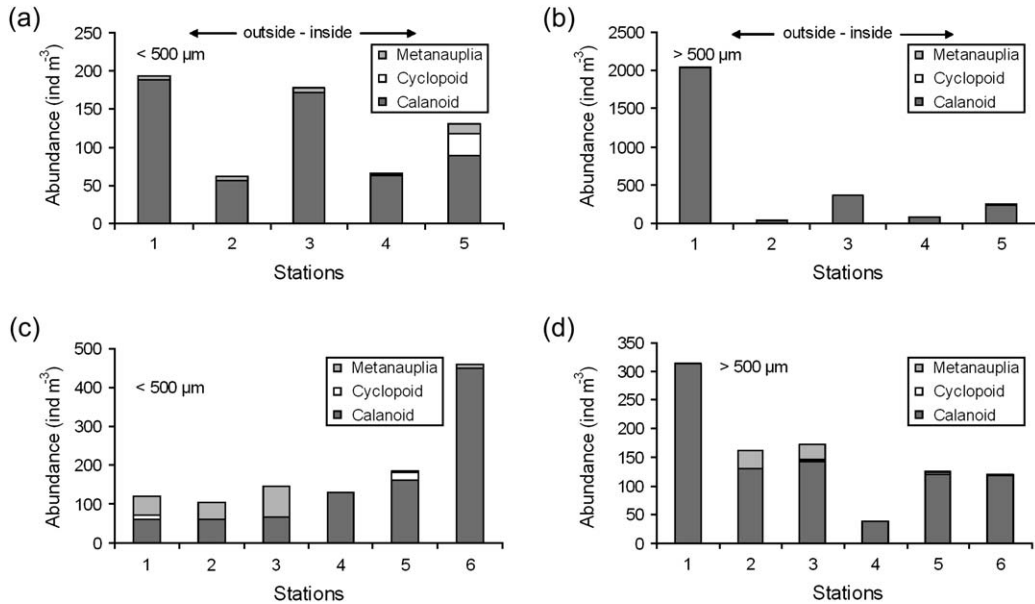


Figure 8. Abundance (number per  $\text{m}^3$ ) of calanoid and cyclopoid copepods and metanauplii of *Rhincalanus* sp. for two size ranges (<500  $\mu\text{m}$  and >500  $\mu\text{m}$ ) along (a and b) the Ninualac Channel, and (c and d) Pulluche Channel, respectively.

sardine (*Strangomera bentincki*), mesopelagic fish such as lightfish (*Maurollicus parvipinnis*), and economically important demersal fish such as *Merluccius australis* and *Macruronus magellanicus* are abundant within the fjords and channels (Balbontín and Bernal, 1997; Bernal and Balbontín, 1999). Of the shallow-water species, *Sebastes capensis* has been reported to be the most abundant (Balbontín and Bernal, 1997).

In our study, rockfish larvae were found during August and November, although abundance was greater in November. Previous work on Chilean fjords also found abundant rockfish larvae throughout the region during spring (Balbontín and Bernal, 1997; Bernal and Balbontín, 1999), including in the northern part of the Moraleda Channel, where we missed two stations in November. In contrast, in central Chilean coastal waters (33°S–36°S), larval *S. capensis* are most abundant earlier in the year (i.e. mid to late winter, Castro *et al.*, 2000; Hernández-Miranda *et al.*, 2003). In southern Chile, there is a marked seasonality in primary production and microphytoplankton composition and abundance (Toro *et al.*, 1999), winter phytoplankton being characterized by low salinity diatoms and spring and summer phytoplankton by marine diatoms (Cassis *et al.*, 2002). This change in microplankton composition and production is coincident with the increase in abundance of larval *S. capensis* in November (Figure 1b–d). Our results, therefore, suggest a potential delay in peak reproduction of this species as latitude increases.

In November, we noted a different spatial distribution of larvae according to ontogenetic stage and age (Figures 1b, c and 2). While pre-flexion larvae were very abundant throughout the channels, post-flexion larvae were found

mainly in the larger Moraleda Channel and in the seaward (outer) part of the transverse channels and over the shelf. There were also differences in hydrographic conditions and in the distribution of potential food particles between the inner and the outer parts of the channels. Areas of marked water column stability (higher Brünt–Väisälä frequency) tended to coincide with greater concentrations of smaller copepods. However, the association between higher stability, smaller copepods, and smaller *S. capensis* larvae was not clearcut, because smaller (pre-flexion) larvae were caught throughout the channels. Our nets may have underestimated the abundance of smaller particles (i.e. copepod eggs and small nauplii), but such a sampling inefficiency should have not affected selectively some areas over others (e.g. inner vs. outer stations). Further, larger *S. capensis* larvae always occurred in the outer part of the channels and over the shelf, where the largest copepods were also found, suggesting an association between potential large size of larval food particles and larger rockfish larvae. Previous studies on other *Sebastes* species have demonstrated that as rockfish larvae grow, their foraging ability also increases, and they prey on a wider range of particle sizes, from copepod eggs to copepodites, and even selecting between calanoid and cyclopoid species (Anderson, 1994). In agreement with this scenario, two sequential non-exclusive hypotheses might be proposed: (i) the smaller particle size of available prey inside the channels associated with lower salinity and temperature might result in poorer condition of larger larvae (which may explain their scarcity and the narrower width increment in the otoliths), and (ii) larger larvae migrate or are transported from the inner part of the channels towards



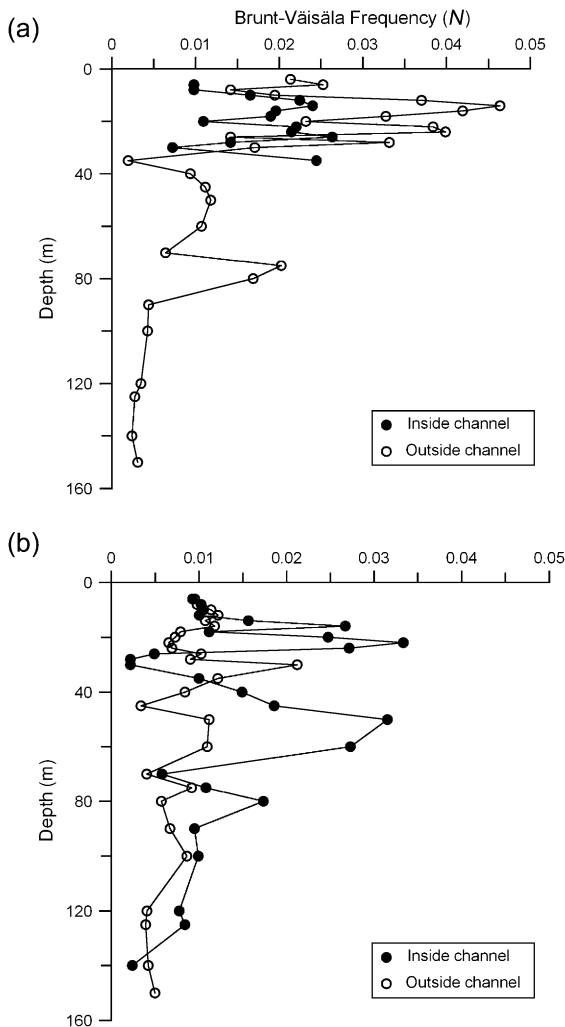


Figure 9. Water column stability calculated as a Brunt-Väisälä frequency ( $N$ ) for the innermost and outermost station of the (a) Pulluche, and (b) Ninualac Channels.

the shelf, where food particles are larger and where faster growth may be achieved (as suggested by the larger numbers of rockfish larvae and the wider rings in their otoliths). The few post-flexion larvae collected in the inner part of the channels were younger than those collected offshore and were located in deep layers, suggesting that they remained inshore in less favourable environmental conditions. Although limited data are currently available to test these hypotheses, they do agree with observations on other species of *Sebastes* on the Scotian Shelf (Drinkwater *et al.*, 2000), as well as with the estuarine circulation pattern observed in the area, in which a shallow layer of low salinity water flows from the head to the outer part of the channels, and subsurface Sub-Antarctic Surface Waters (SSW) enter the channels and fjords at a deeper layer (30–150-m depth; Silva *et al.*, 1998).

We found a linear relationship between otolith radius and SL, similar to that described for *S. saxicola* (Laidig *et al.*, 1996), *S. rastrelliger* (Laidig and Sakuma, 1998), and *Sebastes* spp. from the North Atlantic (Penney and Evans, 1985). Our estimate of the extrusion check radius of *S. capensis* in the Patagonian fjords (10.2–16.8  $\mu\text{m}$ ) is in the range observed for other species of the Northeast Pacific, which vary from 10.5  $\mu\text{m}$  in *S. wilsoni* (Laidig *et al.*, 2004) to 16.9  $\mu\text{m}$  in *S. jordani* (Laidig and Ralston, 1995). Interestingly, species from the Northwest Pacific, particularly off Japan, show larger extrusion check radii (17.6  $\pm$  0.3  $\mu\text{m}$  in *S. thompsoni*, according to Kokita and Omori, 1998; 26.1  $\pm$  1.4  $\mu\text{m}$  in *S. inermis*, according to Plaza *et al.*, 2001), probably because larvae from the latter species extrude at larger sizes than eastern Pacific species.

Larval *S. capensis* showed growth rates during spring (0.148  $\text{mm d}^{-1}$ , Figure 4a) within the range reported for other *Sebastes* species. The growth rate observed during the first 40 days in *S. saxicola* was 0.125  $\text{mm d}^{-1}$  (Laidig *et al.*, 1996), Sakuma and Laidig (1995) reported growth rates of 0.135  $\text{mm d}^{-1}$  for *S. goodie*, and Laidig *et al.* (1991) documented a growth rate for *S. jordani* in its first 20 days of approximately 0.165  $\text{mm d}^{-1}$ . Older larvae grow faster. Laidig *et al.* (1996), Kokita and Omori (1998), and Plaza *et al.* (2003) observed that growth rates of *S. saxicola*, *S. thompsoni*, and *S. inermis*, respectively, increased from 0.32 to 0.47  $\text{mm d}^{-1}$  in larvae and juveniles. Whether or not this increase in growth rate with age also occurs in *S. capensis* is unknown. However, we suspect that the attainment of faster growth by older larvae is probably associated with coastward migration and later settlement, as described for other *Sebastes* species.

In this study, older larvae were found in water of higher salinity, usually to seaward of the channels and mostly within the upper 50 m. Other *Sebastes* spp. larvae found offshore also concentrate in the mixed layer above the pycnocline (Yoklavich *et al.*, 1996; Sakuma *et al.*, 1999; Drinkwater *et al.*, 2000; Moser and Pommeranz, 2000). Several oceanographic processes have been proposed as potential mechanisms to retain larvae adjacent to their original coastal area: upwelling shadows (Wing *et al.*, 1998), stratified Taylor columns (Dower and Perry, 2001) and frontal displacements (Bjorkstedt *et al.*, 2002). *Sebastes* larvae have also been observed associated with drifting seaweed, which they apparently use as a shelter against predation (Kokita and Omori, 1998). Their return to a nearshore juvenile habitat takes place when they attain a larval size of 30–90 mm SL (Wing *et al.*, 1998). We found very few post-flexion larvae in the inner part of the channels, and those we did catch were principally in deeper water. Therefore, it is possible that either those few larvae were retained within the channels as they developed, or they were transported into the channels by means of the deeper, more saline, east-moving layer, which is part of the general estuarine circulation described for the entire region by Silva *et al.* (1998).

The changes in distribution observed in larval *S. capensis* suggest that different habitats are being occupied during the early life stages. This change in ontogenetic larval distribution is probably similar in essence to the changes reported for other *Sebastes* species around the world. However, this similarity is intriguing given that the environmental conditions in the different areas are so different, varying from warmer coastal waters of the tropics (Rodríguez-Graña and Castro, 2003) to high-latitude areas such as the Chilean fjords and channels (this study). The evolutionary forces that drive such habitat change during early ontogeny, and which seem so common for a large number of even non-related taxa (i.e. decapod larvae), remain to be explained.

## Acknowledgements

We thank the officers and crew of the “Vidal Gormaz” and the scientific personnel on board for their help in the collection of the zooplankton samples. Hydrographic data were provided by N. Silva and M. Cáceres. We also thank Claudia Bustos and Cristian Chandía for their help in sorting fish larvae and copepods, respectively. During this study the first author was supported by a CONICYT scholarship for doctorate students, and funding for the study was provided by a CIMAR 8 FIRDOS (CONA) project to LRC.

## References

- Anderson, J. T. 1994. Feeding ecology and condition of larval and pelagic juvenile redfish *Sebastes* spp. *Marine Ecology Progress Series*, 104: 211–226.
- Antezana, T. 1999. Plankton in southern Chilean fjords: trends and linkages. *Scientia Marina*, 63 (Suppl. 1): 69–80.
- Balbotín, F., and Bernal, R. 1997. Distribución y abundancia del ictioplancton en la zona austral de Chile. *Ciencia y Tecnología del Mar*, 20: 55–163.
- Bernal, R., and Balbotín, F. 1999. Ictioplancton de los fiordos entre el Golfo de Penas y Estrecho de Magallanes y factores ambientales asociados. *Ciencia y Tecnología del Mar*, 22: 143–154.
- Bjorkstedt, E. P., Rosenfield, L. K., Grantham, B. A., Shkedy, Y., and Roughgarden, J. 2002. Distributions of larval rockfishes *Sebastes* spp. across nearshore fronts in a coastal upwelling region. *Marine Ecology Progress Series*, 242: 215–228.
- Boje, J. 2002. Intermingling and seasonal migrations of Greenland halibut (*Reinhardtius hippoglossoides*) populations determined from tagging studies. *Fishery Bulletin US*, 100: 414–422.
- Brown, E. D. 2002. Life history, distribution, and size structure of Pacific capelin in Prince William Sound and the northern Gulf of Alaska. *ICES Journal of Marine Science*, 59: 983–996.
- Cameron, W., and Pritchard, D. 1963. Estuaries. *In* The Sea, vol. 2, pp. 306–324. Ed. by M. N. Hill. Interscience Publishers, New York.
- Cassis, D., Muñoz, P., and Avaria, S. 2002. Temporal changes of the phytoplankton between 1993 and 1998 in a fixed station inside Aysen fjord, Chile (45°26'S 73°00'W). *Revista de Biología Marina y Oceanografía*, 37: 43–65.
- Castro, L. R., Salinas, G. R., and Hernández, E. H. 2000. Environmental influences on the winter spawning of the anchoveta *Engraulis ringens* off central Chile. *Marine Ecology Progress Series*, 197: 247–258.
- Dower, J. F., and Perry, R. I. 2001. High abundance of larval rockfish over Cobb Seamount, an isolated seamount in the Northeast Pacific. *Fisheries Oceanography*, 10: 268–274.
- Drinkwater, K., Lochman, S., Taggart, C., Thompson, K., and Frank, K. 2000. Entrainment of redfish (*Sebastes* spp.) larvae off the Scotian Shelf. *ICES Journal of Marine Science*, 57: 372–382.
- Guzmán, D., and Silva, N. 2002. Caracterización física y química y masas de agua en los canales australes de Chile entre Boca del Guafo y Golfo Elefantes (Crucero Cimar-Fiordo 4). *Ciencia y Tecnología del Mar*, 25: 45–76.
- Hernández-Miranda, E., Palma, A. T., and Ojeda, F. P. 2003. Larval fish assemblages in nearshore coastal waters off central Chile: temporal and spatial patterns. *Estuarine, Coastal and Shelf Science*, 56: 1075–1092.
- Kokita, T., and Omori, M. 1998. Early life history traits of the gold-eye rockfish, *Sebastes thompsoni*, in relation to successful utilization of drifting seaweed. *Marine Biology*, 132: 579–589.
- Kong, I. 1985. Revisión de las especies chilenas de *Sebastes* (Osteichthyes, Scorpaeniformes, Scorpaenidae). *Estudios Oceanológicos*, 4: 21–75.
- Laidig, T. E., and Ralston, S. 1995. The potential use of otolith characters in identifying larval rockfish (*Sebastes* spp.). *Fishery Bulletin US*, 93: 166–171.
- Laidig, T. E., Ralston, S., and Bence, J. R. 1991. Dynamics of growth in the early life history of shortbelly rockfish, *Sebastes jordani*. *Fishery Bulletin US*, 89: 611–621.
- Laidig, T. E., and Sakuma, K. M. 1998. Description of pelagic larval and juvenile grass rockfish, *Sebastes rastrelliger* (family Scorpaenidae), with an examination of age and growth. *Fishery Bulletin US*, 96: 788–796.
- Laidig, T. E., Sakuma, K. M., and Nishimoto, M. M. 1996. Description of pelagic larval and juvenile striptail rockfish, *Sebastes saxicola* (family Scorpaenidae) with an examination of larval growth. *Fishery Bulletin US*, 94: 289–299.
- Laidig, T. E., Sakuma, K. M., and Stannard, J. A. 2004. Description and growth of larval and pelagic pygmy rockfish (*Sebastes wilsoni*) (family Sebastidae). *Fishery Bulletin US*, 102: 452–463.
- Loeb, V. J., and Rojas, O. 1988. Interannual variation of ichthyoplankton composition and abundance relations off northern Chile, 1964–83. *Fishery Bulletin US*, 86: 1–24.
- Lopes, P. C. 1979. Eggs and larvae of *Maurollicus muelleri* (Gonostomatidae) and other fish eggs and larvae from two fjords in western Norway. *Sarsia*, 64: 199–210.
- Marteinsdottir, G., Gunnarsson, B., and Suthers, I. M. 2000. Spatial variation in hatch date distributions and origin of pelagic juvenile cod in Icelandic waters. *ICES Journal of Marine Science*, 57: 1182–1195.
- Moser, H. G., and Pommeranz, T. 2000. Vertical distribution of eggs and larvae of northern anchovy, *Engraulis mordax*, and of the larvae of associated fishes at two sites in the southern California Bight. *Fishery Bulletin US*, 97: 920–943.
- Nelson, J. S. 1994. *Fishes of the World*, 3rd edn. Wiley. 600 pp.
- Palma, S., and Silva, N. 2004. Distribution of siphonophores, chaetognaths, euphausiids and oceanographic conditions in the fjords and channels of southern Chile. *Deep-Sea Research II*, 51: 513–535.
- Penney, R. W., and Evans, G. T. 1985. Growth histories of larval redfish (*Sebastes* spp.) on an offshore Atlantic fishing bank determined by otolith increment analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 42: 1452–1464.
- Plaza, G., Katayama, S., and Omori, M. 2001. Otolith microstructure of the black rockfish, *Sebastes inermis*. *Marine Biology*, 139: 797–805.
- Plaza, G., Katayama, S., and Omori, M. 2003. Timing of parturition, planktonic duration, and settlement patterns of the black rockfish, *Sebastes inermis*. *Environmental Biology of Fishes*, 68: 229–239.

- Rodríguez-Graña, L., and Castro, L. R. 2003. Ichthyoplankton distribution off the Peninsula de Mejillones, Chile (23° S, 71° W), under variable hydrographic conditions during the austral summer and winter of the 1997 *El Niño*. *Hidrobiología*, 501: 59–73.
- Sabatés, A., and Olivar, M.-P. 1990. Early development and spawning of *Sebastes capensis* in the Southeast Atlantic. *Marine Biology*, 107: 389–395.
- Sakuma, K. M., and Laidig, T. E. 1995. Description of larval and pelagic juvenile chilipepper, *Sebastes goodie* (family Scorpaenidae), with an examination of larval growth. *Fishery Bulletin US*, 93: 721–731.
- Sakuma, K. M., Ralston, S., and Roberts, D. A. 1999. Diel vertical distribution of postflexion larval *Citharichthys* spp. and *Sebastes* spp. off central California. *Fisheries Oceanography*, 8: 68–76.
- SERNAPESCA. 2002. Anuario Estadístico de Pesca. Subsecretaría de Pesca, Ministerio de Economía, Fomento y Reconstrucción, República de Chile. 140 pp.
- Silva, N., Calvete, C., and Sievers, H. 1998. Masas de agua y circulación general para algunos canales australes entre Puerto Montt y Laguna San Rafael, Chile (Crucero Cimar-Fiordo 1). *Ciencia y Tecnología del Mar*, 20: 17–48.
- Strub, P. T., Mesias, J. M., Montecino, V., Rutllant, J., and Salinas, S. 1998. Coastal ocean circulation off western South America. *In* *The Sea* 11, pp. 273–313. Ed. by A. R. Robinson, and K. H. Brink. John Wiley, New York.
- Toro, J. D., Paredes, P. I., Villagra, J. D., and Senn, C. M. 1999. Seasonal variation in the phytoplankton community, seston and environmental variables during a two-year period and oyster growth at two maricultures sites, southern Chile. *Marine Ecology*, 20: 63–89.
- Valle-Levinson, A., Jara, F., Molinet, C., and Soto, D. 2001. Observations of intratidal variability of flows over a sill-contraction combination in a Chilean fjord. *Journal of Geophysical Research*, 106(C4): 7051–7064.
- Wing, S. R., Botsford, L. W., Ralston, S. V., and Largier, J. L. 1998. Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system. *Limnology and Oceanography*, 43: 1710–1721.
- Woodbury, D., and Ralston, S. 1991. Interannual variation in growth rates and back-calculated birthdate distributions of pelagic juvenile rockfishes (*Sebastes* spp.) off the central California coast. *Fishery Bulletin US*, 89: 523–533.
- Yoklavich, M. M., and Boehlert, G. W. 1987. Daily growth increments in otoliths of juvenile black rockfish, *Sebastes melanops*: an evaluation of autoradiography as a new method of validation. *Fishery Bulletin US*, 85: 826–832.
- Yoklavich, M. M., Loeb, V. J., Nishimoto, M., and Daly, B. 1996. Nearshore assemblages of larval rockfishes and their physical environment off central California during an extended El Niño event 1991–1993. *Fishery Bulletin US*, 94: 766–782.