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Short communication

Spawning and larval survival of the Chilean hake *Merluccius gayi* under later summer conditions in the Gulf of Arauco, central Chile

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Abstract

Five cruises were conducted in the shallow embayment, Gulf of Arauco, central Chile to study abundance and survival of the early stages of Chilean hake, *Merluccius gayi* during the late summer reproductive season (austral summer–autumn transition period). High densities of recently spawned eggs (>3000 eggs × 1000 m^{-3}) and preflexion larvae (>1000 larvae × 1000 m^{-3}) were observed during March 1996. In four of five cruises, larval size distribution moved progressively to larger larvae; however, small-size, recently hatched larvae were dominant (65%) in the last cruise. The change in larval size coincided with intrusion of poorly oxygenated waters (<1 mL L^{-1}) in the Gulf as a result of wind forcing and upwelling events. Cohort mortality estimations vary between −0.086 and −0.141 day^{-1} (i.e., daily losses of 8–11%). The mean mortality rate for the entire period calculated for the eggs and larval stages combined was $Z = -0.065$ day^{-1}, corresponding to a daily loss of 6%. A 1 year monthly time series (December 1999–February 2001) of a coastal station showed also presence of eggs and larval hake during austral mid-spring and late summer and extremely high abundance of preflexion larvae (>8000 larvae × 1000 m^{-3}) in March 2000. The overall results from this study suggest that the Gulf of Arauco is used by *M. gayi* as a spawning and nursery area at the end of the upwelling season when environmental characteristics, such as food availability and nearshore retention are favourable for larval survival.

Keywords: Spawning; Mortality; *Merluccius gayi*; Eggs; Larvae; Upwelling; Humboldt current

1. Introduction

Off the coasts of Peru and Chile, the hake *Merluccius gayi* is a commercially and ecologically important species (Arancibia, 1992) with an annual average catch of 72,500 t between 1989 and 1999 in Chilean waters (SERNAPESCA, 2001). Adults are distributed across the continental shelf and shelf break between 50 and 500 m deep, and are associated with the cold, poorly oxygenated mass waters of the Equatorial Subsurface Water (ESSW) (Avilés et al., 1979; Arancibia, 1992).

Hake spawning occurs in Chile between Antofagasta (23°S) and Puerto Montt (42°S). One of its most important spawning areas is located off Talcahuano, central Chile (Bernal et al., 1997; Vargas and Castro, 2001) (Fig. 1). This area is characterised by a complex topography: a widening of the continental shelf (from ca. 5–10 km in the northern area to ca. 60 km in this zone), and the presence of two important submarine canyons (Sobarzo et al., 2001), as well as several different size embayments (Gulf of Arauco, Concepción Bay) utilised as spawning and nursery areas by epipelagic and mesopelagic species (Castillo et al., 1991; Castro et al., 1993; Landaeta and Castro, 2002).

Off the Talcahuano area, even though hakes spawn throughout most of the year (Balbontín and Fischer, 1981), two main spawning seasons have been identified: a longer season during the austral late-winter and spring (August

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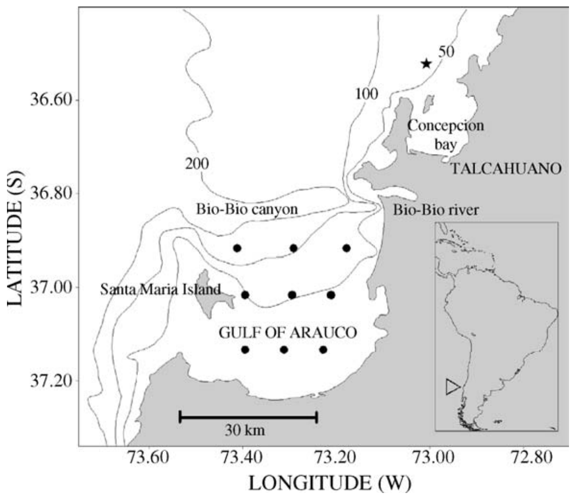

Fig. 1. The Gulf of Arauco, central Chile, indicating the location of the oceanographic stations sampled during March 1996 (black dots). Star shows a coastal station sampled monthly between December 1999 and February 2001. The 50, 100 and 200 m bathymetric contours are shown.

through November) and a shorter spawning season during late summer (March) (Payá et al., 1993; Cerna and Oyarzún, 1998; Alarcón et al., 2004). In the late winter–spring season, the hake spawns about 50–60 km offshore in midwater, associated with upwelling fronts (Vargas and Castro, 2001); subsequently, eggs and preflexion larvae are transported in the subsurface currents to the coast where it has been proposed that settlement occurs (Avilés et al., 1979; Bernal et al., 1997; Vargas et al., 1997). The spawning location during late summer changes: adults migrate from the nearby shelf-break area towards shallower waters (Avilés et al., 1979; Arancibia, 1992) where they finally spawn (Bernal et al., 1997). Although hake constitutes an important demersal fishery off Talcahuano, there is little information on its early-life history, and especially for the late summer spawning period. Reports on aspects such as potential spawning inside the bay, egg and larval transport, and mortality rates during this secondary spawning season do not exist to date.

In the present study, we report the presence of abundant early eggs and larval hake inside the Gulf of Arauco, the largest embayment in the Talcahuano area. Additionally, a 1 year time series of zooplankton samples collected nearshore suggest that during the late summer spawning season, hake spawning may occur nearshore and even inside the bays. Also, we estimated mortality rates (or potential egg and larval loss) during March 1996, when large primary production exportation occurs from the coast in the surface Ekman layer due to the strong, upwelling favourable south winds. This is the first evidence that the Gulf of Arauco, an important spawning zone during late winter and spring for many small pelagic commercially important species (sardines and anchovies), also plays an important role as a spawning and nursery zone for hake during late summer.

2. Methods

2.1. Study area

The Gulf of Arauco (37°10′S, 36°45′W) is a 500 km^2 shallow embayment in central Chile (Fig. 1). It is limited to the west by the Santa María Island and to the north by the Bio–Bio Canyon that extends through the continental shelf. This area has a seasonal influence of coastal upwelling, mainly during the austral spring and summer when winds blow from the south and southwest (Arcos and Navarro, 1986). During the austral winter (May–July) north winds blow and during transition periods (April and August) north–south wind alternation occurs (Sobarzo et al., 2001). During the upwelling season, isopycnals slope upward toward the coast and a semi-permanent eddy over the canyon is noticeable (Djurfeldt, 1989). Additionally, a persistent subsurface, nutrient rich, poleward flow into the Gulf has been observed; this along with a double gyre that causes flow divergence in the southern end of the gulf, may induce the high primary production of the system (Daneri et al., 2000; Valle-Levinson et al., 2003).

2.2. Field and laboratory work

Five cruises were carried out to a nine station grid in the Gulf of Arauco, on March 5, 14, 19, 22 and 27 of 1996 (Fig. 1). Oblique ichthyoplankton tows were carried out from 40 m deep to surface using a standard Bongo net (330 μm mesh, 0.6 m diameter) equipped with a flowmeter. The samples were preserved on board in 4% formaldehyde. Oceanographic data (temperature, conductivity, dissolved oxygen) were obtained using a CTD Sensordata SD2003, and water samples from eight depths (surface, 5, 10, 15, 20, 30, 40 and 60 m) were collected for salinity determinations. Hourly wind data (speed and direction) were obtained from the Carriel Sur Airport, Concepción (36°46′S; 73°04′W). Sea Surface Temperature images (NOAA 14) were obtained for the entire sampling period. Current meter data and the general circulation pattern in the Gulf of Arauco throughout the sampling season have been described elsewhere (Parada et al., 2001).

All zooplankton samples from the five cruises were sorted, and all eggs and larvae of *M. gayi* were identified, separated and counted. Egg and larval densities were expressed as individuals per 1000 m^3. Eggs were staged in three-age classes according to Fischer (1959): stages I–III (undeveloped embryo), stage IV (early embryo) and stage V (prehatching). Standard length (SL) of undamaged larvae ($N = 799$) was measured to the nearest 0.1 mm with a calibrated ocular micrometer fitted to a Nikon stereomicroscope, and corrected for shrinkage according to algorithms proposed by Fowler and Smith (1983) for silver hake larvae. Kolmogorov–Smirnov tests were used to compare the frequency distributions of size for hake larvae between cruises.

To analyse the temporal pattern of spawning of Chilean hake in the coastal area, a nearshore station (Fig. 1) was sampled monthly between December 1999 and February 2001 following the same procedure used in the Gulf of Arauco.

2.3. Larval growth and mortality rates

A lineal growth model was utilised to estimate the age of *M. gayi* larvae (SL = 2.5 + 0.15 age). In the model, the intercept was set at 2.5 mm, which corresponds to the smallest larval length reported for this species in literature (Vargas and Castro, 2001) as well as the smallest larvae measured in this study. A value of 0.15 was utilised as the model's slope, which corresponds with larval growth rates estimations (mm day^{-1}) from otolith analysis for several hake species (*M. productus*, 0.16 mm day^{-1}, Bailey, 1982; 0.15 mm day^{-1}, Butler and Nishimoto, 1997; 0.14–0.28 mm day^{-1}, Cass-Calay, 1997; *M. bilinearis*, 0.17–0.18 mm day^{-1}, Jeffrey and Taggart, 2000; *M. hubbsi*, 0.16 mm day^{-1}, Brown et al., 2004) as well as for *M. gayi* larval growth rates estimated for the 1999 winter (0.14 mm day^{-1}) in the same area (Landaeta unpublished data).

Daily cohort mortality rates were estimated utilising the converted length frequency method (Essig and Cole, 1986). The instantaneous mortality rate (Z) was estimated for four daily cohorts from a negative exponential model of decline: $N_t = \mathrm{No}\, e^{-Zt}$, where N_t is the number of larvae at age-class t in days, No is the number of eggs. Larvae belonging to any of those four cohorts were identified by back-calculating their spawning dates from their egg stages and larval age at the date of capture. ANCOVA (multiple-slope test, Zar, 1999) was utilised to determine whether differences in mortality rate existed between daily cohorts estimates. Also, a mean mortality rate during March 1996 was calculated from the egg and larvae pooled-age distribution for the five sampled dates.

3. Results

3.1. Wind and oceanographic conditions

The wind regime during 1996 followed a seasonal pattern of moderate (~10 m s^{-1}), south winds from austral summer through mid-autumn, changing to strong winds (15–20 m s^{-1}) from the northern quadrant during the austral winter. Southwest winds were dominant throughout March 1996; however, north-wind events occurred sporadically between days 11–13, 19–20, 23–24 and 29–30. A strong thermocline and well-defined pycnoclines and oxyclines between 10 and 25 m occurred during each cruise. The upper layer reached values between 13 and 15 °C and was well-oxygenated (>6 mL L^{-1}), except for March 5, when oxygen concentrations only reached 2 mL L^{-1}. Below 25 m depth, the water column was colder (11 °C) and less oxygenated (<3 mL L^{-1}) than the upper layer. During the first (March 5) and fifth (March 27) cruises, very low-oxygen concentrations occurred below 40 m (<1 mL L^{-1}), characteristic of the Equatorial Subsurface Water (ESSW) that flows poleward and is frequently located underneath the Humboldt Current (Sobarzo et al., 2001). The presence of this cold, low-oxygen content water nearshore and inside the Gulf combined with south winds are indicative of the upwelling events that occurred during March 1996.

3.2. Egg and larval abundance

A total of 789 eggs and 1134 larvae was collected during March 1996 in the Gulf of Arauco. Average densities of early-life stages of the Chilean hake during the five cruises varied by more than an order of magnitude, ranging between 16–619 eggs × 1000 m^{-3} and 49–617 larvae × 1000 m^{-3} (Table 1). Higher abundance of total eggs was observed in the first (March 5) and third (March 19) cruises, reaching values of 804 and 3576 eggs × 1000 m^{-3}, respectively (Table 1). Eggs were located mainly in the middle area of the Gulf, in the vicinity of Santa María Island, and associated with bottom depths deeper than 50 m. Most eggs (>80%) for all the cruises were recently spawned (stages I–III), indicating that Gulf of Arauco is an important spawning zone for the Chilean hake during its second reproductive season.

Larval densities showed high variations in number inside the Gulf of Arauco. Larvae were abundant during the first (March 5) and last (March 27) (>1000 larvae × 1000 m^{-3}) (Table 1). Maximum density occurred at the Gulf entrance during the first cruise and in its southern end in the following weeks. Larval density higher than 500 × 1000 m^{-3} occurred in several areas of the Gulf at the end of March.

Table 1
Summary statistics for collections of chilean hake eggs (total and by development stage) and larvae in the Golfo de Arauco during March 1996

	Sampling date				
	5 March	14 March	19 March	22 March	27 March
No. of samples	9	9	9	9	8
Total eggs					
Mean	353.8	82.8	618.5	49.5	15.9
Max	804.0	188.4	3576.0	106.7	19.9
Stages I–III					
Mean	274.1	98.3	866.4	42.9	13.5
Max	593.8	150.7	3160.7	81.3	14.9
Stage IV					
Mean	79.7	25.9	90.9	9.3	5.0
Max	229.7	37.7	239.3	7.2	5.0
Stage V					
Mean	–	–	45.5	14.8	–
Max	–	–	176.0	20.3	–
Larvae					
Mean	616.8	84.5	119.5	49.4	340.0
Max	1093.3	339.0	335.8	114.1	1007.4

Densities are given in ind × 1000 m^{-3}.

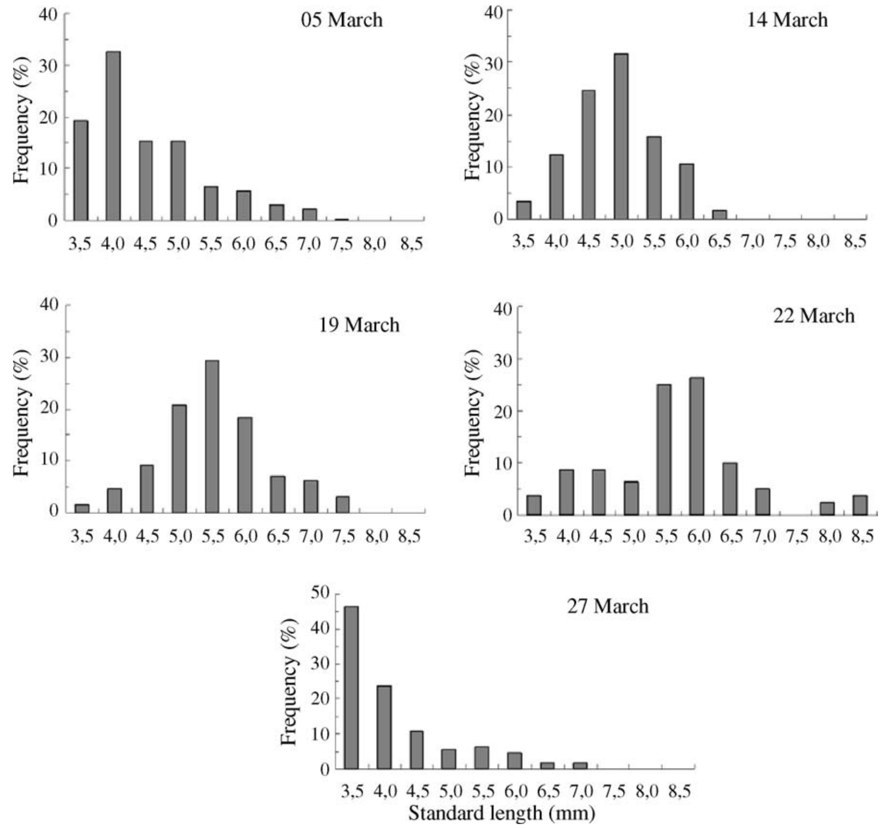

Fig. 2. Larval size distribution of Chilean hake during five cruises in the Gulf of Arauco, central Chile in March 1996.

3.3. Larval size distributions

All larvae collected were in preflexion stage. Larval hake size varied between 2.5 and 8.9 mm SL during the five cruises (Fig. 2). During the first cruise, the larval size mode was 3.5 mm. In four of five cruises, larval sizes moved progressively from smaller (mode = 3.5 mm SL in March 5) to larger sizes (modes: 4.7 mm in March 14, to 4.9 mm in March 19, and to 5.2 mm SL in March 22). However, in the last cruise (March 27) when a strong upwelling event occurred, no larvae larger than 7.5 mm SL were observed in the samples, and younger larvae (<4.5 mm SL) represented more than 65% of total hake early stages (Fig. 2). Comparing the size structure for the five cruises with the Kolmogorov–Smirnov test, all combinations were significantly different ($P < 0.01$).

3.4. Mortality rates

Individual cohort mortality rates were estimated for hake larvae originated from eggs occurring at stages I–III, and IV and V for March 5 and 14 (Table 2). Accordingly, we estimated cohort mortality rates for daily cohorts spawned on March 3, 5, 12 and 14. Instantaneous cohort mortality rates (egg and larvae included) ranged between −0.141 and −0.086 day^{-1}, and were not different among cohorts (ANCOVA; $P > 0.1$; Table 2). The mean mortality rate estimated for the entire period and calculated for all eggs and larval stages pooled was $Z = -0.065$ (Fig. 3), which corresponds to a 6% daily loss.

3.5. Time series

In the nearshore station, hake eggs were found during February–March and November, varying from 13 to 546 eggs × 1000 m^{-3} with a maximum density in November (Fig. 4). Similarly to eggs, larval *M. gayi* were collected during austral mid-spring and late summer months. An extremely high value of preflexion larvae was observed during March 2000 (8042 larvae × 1000 m^{-3}) (Fig. 4), confirming the presence of a secondary spawning event of this species in nearshore waters.

Table 2
Spawning date; egg state, growth rate, mortality equation, R^2, and daily cohort loss for different cohorts spawned during March 1996 in the Golfo de Arauco; *t* is time in days

Spawning date 1996	Egg stage	Mortality equation	R^2	Daily loss (%)
3 March	Stages I–III	$N_t = 97\,e^{-0.141t}$	0.45	13
5 March	Stage IV	$N_t = 68\,e^{-0.120t}$	0.63	11
12 March	Stages I–III	$N_t = 35\,e^{-0.086t}$	0.22	8
14 March	Stage IV	$N_t = 20\,e^{-0.113t}$	0.58	11

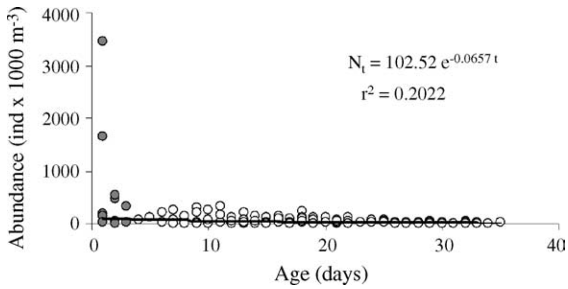

Fig. 3. Mean age frequency distribution for the entire sampling season, showing the mortality curve for combined egg (grey dots) and larval (white dots) of the Chilean hake during March 1996.

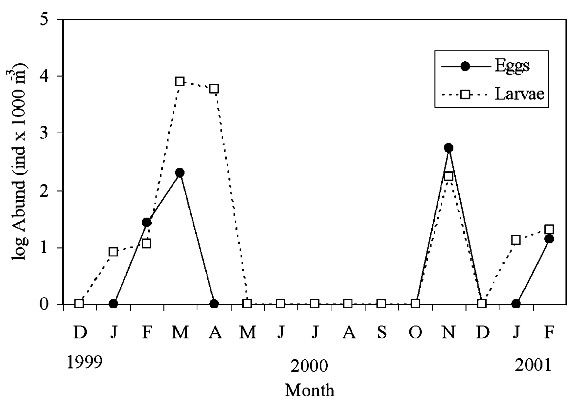

Fig. 4. Logarithmical abundance of total eggs and larvae collected in a coastal station between December 1999 and February 2001.

4. Discussion

Equator-facing bays adjacent to eastern boundary currents, such as Gulf of Arauco, are areas of high productivity and retention of holo and meroplanktonic larvae (Castro et al., 1993; Wing et al., 1998). Along central Chile, the highest primary production values have been observed in the Gulf of Arauco (Daneri et al., 2000). This gulf is a spawning and nursery area for several pelagic species, such as anchoveta *Engraulis ringens* and sardine *Sardinops sagax* (Castillo et al., 1991). Our results suggest this area is also important for the hake during late austral summer.

A high abundance of recently spawned eggs (stages I–III) (>3100 eggs × 1000 m^{-3}, Table 1) and small larvae (>600 ind × 1000 m^{-3}) was found inside the Gulf during March 1996. For the same year, Vargas and Castro (2001) found early-life stages of hake over the shelf but no eggs or larvae inside the Gulf during spring, which is the main spawning season. The egg density observed in March 1996 is two orders of magnitude higher than in spring 1996 (∼50 eggs × 1000 m^{-3}; Vargas and Castro, 2001). Previous studies on hake spawning in the Talcahuano area have reported that spawning occurs preferentially over the shelf or at the shelf-break zone during spring (Avilés et al., 1979; Bernal et al., 1997; Vargas et al., 1997; Vargas and Castro, 2001), which is similar to other *Merluccius* species worldwide (Álvarez et al., 2001; Olivar et al., 1988, 2003). Therefore, our results on

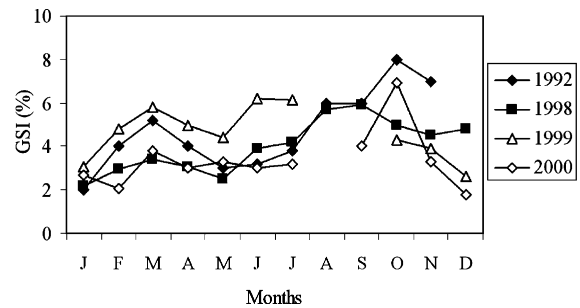

Fig. 5. Monthly trend in the Gonadosomatic index (GSI) calculated for female Chilean hake captured off Talcahuano area, central Chile during 1992 (modified from Cerna and Oyarzún, 1998) and 1998–2000 (modified from Alarcón et al., 2004).

hake spawning off Talcahuano confirm two spawning seasons (mid-spring and late summer) estimated by Gonadosomatic Index data (Fig. 5) and suggest a change in spawning locations between seasons from offshore in spring to inshore waters or in the Gulf in late summer. An alternative hypothesis to explain high egg and young larvae density within the Gulf is their potentially faster transport from the shelf break via the subsurface water entering the Gulf during the upwelling season. This transport mechanism has been proposed for hake larvae during austral spring based on their increase in size distribution between the shelf break and the coast as well as their subsurface distribution (Vargas et al., 1997; Vargas and Castro, 2001). This hypothesis is also in agreement with observations of adult hake that preferably reside in the ESSW during their reproductive season (Avilés et al., 1979; Arancibia, 1992). In our study, ESSW was observed throughout the sampling period in the layer below the pycnocline, and even near the surface during the first and last sampling date. Moreover, higher abundance of recently hatched and smaller larvae occurred during the first (March 5) and last (March 27) cruises (Fig. 2), which also coincided with strong south-westerly, upwelling inducing winds and with subsurface flow data collected from current meters during this study at the mouth during this study (Parada et al., 2001). However, since this same transport process has been observed during spring when eggs have not been abundantly observed inside the Gulf and when a wind alternation also occurs (Vargas and Castro, 2001), the transport hypothesis alone does not fully account for the higher egg abundance inside the Gulf in late summer. For this high egg abundance to occur inside the Gulf in late summer, a combination of a closer-to-shore spawning (as occurred in the Valparaiso area, 32°S, Bernal et al., 1997, and observed in the coastal time series, Fig. 4) and subsequent subsurface transport is proposed.

Chilean hake larvae showed a modal progression from yolk-sac larvae to 4 mm SL, inside the Gulf between March 5 and 22 (Fig. 2). This result may indicate the maintenance of a similar sized group of early larval stages of hake in the Gulf for at least 2 weeks (i.e., growing at rate of 0.15 mm day^{-1}). This estimation of potential retention time is within the range of residence time for recently upwelled water inside the Gulf (21 days), as proposed by Parada et al. (2001) for the same sampling period. For this fluctuating wind season, alternating circulation patterns in the Gulf have been observed. During strong south (north) winds, the surface and subsurface layer moves anticlockwise (clockwise) and the main outflow from the Gulf occurs at the eastern (western) flank. During transition winds, a surface layer moves anticlockwise and the subsurface in a clockwise direction. Accordingly, retention of the hake's early-life stages in the Gulf may have occurred for several weeks considering that during the study alternating winds occurred.

Early stages of the hake collected in the Gulf of Arauco experience a daily cohort loss estimated between 8 and 13% (Table 2). Similarly, mean loss (mortality) rates estimated for the entire period (pooled-age frequency distributions) reached $Z = -0.065$ (6% daily). These estimated cohort and mean loss rates (Fig. 5) were lower than the patchiness-based mortality rates previously calculated for larvae captured in the Gulf and in adjacent areas during early spring 1991 (0.098–0.382 day^{-1} for larvae 4–11 mm SL, which correspond to daily losses between 9 and 32%) (Vargas et al., 1996), but they are within the upper range for other demersal spawning fish in other environments (Campana et al., 1989; Horne et al., 1999; Anderson and Rose, 2001). Compared with other species in the same upwelling system, our estimates are lower than the daily cohort mortality rates estimated for egg and larval anchoveta during the 1995 and 1996 winters (9–52 and 25–35% daily, respectively; Castro and Hernández, 2000).

Transport out of benign nursery zones may reduce their survival chances (Bailey, 1981). During our study, food supply did not seem to be limiting since spawning still occurred during the highly productive upwelling season in the area (Daneri et al., 2000) and also given the hake is capable of capturing a wide food-size range under normal field conditions (Valenzuela et al., 1996; Balbontín et al., 1997; Cass-Calay, 2003). Transport out of the Gulf may be a source of egg and larval loss from the system. However, the alternation of winds and circulation in the Gulf in our study may have reduced the exportation of early-life stages and thus may have lowered our cohort and mean loss mortality estimations. Therefore, the relatively benign feeding conditions in the area and the decreased chances of exportation from the Gulf (when compared with the season of stronger south winds in early summer) may be favourable for survival of the young Chilean hake *M. gayi* in the area in late summer.

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