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Seasonal and annual variation in Chilean hake *Merluccius gayi* spawning locations and egg size off central Chile

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ABSTRACT

Variability in Chilean hake reproductive tactics off central Chile was assessed by analyzing ichthyoplankton samples from nine oceanographic cruises (1996–2005) and through experimental trials with early life stages (eggs, yolk-sac larvae) during the main (austral spring) and secondary (late summer–early autumn) spawning seasons. Abundant eggs in the plankton (1300–2000 eggs per 10 m²) and historical adult reproductive data showed the highest reproductive activity in austral spring, with large egg aggregations near shelf break (50–100 m depth). Large, recently spawned eggs (1.15–1.20 mm diameter) were advected nearshore by coastward subsurface flows in the spring upwelling season. Experimental trials indicated that recently hatched larvae (3.4–3.5 mm) consumed their yolk-sac (0.17–0.41 mm³) in 3–4 days at 10–12 °C; plankton sampling indicated that larval hake remained at mid-depth (50–100 m) without showing daily vertical migrations until completing their caudal fin formation (~15 mm). During the secondary reproductive peak, hake spawned nearshore, when smaller eggs (0.95–1.13 mm) and recently hatched larvae (2.2–2.6 mm notochord length) occurred in surface waters (0–10 m depth). Their relatively large yolk-sac volumes (0.57 ± 0.11 mm³) provided endogenous nourishment for at least 5 days at 10 °C, according to experiments. In the field, preflexion larvae occurred mainly in the mixed layer (0–25 m) and started ontogenetic daily vertical migrations at 7 mm. A strong decline occurred after 2002 in the adult Chilean hake biomass (estimated by hydroacoustic surveys) and body size, coinciding with variations in spawning locations (more coastward in early spring 2004 and 2005) and decline in egg size. Thus, recent variations in Chilean hake reproductive tactics may reflect an indirect effect of declines in the parental population size.

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1. Introduction

Oceanographic processes on different scales of time and space modify the success and survival of marine organisms throughout their life cycle (Cowen and Castro, 1994; Sponaugle et al., 2002) and may also modulate their phenotypes during different life stages. Parental phenotypes also influence those of the offspring (i.e., via parental effects; Bernardo, 1996). Marine fishes and other oviparous organisms select the environment in which their eggs will incubate (Roosenburg, 1996) and may vary the quality and quantity of energetic resources provided to the egg (Furuuta et al., 2002; Riveiro et al., 2004) by adjusting the egg size as a result of adaptive phenotypic plasticity (Chambers and Leggett, 1996; Bize et al., 2002; Castro et al., 2002; Einum and Fleming, 2002). The choice of the spawning location, in turn, may be associated with the selection of oceanographic processes that might, in some envi-

ronments, enhance retention (Cowen and Castro, 1994; Castro et al., 2000; Landaeta and Castro, 2006a) and, in others, enhance advection to nursery grounds (Smith and Suthers, 1999; Landaeta and Castro, 2002, 2006b). Other examples of parental influence are the change in egg size observed in both demersal and epipelagic fish spawners as the spawning season progresses (Hinckley, 1990; Llanos-Rivera and Castro, 2004) and variations in egg quality throughout the reproductive season (Riveiro et al., 2004; Castro et al., 2009). These may be influenced by variations in the size of spawning females and/or by a shift in energy allocations from reproduction to growth. Interactions between physical processes and parental effects, thus, are likely to occur during the vulnerable early life stages, thereby reducing the chances of mortality (Sponaugle et al., 2002; Green and McCormick, 2005; Trippel et al., 2005).

The Chilean hake *Merluccius gayi* is a demersal marine fish inhabiting the cold, poorly oxygenated waters of the South Pacific off South America. It supports an important industrial and artisanal fishery in Peruvian and Chilean waters but, recently and until 2009, its adult biomass and size have declined sharply (Tam et al., 2006). Off central Chile, hake spawns year-round, with the main spawning

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season from late austral winter through spring (August–November) and a second spawning peak in late summer (March–April) (Baltontín and Fischer, 1981; Cerna and Oyarzún, 1998; Alarcón et al., 2004; Landaeta and Castro, 2006a). In austral spring, when the frequency of equatorward (south) winds that favor upwelling events increase (Figueroa and Moffat, 2000), larger hake (>50 cm total length, TL) spawn about 50–60 km offshore (Bernal et al., 1997; Vargas and Castro, 2001; Alarcón et al., 2004), subsequently, eggs and preflexion stage larvae are transported to the coast through the subsurface flow that compensates the surface offshore Ekman layer during upwelling events (Vargas et al., 1997; Sobarzo and Djurfeldt, 2004). During the transitional period from south to north winds (Parada et al., 2001), which coincides with the late summer secondary spawning peak, the spawning location, oceanographic conditions, and female spawners change. In this period, small and medium-sized adults (<50 cm TL) occur and spawn in shallower waters and within gulfs and bays (Alarcón et al., 2004; Landaeta and Castro, 2006a). A strong homing behavior on the part of smaller-sized adults and the subsequent migration of larger (older) adults to deeper waters may partially explain these observed differences in size and spawning sites for adult Chilean hake in central Chile between spawning seasons; however, these topics still need to be tested.

No information is available on variability in the offspring's characteristics or the early life history between spawning seasons, although the biological characteristics of the adults and meteorologic/oceanographic conditions are known to be different in these two periods (size structure, wind direction, upwelling conditions). In the same area, the biological characteristics of recently spawned eggs (i.e., size, lipid content) and yolk-sac larvae of other species such as the anchoveta *Engraulis ringens* vary from the main winter spawning season (Castro et al., 2000) to the end of the reproductive season late in spring (Castro et al., 2004, 2009; Llanos-Rivera and Castro, 2004, 2006). This study analyzes ichthyoplankton samples collected during nine oceanographic cruises and experimental trials carried out with early life stages to assess the seasonal changes in the spawning characteristics (horizontal and vertical distribution of recently spawned eggs, vertical migration of young larvae) and the variability in early life stage features such as egg size, larval size at hatching, yolk-sac quantity, and absorption times. We also explore the relationship between spawning and early life stage characteristics and the reduced biomass and adult body length observed in the local hake population since 2002.

2. Material and methods

2.1. Field and laboratory work

A series of oceanographic cruises carried out between 1996 and 2005 were utilized to determine seasonal variations in Chilean hake spawning locations (area, depth range) and egg sizes off central Chile (Tables 1 and 2). The sampled area included the continental shelf and adjacent shelf break between 33° and 37°30'S

(Fig. 1). At each station, temperature and salinity profiles were obtained from CTD casts (Seabird SBE-19) from the surface to 300 m depth or near the bottom. Also, zooplankton samples were collected at all stations with oblique tows and an opening–closing 1 m²-mouth Tucker trawl (300 µm mesh size) or a standard Bongo net (60 cm diameter, 300 µm mesh size). In October 1996, two strata were sampled (0–40 and 40–100 m), in November 2001 and March 2002, two and four strata were sampled according to bottom depth (0–10 and 10–25 m at stations with depth <60 m; 0–50, 50–100, 100–150, and 150–250 m over the slope region). In September 2004 and 2005, oblique tows were carried out from 100 m depth to the surface with a standard Bongo net. A General Oceanics flowmeter was mounted in the net frames to estimate the filtered volume. The towing speed was 1–2 knots. Filtered tow volumes in October 1996 ranged from 69 to 706 m³/tow (mean: 348 m³/tow), in November 2001 from 17 to 589 m³/tow (mean: 142 m³/tow), in March 2002 from 12 to 217 m³/tow (mean: 96 m³/tow), in September 2004 from 7 to 200 m³/tow (mean: 48 m³/tow), and in September 2005 from 15 to 142 m³/tow (mean: 57 m³/tow). All samples were preserved onboard in 10% formalin buffered with sodium borate.

In the laboratory, all zooplankton samples from the five cruises were sorted, and all eggs and Chilean hake larvae were identified, separated, and counted. Eggs and larval densities were expressed as individuals per 10 m² for mapping the horizontal distribution; individuals per 1000 m³ were used to depict the vertical distribution of eggs and larvae. Eggs were measured and staged in three age classes according to Fischer (1959): stage 1 (undeveloped embryo), stage 2 (early embryo), and stage 3 (pre-hatching). Larvae were measured and classified according to the bending of the notochord in preflexion and postflexion stages (pooled flexion and postflexion stages). Eggs and larvae were measured to the nearest 0.01 mm with a calibrated ocular micrometer fitted to a Nikon stereomicroscope. Notochord length (NL) was measured in preflexion larvae from the tip of the mouth to the tip of the notochord; for postflexion larvae, standard length (SL) was measured from the tip of the mouth to the base of the hypurals. Flexion in larval hake occurs at ~10 mm (Santander and de Castillo, 1969). Parametric tests were used on log-transformed abundance to compare the vertical distribution of larval hake, when the assumptions of homogeneity of variance and normality were not rejected (Levene's test and Kolmogorov–Smirnov test, respectively). Otherwise, non-parametric tests were run.

We tested whether vertical migrations occurred in different size groups of hake larvae by considering the frequency of the larval weighted mean depth for day and night over the entire area (Bailey and Picquelle, 2002) using an unpaired *t*-test or Mann–Whitney *U* test, according to the normality of data.

To establish the variability of Chilean hake egg diameter along time, zooplankton samples from nearshore waters off Talcahuano were also used. These samples were collected with Bongo nets between March 1996 and March 2000 at stations with <90 m depth (Table 2). In this case, information is given for all egg stages

Table 1
Summary of the main characteristics of the surveys and range of water column conditions (temperature, salinity and density) utilized to describe the horizontal distribution of Chilean hake eggs and larvae.

Sampling period	Season	Sampled area	Number of stations	Number of samples	Number of strata	Gear	Temperature (°C)	Salinity	Density (sigma-t)
24 September–30 October 1996	Mid spring	33°–37°30'S	116	228	2	Tucker	10.7–14.4	33.2–34.8	25.4–26.6
7–12 November 2001	Mid Spring	35°–37°S	65	172	2–4	Tucker	9.3–14.3	33.4–34.6	25.1–26.7
7–12 March 2002	Late summer	35°–37°S	66	181	2–4	Tucker	10.6–18.3	32.7–34.7	24.5–26.5
21 August–19 September 2004	Late winter	34°30'–37°S	38	38	integrated	Bongo	11.1–13.0	32.0–34.2	24.0–26.2
30 August–21 September 2005	Late winter	33°–37°S	48	48	integrated	Bongo	11.0–13.5	31.0–34.6	23.5–26.5

Table 2

Statistics of egg size from different oceanographic surveys carried out off central Chile. Values in mm. SD = standard deviation; CV = coefficient of variation.

Sampling period	Mean	SD	CV	Min	Max	N	Gear
5–27 March 1996	1.015	0.027	2.648	0.950	1.075	56	BONGO
24 September–30 October 1996	1.188	0.035	2.910	1.125	1.275	113	Tucker
23–28 August 1997	1.153	0.095	8.255	1.016	1.302	34	BONGO
9–14 July 1999	1.214	0.038	3.130	1.120	1.302	55	Tucker
28 March 2000	1.128	0.058	5.175	1.042	1.276	36	BONGO
7–12 November 2001	1.208	0.032	2.626	1.125	1.275	106	Tucker
7–12 March 2002	1.109	0.052	4.670	1.000	1.250	101	Tucker
21 August–19 September 2004	1.095	0.038	3.443	1.008	1.200	87	BONGO
30 August–21 September 2005	1.066	0.046	4.287	0.960	1.200	166	BONGO

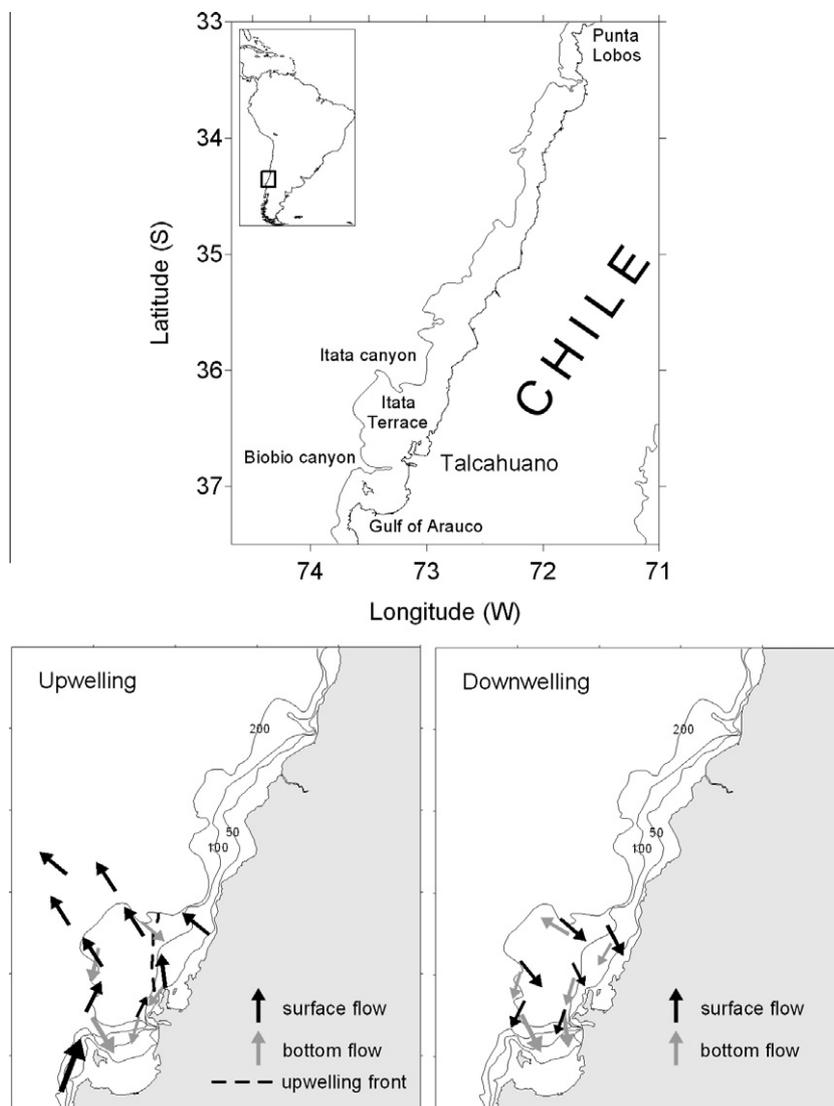


Fig. 1. Map and sketches showing the study area and the main flows during upwelling and downwelling conditions. Modified from Sobarzo and Djurfeldt (2004).

because there were no significant differences in diameter among stages for a given time period (for all cases, $p > 0.01$).

Hourly wind data (speed, direction) were obtained at the Carriel Sur Airport Meteorological Station in Talcahuano ($36^{\circ}46'S$, $73^{\circ}03'W$, 12 m over sea level) and are presented here as daily mean speeds on the v -axis (north–south direction) to indicate periods of winds favorable for upwelling events (negative values) or for downwelling and the coastal retention of surface waters (positive values).

2.2. Experimental protocol

To determine potential variations in early stage features (egg size, larval size at hatching, yolk-sac volume at hatching) between the maximum Chilean hake reproductive seasons, experimental trials were carried out in May (austral autumn) and October (spring) 2004, using early (stage 1) hake eggs collected from the field in the nearshore waters off Dichato ($36^{\circ}30'S$). Zooplankton samples were collected by oblique tows with a standard Bongo net at <1 knot ves-

sel velocity. Once on board, samples were kept in the dark in plastic jars with cool water and immediately transported to the Universidad de Concepción Marine Station in Dichato. Hake eggs were identified and measured under stereomicroscopes and individually placed in 30-mL sterile vials filled with filtered (0.45 μm), UV-sterilized seawater. Vials were transferred to one (May trials) or two (October trials) water baths maintained at 10 or 12 $^{\circ}\text{C}$, temperature at which hake eggs are normally exposed in the wild. Half of the seawater in each vial was replaced daily throughout the experiment. Vials were checked daily to determine egg and larval development stages. After hatching, individuals were measured daily for larval length and yolk-sac length and width until total absorption of yolk reserves. Yolk-sac volume was estimated considering the yolk-sac as an ellipsoid ($V = 4/3 \pi a * b^2$, where a is half the yolk-sac length and b is half the yolk-sac width). The relationship between size at hatching and egg diameter, and between yolk-sac volume per unit of larval size and size of larvae at hatching was explored by using least squares linear regressions.

3. Results

3.1. Environmental conditions

Alongshore winds (north–south direction) showed a clear seasonal pattern during 1996 and between 2001 and 2004 in central Chile (Fig. 2). Upwelling-favorable winds (south winds, negative values) were dominant during austral summer (January–March) and spring (September–December), during late autumn and winter, wind direction and intensity changed and was dominated by north winds (Fig. 2). Oceanographic cruises (gray bars in Fig. 2) were carried out when south winds dominated, i.e., when the meteorological conditions favored the occurrence of upwelling events. In October 1996, the mean intensity was -1.94 m s^{-1} (± 1.19), showing an increase in south wind intensity throughout the sampling period; similar results were obtained in November 2001 ($-1.19 \pm 1.10 \text{ m s}^{-1}$) and September 2004 ($-1.49 \pm 1.22 \text{ m s}^{-1}$). In spring 2004, strong south wind events were also recorded (up to -4.02 m s^{-1} ; Fig. 2). Finally, in March 2002, wind direction and intensity were more variable, ranging from 1.94 to -1.54 m s^{-1} (mean: $-0.28 \pm 1.48 \text{ m s}^{-1}$) when the winds switched from south to north (Fig. 2).

Environmental conditions of the water column varied among surveys. Wide range of temperature was observed during March 2002 (Table 1) when an intrusion of warm waters ($16\text{--}18^{\circ}\text{C}$) occurred in the northern area. Temperature ranges were similar during austral spring 1996 and 2001 (from 9.3 to 14.4°C), as well as during late winter 2004 and 2005 ($11.0\text{--}13.5^{\circ}\text{C}$). Salinity was lower during late winter conditions ($31\text{--}32$), associated mainly at stations located near rivers and affected by heavy rainfall (not shown). These conditions reduced seawater density during winter ($23.5\text{--}24$ units of sigma- t) compared with austral spring and late summer conditions (up to 26.7 units of sigma- t) (Table 1).

3.2. Horizontal distribution of eggs and larval *Merluccius gayi* (1996–2005)

In October 1996, eggs (stages 1–3) were aggregated in high abundances (up to 1300 eggs per 10 m^2) south of the Itata canyon and mainly near the shelf break, with a secondary area along the coast from 33°S to $34^{\circ}30'\text{S}$ (Fig. 3). In the main spawning zone, eggs in different stages of development were located in the same area; preflexion larvae were collected closer to shore, mainly over the wide continental shelf off Talcahuano (the Itata Terrace, Fig. 3). In the northern area ($<35^{\circ}\text{S}$), eggs in late development (stages 2–

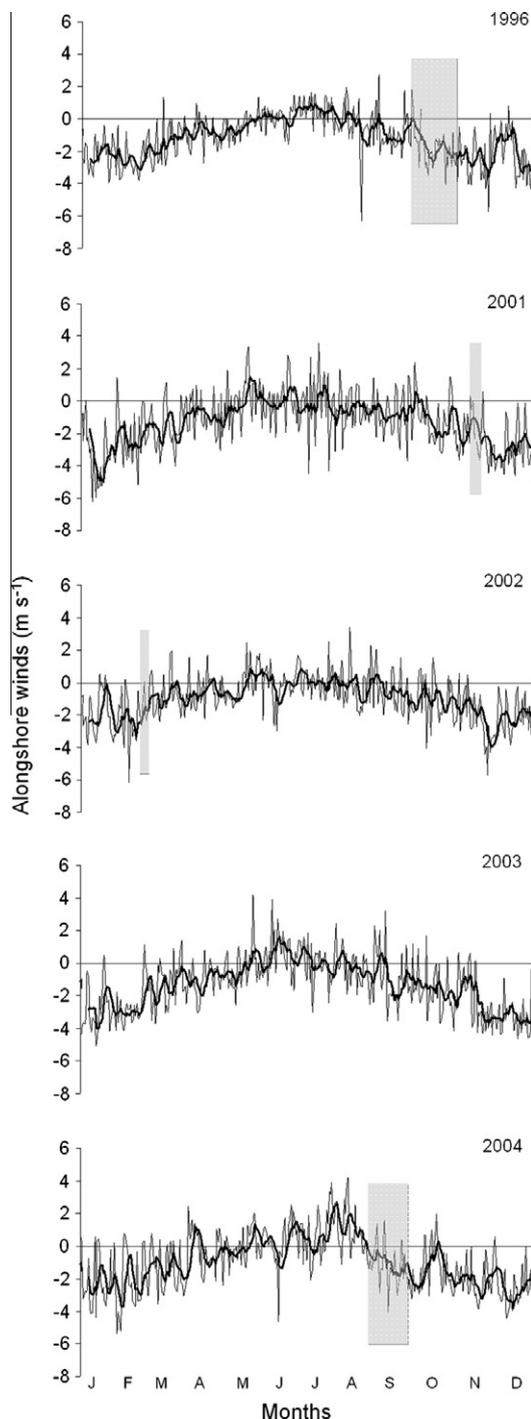


Fig. 2. Daily variability in the alongshore winds (m s^{-1}) off central Chile in 1996 and between 2001 and 2004. North winds have positive values and south winds are negative. Bold continuous line corresponds to a 7-day moving average. South winds are conducive to upwelling conditions. Gray areas correspond to ichthyoplankton sampling.

3) were collected in offshore waters and few preflexion larvae occurred over the shelf (<30 larvae per 10 m^2).

Higher spawning activity identified in November 2001 was located in the same area depicted for October 1996, i.e., south of the Itata canyon, with a peak abundance of ~ 2000 eggs per 10 m^2 (Fig. 3). Hake reproduction also occurred over the narrow continental shelf at 35°S , as revealed by the high number of stage 1 eggs ($200\text{--}450$ eggs per 10 m^2). Eggs with early embryos (stage 2) were collected mainly over the Itata Terrace and nearer the coast.

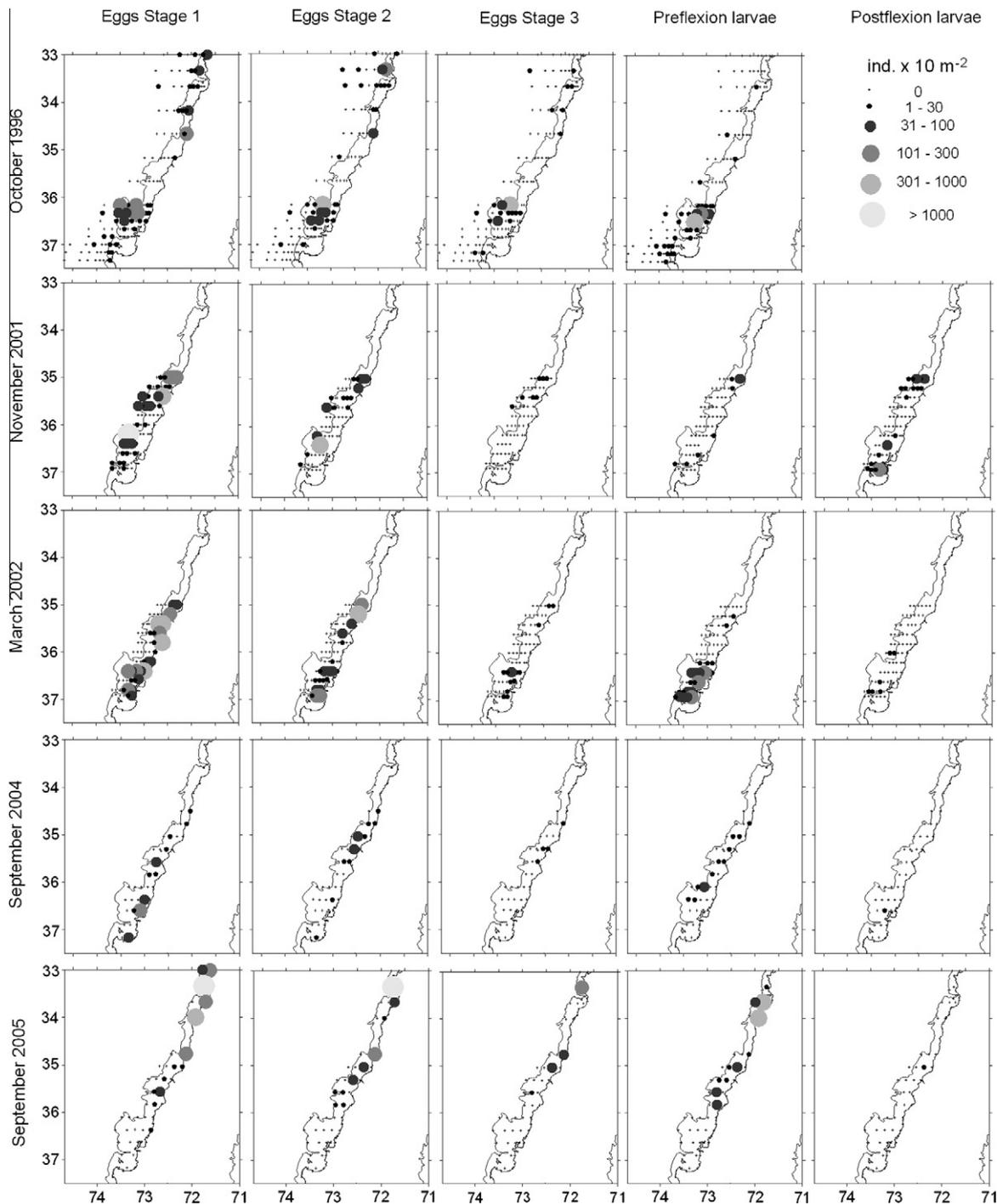


Fig. 3. Horizontal distribution of Chilean hake eggs and larvae from 1996 to 2005 off central Chile.

Preflexion and postflexion larvae were collected coastward; larger larvae were more abundant than smaller larvae, particularly in the Gulf of Arauco (102 larvae per 10 m^2 , Fig. 3).

In March 2002, spawning occurred near the coast all along the sampled area (35–37°S). Recently spawned eggs (stage 1) were abundant to the north and south of the Itata canyon (400–585 and 140–306 eggs per 10 m^2 , respectively; Fig. 3). The other embryonic stages showed a similar spatial distribution. Pre- and postflexion larvae were collected almost exclusively over the Itata Terrace. Preflexion stages were abundant (up to 236 larvae per 10 m^2) and larger larvae were found near the Itata and Biobío canyons (Fig. 3).

In September 2004 and 2005, the spawning area changed noticeably compared with previous cruises carried out during austral spring. Horizontal hake egg distributions in September 2004 were similar to those observed in March 2002, i.e., spawning occurred nearshore to the north and south of the Itata canyon. Although eggs in late development (stages 2–3) were collected mainly north of 36°S, preflexion larvae were found between 34°30' and 36°30'S, were more abundant south of the Itata canyon, and were found slightly more offshore than eggs (Fig. 3). Only one postflexion specimen was caught with the Bongo nets over the continental shelf off Talcahuano.

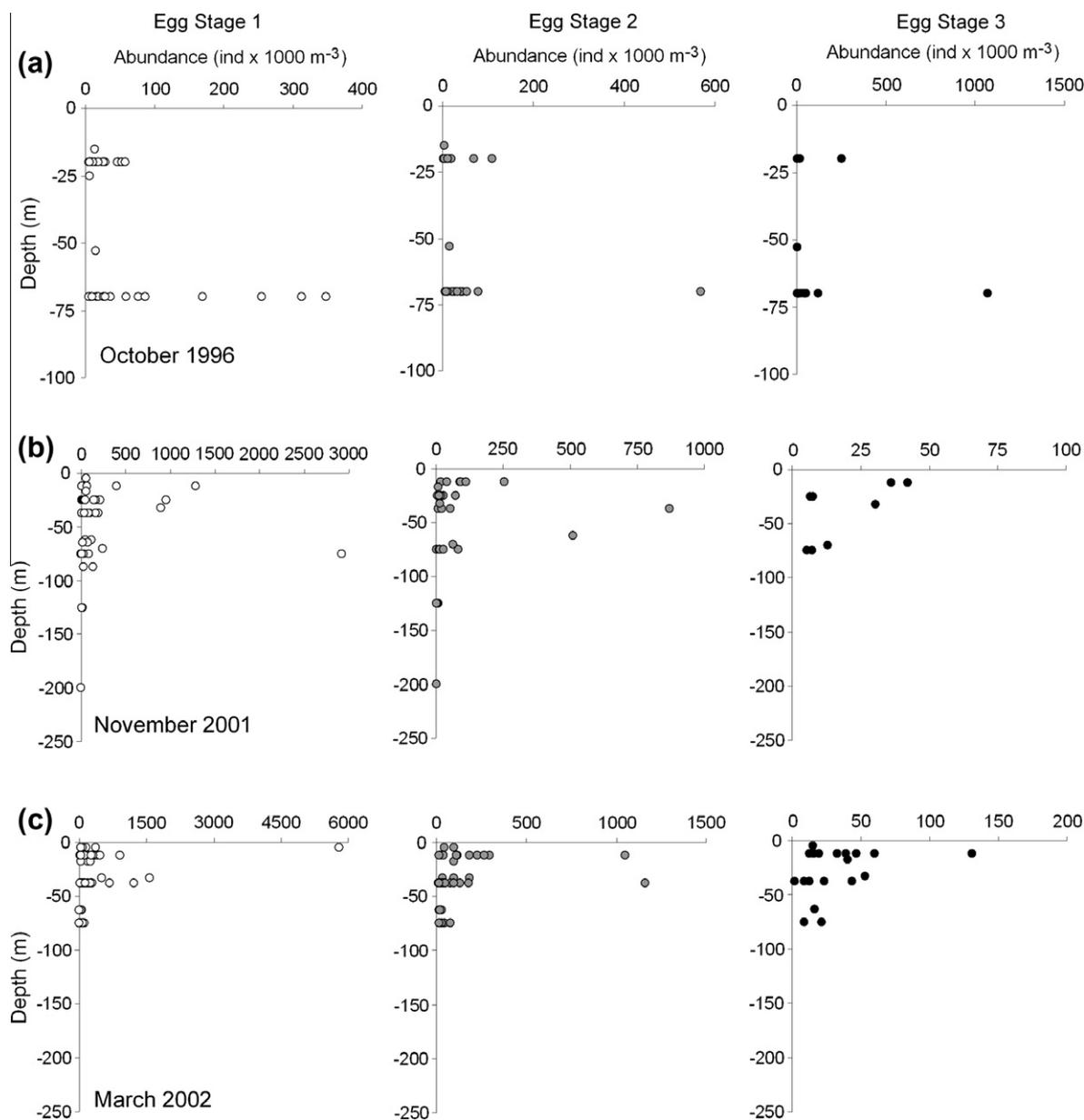


Fig. 4. Mean depth (m) of hake eggs by developmental stage in (a) October 1996, (b) November 2001 (offshore spawning) and (c) March 2002 (inshore spawning).

In September 2005, *M. gayi* spawning was detected very close to shore between 33° and 36°S. The highest abundances (1820 eggs per 10 m²) were located mainly south of Punta Lobos (for all egg stages), and no evidence of spawning or larval presence was detected over the Itata Terrace. The egg and preflexion larval distribution were similar but contrasted strongly with the distribution observed in October 1996 (Fig. 3). Differences between 2004 and 2005 may be partially due to differences in coverage during those cruises. Northern part of the area was not covered in September 2004, and that was the area with the highest eggs abundance in 2005.

3.3. Vertical distribution of early hake stages

The vertical distribution of *M. gayi* eggs and larvae was analyzed separately for October 1996, November 2001, and March 2002. Ontogenetic and seasonal changes in the vertical hake egg and larval distribution were detected (Figs. 4 and 5). In austral spring, recently spawned eggs (stage 1) were collected throughout the water

column (surface to 100 m depth in October 1996, surface to 250 m depth in November 2001), with the highest abundances (312 and 2920 eggs per 1000 m³, respectively) between 50 and 100 m (Fig. 4). Both abundance peaks occurred south of the Itata canyon (Fig. 3). In October 1996, eggs spawned south of the Itata canyon were aggregated at mid-depths throughout embryonic development (Fig. 4). Preflexion larvae caught during this cruise (day and night, $n = 673$) were found at mid-water (Fig. 5a) without evidence of diel vertical migrations (DVM, Mann–Whitney test, $U = 860$, $p = 0.295$).

In November 2001, stage 1 and 2 hake eggs occurred down to 250 m, with most eggs collected above 100 m depth and peaks between 50 and 75 m. The oldest egg stages were only found above 100 m depth (870 eggs per 1000 m³ at 25–50 m depth). Small and medium-sized hake larvae (4–14 mm, $n = 35$) were found in the subsurface layer (50–75 m depth), without diel changes in their depth distribution (t -test, $p = 0.45$). Larger larvae (>14 mm, $n = 176$) occurred in the 50–100 m layer in the day, migrating to shallower waters at night (~25 m deep; Mann–Whitney test,

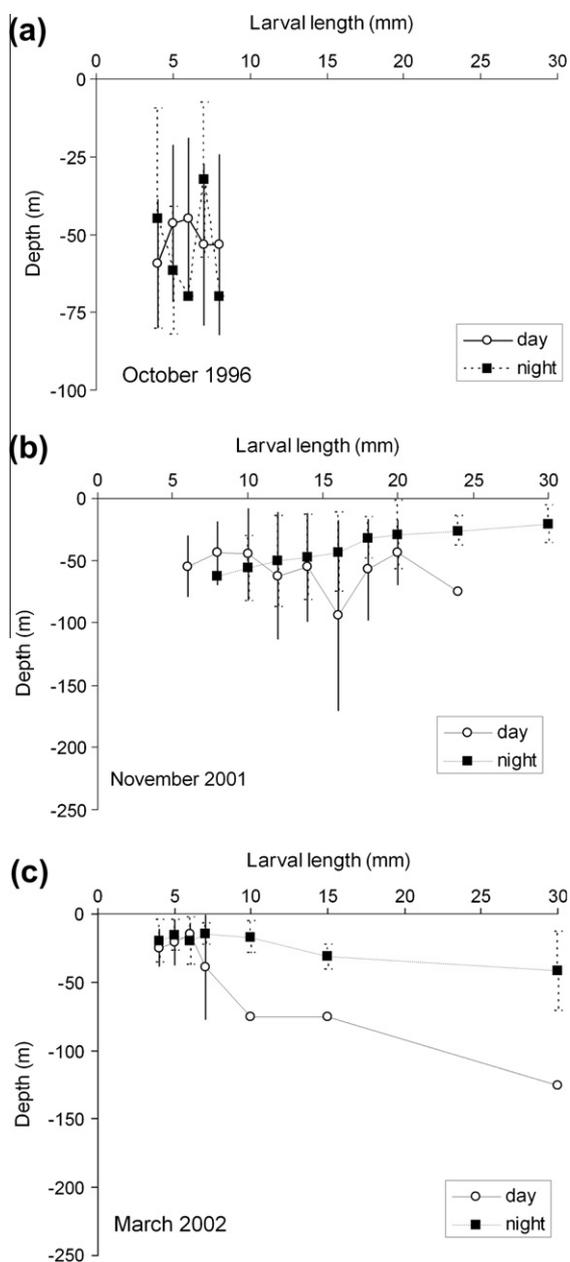


Fig. 5. Daily and ontogenetic variability in the mean depth distribution of hake larvae in (a) October 1996 (offshore spawning), (b) November 2001 (offshore spawning) and (c) March 2002 (inshore spawning). Open (white) circles indicate the depth distribution during day (night) hours, and bars indicate 1 SD.

$U = 570$, $p = 0.015$). Fig. 5b shows that, as the larvae grew, they tended to approach the surface at night, coinciding with their movement in the shallow Gulf of Arauco (<50 m depth).

In late summer 2002, spawning seemed to occur in shallower waters as hake eggs were found only in the first 100 m of the water column (Fig. 4), recently spawned eggs were most abundant (5797 eggs per 1000 m³) at the surface (0–10 m deep). Eggs in late developmental stages were collected mainly over 50 m depth (Fig. 4). Hake larvae smaller than 7 mm NL were collected in surface waters (<25 m deep, $n = 374$) and shallower than previous surveys (Mann–Whitney test, $U = 593$, $p < 0.001$). No evidence of diel migrations was detected in larvae of this size range (t -test, $p = 0.57$). However, with the appearance of the first hypural rays in the caudal fin (7–8 mm NL, $n = 18$; Santander and de Castillo, 1969), hake larvae deepened in the water column to 70–125 m during the day and

migrated to shallower waters (20–40 m deep) at night (Mann–Whitney test, $U = 44$, $p = 0.048$; Fig. 5c). Net avoidance by large *M. gayi* larvae during the day was probably low, as we collected larvae up to 20 mm SL in the first 50 m in day time hours.

3.4. Larval size distribution

Larval size distribution was unimodal and largely dominated by small preflexion larvae, typically <6 mm NL (Fig. 6), irrespective of the gear used (Table 1). An exception was detected in November 2001, when larger postflexion larvae dominated and constituted around 88% of total larval hake (Fig. 6). Larvae caught in October 1996 and late winter 2004–2005 showed a reduced size range, varying from 2.92 mm NL (October 1996) to 10.21 mm SL (September 2005). In November 2001 and March 2002, the larval size distribution was wider (3.96–28.65 mm SL in mid spring, 3.13–27.19 mm SL in late summer).

3.5. Seasonal and inter-annual variability in Chilean hake egg diameter

Noticeable seasonal and inter-annual differences in egg size (diameter) were detected in *M. gayi* eggs (Fig. 7, Table 2). Between 1996 and 2002, hake eggs collected over the continental shelf decreased significantly in size from winter–spring spawning to late summer spawning, i.e., eggs spawned in mid-winter and spring were larger than eggs spawned in late summer (Mann–Whitney test, $U = 5774$, $p < 0.001$). Also, inter-annual differences in egg size were found within seasons (late winter–spring eggs: Kruskal–Wallis ANOVA, $H = 20.36$, $p = 0.001$; late summer eggs: Kruskal–Wallis ANOVA, $H = 101.33$, $p < 0.001$), i.e., hake eggs collected in March 1996 were significantly smaller than eggs spawned in March 2000 and March 2002 (Mann–Whitney test 1996–2000, $U = 36$, $p < 0.001$; Mann–Whitney test 1996–2002, $U = 280$, $p < 0.001$). However, between March 2000 and 2002, the diameters did not differ (Mann–Whitney test 2000–2002, $U = 1651$, $p = 0.415$).

After 2002, the seasonal pattern of egg sizes varied. Hake eggs collected in late winter–early spring 2004 and 2005 were significantly smaller than eggs spawned between spring 1996 and 2002 (t -test, $p < 0.001$), but were similar in diameter to those spawned in March (Mann–Whitney test, $U = 24,246$, $p = 0.900$). Also, there was a significant decrease in egg diameter between September 2004 and September 2005 (Fig. 7; t -test, $p < 0.001$).

3.6. Effect of egg size on early larval characteristics

There was a significant difference in the diameter of live hake eggs collected off Dichato (36°30'S) between May (smaller) and October 2004 (larger) (Mann–Whitney test, $U = 5$, $p < 0.001$). Similarly, recently hatched larvae in May were significantly smaller than hake larvae hatched in October (Mann–Whitney test, $U = 0$, $p < 0.001$). Temperature had no effect on larval size at hatching in the October experiments (10 °C vs. 12 °C, Mann–Whitney test, $U = 58$, $p = 0.464$). A significant, simple linear model explained the relationship between Chilean hake egg diameter and larval size at hatching (Fig. 8a): $LH = -3.66 + 6.169 ED$, where LH is the length at hatching (mm) and ED is the egg diameter.

However, there was no significant relationship between egg diameter and yolk-sac length or yolk-sac volume at hatching. At the same water temperature (10 °C), recently hatched larvae in October and May had similar amounts of yolk, regardless of egg size (for yolk-sac length: Mann–Whitney test, $U = 150$, $p = 0.571$; for yolk-sac volume: Mann–Whitney test, $U = 141$, $p = 0.404$). Although eggs maintained at 12 °C in October showed lower yolk quantities (Table 3), no significant differences were detected between the 10 vs. 12 °C trials (Kolmogorov–Smirnov test, $p > 0.1$).

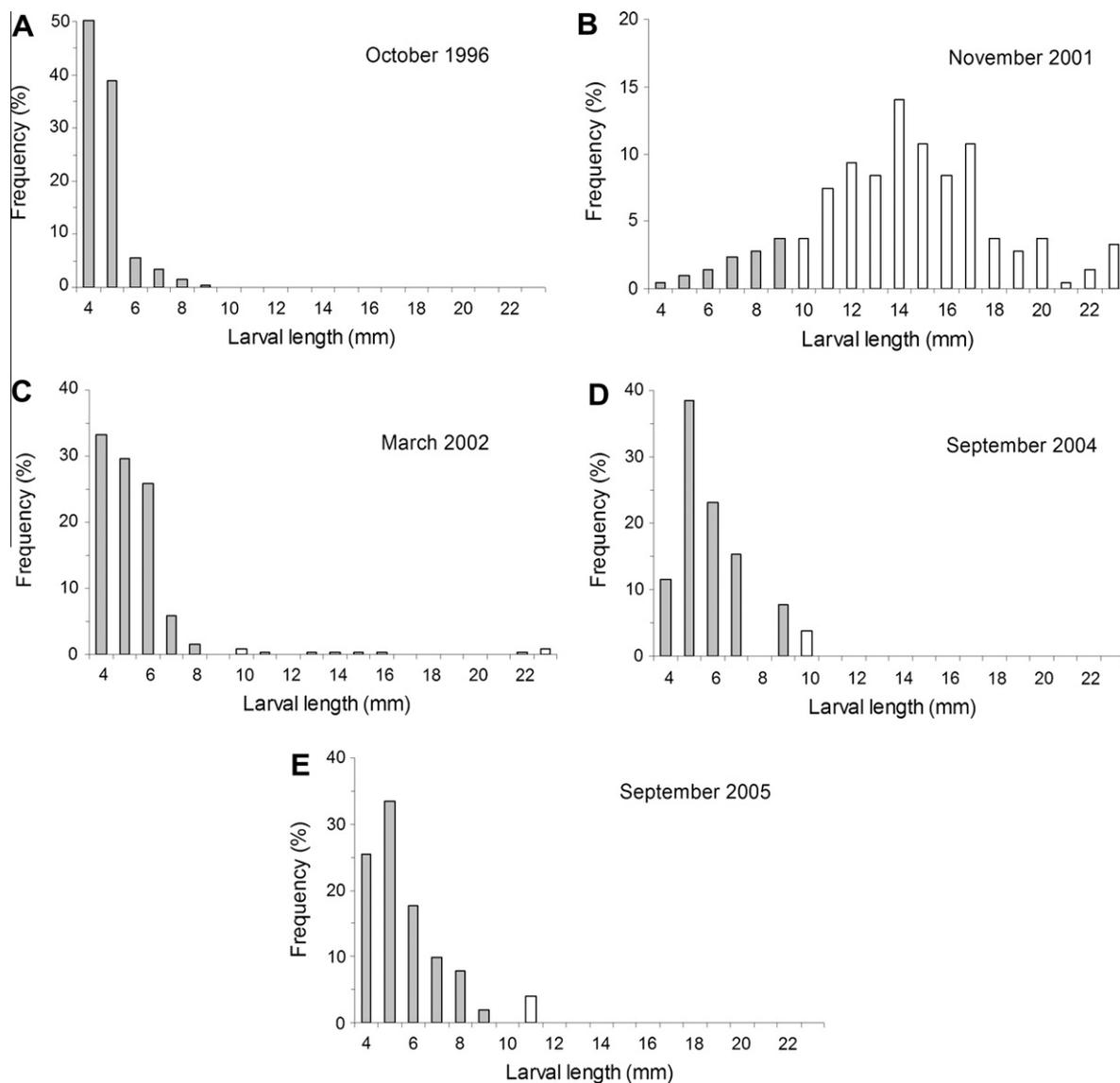


Fig. 6. Length frequency of *Merluccius gayi* larvae during long oceanographic cruises (1996–2005). Shaded bars represent preflexion larvae and clear bars represent postflexion larvae.

The yolk-sac volumes per unit of larval length (YSpL) had a significant negative linear relationship (Fig. 8b), with $YSpL = 0.52 - 0.13 SH$, where SH is the size at hatching. This means that smaller larvae had relatively more yolk reserves per unit of length than larger larvae (Mann–Whitney test, $U = 42$, $p < 0.001$). Finally, in spite of different yolk-sac consumption rates at the same temperature in May and October (slower in May; Table 3; Fig. 9), we were not able to detect differences in larval growth rates between months despite their apparent differences (0.292 mm d^{-1} in May vs. 0.112 mm d^{-1} in October; ANOVA, $p > 0.05$). In agreement with these results, larval length at the end of the yolk-sac stage was similar for both seasons (Table 3).

4. Discussion

Hakes of the genus *Merluccius* have developed several reproductive tactics to enhance survival of their early stages, including retention and/or transport to favorable nursery and recruitment zones (Ciechomski and Weiss, 1974; Chang et al., 1999; Steves and Cowen, 2000; Alvarez et al., 1995, 2001, Olivar et al., 2003;

Brown et al., 2004; Bustos et al., 2007). Off central Chile, hake reproductive tactics include early spawning by larger adults in spring and later spawning of younger/smaller adults in late summer–early autumn (Alarcón et al., 2004). This seasonal change in dominant spawning adults results in differences in the characteristics of the early life stages as well as changes in the spawning location. In austral spring, schools of larger hakes (>50 cm total length) concentrate to reproduce over the continental shelf break between the Itata and Biobío canyons. This spawning area was detected through ichthyoplankton from the early 1970s to 2001 (Bernal et al., 1997; Vargas et al., 1997; Vargas and Castro, 2001; this study), showing a temporal persistence over the last three decades. In the spring spawning season, when meteorological conditions are favorable for the occurrence of upwelling events (i.e., high incidence of south winds, saltier waters in surface, Table 1, Fig. 2), large hake eggs (1.15–1.21 mm diameter; Table 2), resulting in large larval sizes at hatching (experimental trials, Table 3), occur at 50–100 m depth (Vargas and Castro, 2001; Fig. 4), these larvae are advected onshore in the subsurface layer that compensates the offshore-moving surface Ekman layer during upwelling events (Fig. 1). Later, during ontogenetic development, hake larvae carry out DVM (>14 mm

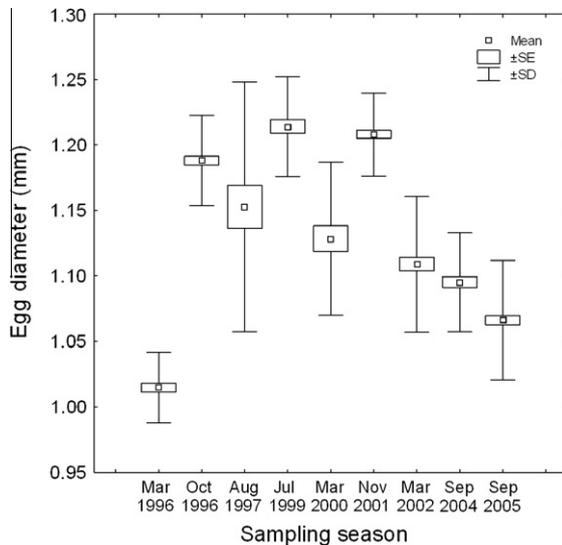


Fig. 7. Seasonal and inter-annual egg size variability (diameter) of *Merluccius gayi* off central Chile. March samples (1996, 2000 and 2002) correspond to late summer spawning, and the remaining samples correspond to early spring spawning.

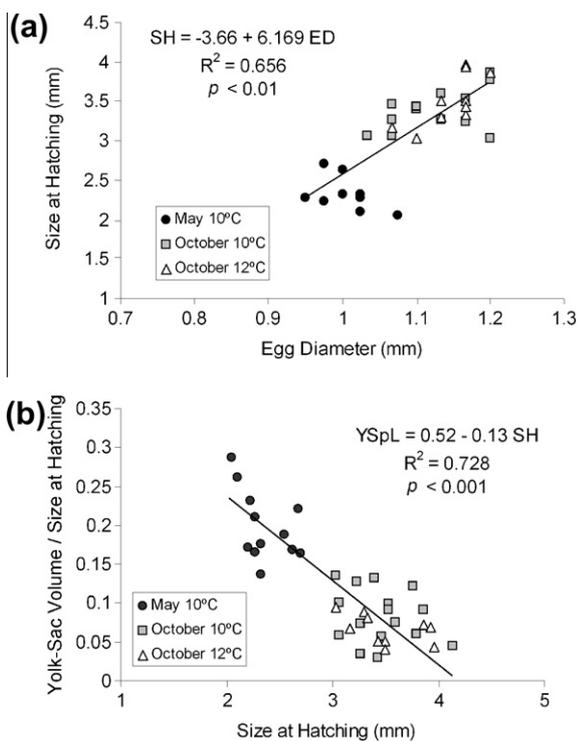


Fig. 8. (a) Relationship between larval length at hatching and egg diameter. (b) Relationship between yolk-sac volume per unit of larval length and larval length at hatching. The solid line represents the least square regression line. The key indicates the time and temperature at which the eggs were incubated.

SL) until arriving at coastal areas, including the Gulf of Arauco (Fig. 5). These areas are rich in larval food and likely settlement sites (Fig. 3). In late summer and early autumn, when rapid changes in the wind direction and speed occur and wind-driven upwelling reduces its intensity (Fig. 2) and warm waters occurs off-shelf (Table 1), small and medium-sized hakes (<55 cm TL; Alarcón et al., 2004) migrate to the coast and even into the bays (Landaeta and Castro, 2006a), spawning smaller eggs (<1.15 mm; Table 2) in the mixed layer (<25 m; Fig. 4). Experimental trials showed that, in these areas

and seasons, small yolk-sac larvae hatch with relatively large yolk reserves (Table 3; Fig. 9) and plankton samples revealed that larval hake persist in surface waters up to ~7 mm NL, when they begin DVM (Fig. 5b). What triggers the DVM in hake larvae is still unknown, but it may be related to changes in meteorological conditions (wind-generated turbulence), water column structure (mixed vs. stratified conditions), foraging behavior, advective transport and/or topography. Upwelling fronts (Vargas and Castro, 2001) and abrupt changes in wind direction and speed in March and April (Fig. 2; Parada et al., 2001) may reduce chances in offshore advection of hake eggs and larvae during late summer, producing lower mortality rates (0.065 day^{-1} ; Landaeta and Castro, 2006a) than in spring ($0.1\text{--}0.38 \text{ day}^{-1}$; Vargas et al., 1996). These mortality rates are also low compared with those estimated for other hake larvae ($0.23\text{--}0.41 \text{ day}^{-1}$ in *Merluccius productus*, Hollowed, 1992; $0.12\text{--}0.27 \text{ day}^{-1}$ in *Merluccius hubbsi*, Brown et al., 2004), but similar to those obtained for *Merluccius merluccius* in the Bay of Biscay ($0.09\text{--}0.16 \text{ day}^{-1}$, Alvarez and Cotano, 2005).

The Chilean hake reproductive tactic (i.e., eggs concentrated in mid-water depths over the shelf-break and larvae found over the shelf during the main spawning season) is similar to that of *Merluccius capensis* in the Benguela system (Sundby et al., 2001), *M. productus* off California (Moser et al., 1997), and *M. merluccius* in the Bay of Biscay (Alvarez et al., 1995, 2001) and Mediterranean waters (Olivar et al., 2003). Spawning behavior in shallow coastal waters has been observed for the Argentinean hake *M. hubbsi* (Ciechowski and Weiss, 1974) and the silver hake *Merluccius bilinearis* (Jeffrey and Taggart, 2000), with eggs and larvae remaining over the shelf up to 35–40 days, when settlement occurs (Steves and Cowen, 2000). Other hake species display a different reproductive tactic, with reproduction occurring in fjord-like environments (*M. productus* in Georgia Basin, Bailey and Yen, 1983; Bollens et al., 1992; *Merluccius australis* in southern Chile, Bustos et al., 2007).

Some pelagic and demersal marine fishes have been shown to reduce mean egg size and quality as the reproductive season progresses (Hinckley, 1990; Chambers and Waiwood, 1996; Kjesbu et al., 1996; Llanos-Rivera and Castro, 2004; Riveiro et al., 2004; Macchi et al., 2006; Castro et al., 2009). The variation of egg size in oviparous organisms is not clearly understood, but it is commonly correlated with female phenotypes, environmental variability, and harvest selection (Einum and Fleming, 2002; Walsh et al., 2006). Female cods with multiple batches produce smaller eggs during the course of spawning. Also, first-time spawners that reproduce at the end of the spawning season produce smaller and fewer eggs. *Gadus morhua* females that grow more in length and lose the least weight during the spawning season also have larger eggs (Chambers and Waiwood, 1996; Kjesbu et al., 1996). Similarly, in *M. hubbsi*, the oocyte dry weight of large females (>55 cm TL) decreases as the spawning period progresses (November–March; Macchi et al., 2006). At a population level, the harvesting of large fish (age truncation; Berkeley et al., 2004) may also cause a reduction in the mean egg volume and larval size at hatching (Walsh et al., 2006). In our study, changes in Chilean hake egg sizes were detected between spawning seasons (winter–spring vs. late summer–fall) after an abrupt decrease in population biomass and the change in adult sizes in 2004 and 2005 (Fig. 10).

4.1. Variability in seasonal spawning characteristics of hake after 2002

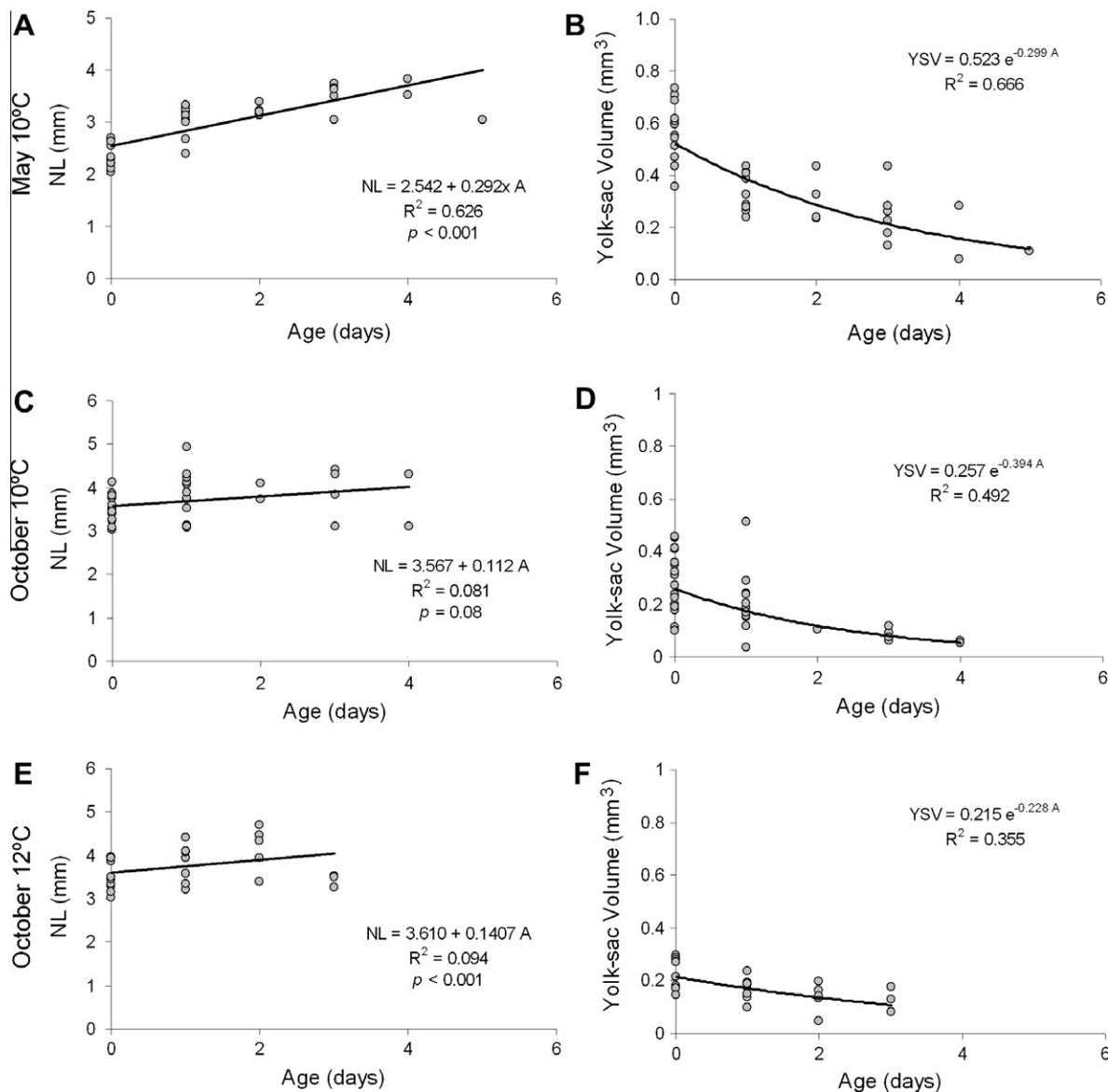
Adult Chilean hake biomass (estimated by hydroacoustic surveys; Fig. 10a) and size were progressively reduced from 1999 (Fig. 10b) and declined during 2004 and 2005 off central Chile (Fig. 10c), coinciding with the absence of a major spawning area south of the Itata canyon, increased coastal spawning in early spring, and the decline in egg size during 2004 and 2005. No studies

Table 3

Summary of characteristics of early life stages (eggs and yolk-sac larvae) from experiments carried out in May and October 2004.

Month	Temperature (°C)	Egg diameter (mm)	Size at hatching (mm)	Yolk-sac length at hatching (mm)	Yolk-sac volume at hatching (mm ³)	Growth rate* (mm d ⁻¹)	Size at the end of yolk* (mm)	Duration of yolk-sac (d)
May	10	1.00 ± 0.04	2.34 ± 0.24	1.23 ± 0.04	0.57 ± 0.11	0.292	4.00	5
October	10	1.13 ± 0.06	3.40 ± 0.26	1.32 ± 0.15	0.29 ± 0.12	0.112	4.01	4
October	12	1.15 ± 0.05	3.50 ± 0.32	1.18 ± 0.08	0.23 ± 0.06	0.141	4.03	3

* Estimated from linear regressions.

**Fig. 9.** Larval growth and yolk-sac absorption rates during endogenous feeding in early *Merluccius gayi* larvae, obtained experimentally in May and October 2004.

to date have discussed the possibility that modifications in spawning characteristics (location, egg size) might be a consequence of age/size variability by the harvesting of the hake population. Also, fishing pressure may stress females during the spawning season, producing high levels of cortisol that result in short larvae (McCormick, 1998). Recently, Funes-Rodriguez et al. (2009) have shown that reduced abundance of larval hake *M. productus* suggested a fishery effect for large adults of the coastal migratory population, starting in 1966. In 2007, for the fifth consecutive year, the population biomass of Chilean hake was far below the normal historical

levels observed before 2002 (278,700 tons estimated by hydroacoustic survey, 80% juveniles¹).

Other fish components of the demersal assemblage off central Chile such as bigeye flounder *Hippoglossina macrops* and the mid-water fish *Maurollicus parvipinnis* have evolved convergent reproductive tactics in the area (Landaeta and Castro, 2002; Landaeta

¹ Final report Project FIP 2007-16 "Hydroacoustic evaluation of common hake, year 2007", freely available in Spanish at www.fip.cl.

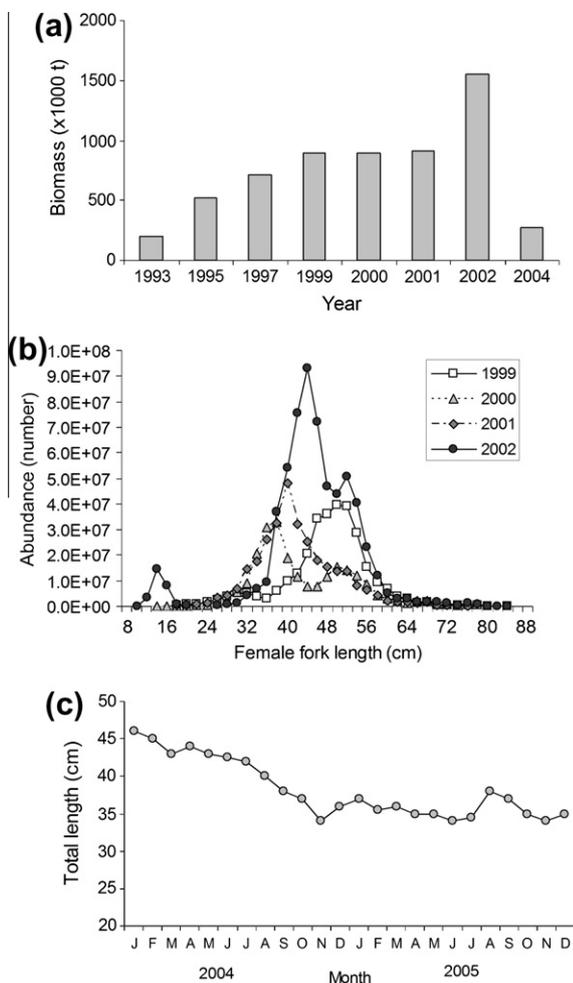


Fig. 10. (a) Adult hake biomass estimated by hydroacoustic surveys off central Chile from 1993 to 2004. (b) Size structure of female hake (fork length) between 1999 and 2002 off central Chile. (c) Mean adult size (total length) of Chilean hake between January 2004 and December 2005 captured off central Chile. Data freely available in Spanish at www.fip.cl.

et al., 2006). These tactics involve reproduction during the same seasons, the use of subsurface currents to move eggs and larvae nearer the rich coastal areas, and ontogenetic changes in vertical distribution. *H. macrops* is also intensively fished. However, since the spawning areas of the bigeye flounder did not change after 2002 as did that of the Chilean hake, we believe the observed modifications in the reproductive tactic of *M. gayi* may be more associated with intensive fishery pressure than with short-term changes in the physical environment off central Chile.

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