

Distribution patterns, larval growth and hatch dates of early stages of the mote sculpin *Normanichthys crockeri* (Scorpaeniformes, Normanichthyidae) in the upwelling ecosystem off central Chile

Patrones de distribución, crecimiento larval y fecha de eclosión de los estados tempranos del mote *Normanichthys crockeri* (Scorpaeniformes, Normanichthyidae) en el ecosistema de surgencias de Chile central

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Resumen.– Se examinó la variabilidad en la distribución espacial y temporal de los estados tempranos del mote *Normanichthys crockeri* en el ecosistema de surgencias de Chile central, utilizando la información de una serie de seis cruceros oceanográficos, crecimiento larval basado en otolitos, y experimentos de desarrollo embrional. Los adultos desovan durante todo el año en aguas superficiales cerca de penínsulas y dentro de bahías a lo largo de Chile central, reduciendo la advección costa afuera. Se observaron densidades de huevos de 16-788 10 m⁻². Eclosionan larvas pequeñas (~2,7 mm de longitud corporal) alimentadas endógenamente por 6 días. Las larvas en pre y postflexión de *N. crockeri* se retienen sobre la plataforma continental o cerca de la costa, y están ubicadas verticalmente en la capa de mezcla de la columna de agua. No se detectó evidencia de migración vertical diurno-nocturna en las larvas durante primavera y verano. Las larvas de *N. crockeri* mostraron tasas de crecimiento lineal de 0,15-0,20 mm día⁻¹ en los primeros tres meses de vida durante primavera y verano. Comparada con las tácticas reproductivas de otros peces pelágicos menores del área (*Engraulis ringens* y *Strangomera bentincki*), *N. crockeri* coincidió espacialmente en las áreas de desove, aunque las larvas presentaron tasas de crecimiento más lentas.

Palabras clave: Ictioplancton, desove, otolito, Pacífico suroriental

Abstract.– The variability of spatial and temporal distribution of early stages of the mote sculpin *Normanichthys crockeri* from the upwelling ecosystem off central Chile was examined using a series of six oceanographic cruises, otolith-based larval growth, and experimental trials. Adults spawned year-round in surface waters near capes and inside bays along central Chile, which reduced offshore advection. Egg densities of 16-788 10 m⁻² were observed. Small larvae (~2.7 mm body length) hatched after a few days and fed endogenously for 6 days. Pre and postflexion larval *N. crockeri* were retained over the shelf and near the coast and were vertically located in the mixed layer of the water column (from surface to ~ 50 m depth). No evidence of diel vertical migration was detected in larvae during the austral spring and summer seasons. *N. crockeri* larvae showed linear growth rates of 0.15-0.20 mm day⁻¹ in the first three months of life during spring and summer. Compared with the reproductive tactics of other small pelagic fishes from the area (*Engraulis ringens* and *Strangomera bentincki*), *N. crockeri* shared the same spawning areas; however larvae showed slower growth rate.

Key words: Ichthyoplankton, spawning, otolith, southeast Pacific

INTRODUCTION

In eastern boundary current ecosystems such as Humboldt ecosystem in the South Pacific Ocean, equatorward winds induce upwelling of nutrient-rich subsurface waters, with a

subsequent high primary production (Montero *et al.* 2007). The high primary production and biomass of microalgae sustains highly concentrated schools of herbivorous small

pelagic fishes, such as common sardine (*Strangomera bentincki*) and anchoveta (*Engraulis ringens*) (Barange *et al.*, 2005, Pedraza-Garcia & Cubillos 2008). In the area, coastal small pelagic fishes have evolved reproductive tactics to reduce advective transport from the coastal food-rich environment by spawning large amounts of small pelagic eggs (Cubillos *et al.* 2007) during seasons when upwelling events are scarce or absent, and when the abundance of gelatinous predators is low (Castro *et al.* 2000). This tactic, together with fast growing larval stage (e.g., 0.40-0.57 mm day⁻¹ for larval *E. ringens*, Hernández & Castro 2000, 0.48 mm day⁻¹ for larval *Sardinops sagax*, Gaughan *et al.* 2001) may account for the success of these taxa in a productive environment. On the other hand, there is scarce knowledge about reproductive tactics and early life history of other highly abundant small pelagic fishes inhabiting upwelling areas, such as the mote sculpin, *Normanichthys crockeri* Clark, 1937 (Scorpaeniformes, Normanichthyidae).

The *N. crockeri* is a schooling, small-bodied (up to 11 cm total length) and short-lived pelagic fish endemic to the southeast Pacific, which inhabits coastal waters from Chimbote, Peru to 44°S, southern Chile (Vegas & Pequeño 1993, Landaeta & Castro 2006a, Bustos *et al.* 2008). Adults feed on zooplankton, mainly copepods (Sepúlveda *et al.* 2004) and show trophic interactions with several taxa, being preyed upon by coastal fishes (Vargas *et al.* 1999, Oyarzún *et al.* 2001, González & Oyarzún 2003), seabirds (García-Godos & Goya 2006) and marine mammals (Soto *et al.* 2006). Currently the eggs are unknown, while the larval stages are characterized by a slender body and large pectoral fins (Balbontín & Pérez 1980, Vélez *et al.* 2003). Larvae feed on copepod eggs, copepodites and adult copepods (Balbontín *et al.* 1997). Spawning sites, early nursery areas and larval dynamics are unknown. This information is important from the ecological and fishery perspective, considering the fast increase of landings experienced along Chile in recent years (from 9,300 ton in 2003 to ~ 67,000 ton in 2008). The fishing period of this species off central Chile waters occurs during austral summer (February-May) and early spring (September-October), and it is part of the by-catch of small pelagic fisheries (G. Aedo, pers. comm.¹). The hypothesis of this study is that early life history of this species is similar to other small pelagic fish, such as anchoveta and sardine, *i.e.*, spawning in coastal, shallow waters during winter season, and fast growing larval stage. In this paper the objectives were 1) to describe the

spatio temporal and vertical distribution of *N. crockeri* and 2) to estimate larval growth of *N. crockeri* in the upwelling ecosystem off central Chile coastal waters.

MATERIAL AND METHODS

COLLECTION OF THE SAMPLES AND LABORATORY ANALYSIS

A series of six surveys carried out over the continental shelf off central Chile between 33°S and 37°S were utilized to describe egg and larval distribution of *N. crockeri* (Fig. 1). A grid of 108 stations from inshore (5 km) to a maximum of 110 km offshore was sampled during the austral spring 1996 (25 September-29 October) onboard the RV Abate Molina. Conductivity-temperature-depth (CTD) (Sensordata® SD2003) casts to 100 m depth were conducted at each station in the sampling grid. Oblique tows were carried out at each station during day and night hours using a 1m² Tucker trawl (250 µm mesh size) with a General Oceanics® flowmeter mounted in the frame

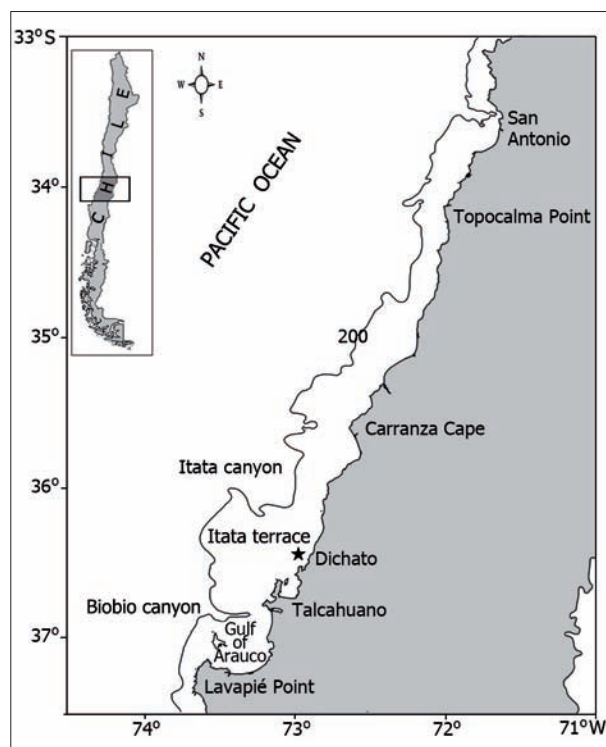


Figure 1. Central Chile study area, indicating the main topographic characteristics of the zone. The line corresponds to the 200-m isobath and the star indicates the location of the coastal time series / Área de estudio en Chile central, indicando las principales características topográficas de la zona. La línea corresponde a la isóbata de 200 m y la estrella indica la ubicación de la serie de tiempo costera

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of the net. Two depths strata were sampled, 0-40 m and 40-100 m. Towing speed was 2-3 knots. Volume filtered in each tow (range = 69-706 m³ tow⁻¹; mean = 348 m³ tow⁻¹) was estimated taking into account the net mouth area and towing duration. Onboard, the samples were divided using a Folsom splitter and one subsample (*i.e.*, 50% of the whole) was preserved in 10% formalin buffered with sodium borate. The other subsample was preserved in 90% ethanol.

Two cruises were carried out during 7-11 November 2001 (austral spring) and 7-12 March 2002 (austral late summer) between 35° and 37°S onboard the RV Abate Molina. Eleven transects with 6-7 stations each were sampled during both surveys. A CTD cast (Seabird® SB-19) was conducted at each station to 250 m or near the bottom. Oblique tows at speeds of 2-3 knots were carried out using a 1 m² Tucker trawl (300 µm mesh size) with a General Oceanics® flowmeter mounted in the frame of the net to estimate filtered volume. Volume ranged between 17-598 m³ tow⁻¹ (mean = 142 m³ tow⁻¹) during November 2001, and between 12-217 m³ tow⁻¹ (mean = 96 m³ tow⁻¹) during March 2002. Depth strata were variable, ranging from 0-10, 10-25 m in nearshore waters, 0-25, 25-50, 50-75 and 75-100 m deep over the shelf, and 0-50, 50-100, 100-150 and 150-250 m deep at the shelf break area. Samples from each depth strata were preserved in 10% formalin and 90% ethanol.

During September 2004 and 2005 (austral late winter), 41 and 48 stations were surveyed, respectively, over the continental shelf between San Antonio (33°18'S) and Gulf of Arauco (Fig. 1) onboard the RV Kay-Kay. At each station CTD casts (Seabird SB-19) and an oblique Bongo (60 cm diameter, 300 µm mesh size, with General Oceanics® flowmeter) tow to 80 m depth or near the bottom, were conducted during day and night hours, following Smith & Richardson (1977). Towing speed was 2 knots. Filtered volume ranged from 7 to 200 m³ tow⁻¹ (mean = 48 m³ tow⁻¹) for the 2004 survey, and from 15 to 142 m³ tow⁻¹ (mean = 57 m³ tow⁻¹) for the 2005 survey. The right sample was preserved in 10% formalin buffered with sodium borate and the left sample was preserved in 90% ethanol.

Between July 2004 and June 2006, monthly samples of zooplankton were collected at three coastal stations located 5 nautical miles from the shore (Fig. 1), onboard RV Kay-Kay. Oblique samples were collected with a standard bongo net (60 cm diameter, 300 µm mesh size, General Oceanics® flowmeter), from 40 m depth

to surface. Once onboard, samples were fixed in 10% formalin buffered with sodium borate.

All fish eggs and larvae were sorted from the plankton samples at the laboratory. Identification of larval *N. crockeri* was carried out utilizing characters described by Balbontín & Pérez (1980) and Vélez *et al.* (2003). Egg and larval densities were expressed as individuals 10 m⁻² for examination of horizontal distribution patterns (integrated samples) and as individuals 1000 m⁻³ for examination of vertical distribution (only Tucker trawl samples). Developmental stages of all larvae were classified as preflexion or postflexion (flexion and postflexion larvae pooled). In addition, undamaged larvae from the 2001 and 2002 surveys (N = 66 and 812, respectively) were measured to the nearest 0.1 mm with a calibrated ocular micrometer fitted to a Nikon® stereomicroscope.

Non-parametric tests (Mann-Whitney U test) were run to compare the vertical distribution of early stages of *N. crockeri*. Additionally, the centroid depth distribution (CDD) of pre- and postflexion larvae collected during November 2001 and March 2002 were calculated separately for each station according to the formula:

$$CDD = \frac{\sum(pk \times zk)}{\sum pk}$$

where p_k is the number of organisms at stratum k (abundance standardized to individuals 1000 m⁻³), and z_k is the mean depth of stratum k . To establish if vertical migration occurred in both groups, the calculated centroid depths during day and night hours were compared using Mann-Whitney U-test.

EGG IDENTIFICATION

Normanichthys crockeri eggs were identified using the series method described by Neira *et al.* (1998), from zooplankton samples collected between 1996 and 2005. The method consists of positively identifying the largest available larva, using known adult characters and subsequently linking this specimen with progressively smaller specimens by using general morphological and pigment characters until a developmental series is assembled. Eggs and yolk-sac larval identifications were confirmed through laboratory reared eggs collected onboard the RV KayKay with oblique Bongo nets tows in the nearshore waters off Dichato, Chile (36.5°S) during October 2000. Samples were placed separately in a 4 L plastic jar inside a cooler with icepacks and immediately

transported to the Universidad de Concepción, Estación de Biología Marina at Dichato (36°30'S), where early life stages of *N. crockeri* were separated under stereomicroscopes and incubations were carried out. Early stage eggs (*i.e.*, without evidence of embryo) were initially maintained in 1 L glass jars with ultraviolet-irradiated and filtered seawater (0.5 µm) inside a water bath at 12°C and a photoperiod of 12L:12D. One-third of the seawater was replaced daily. Once hatching occurred, yolk-sac larvae and preflexion larvae were maintained without food until death. Recently hatched larvae (N = 38) were anesthetized and measured under a stereomicroscope and dim light in the Marine Station at Dichato.

OTOLITH MICROSTRUCTURE, LARVAL GROWTH, AND HATCHING DATES

A total of 90 ethanol-preserved *N. crockeri* larvae were removed from the November 2001 (N = 19, 4.0-11.2 mm larval length) and March 2002 surveys (N = 71, 5.7-16.0 mm larval length). The larvae were placed on a glass slide, with a drop of water, and left and right sagitta otoliths were removed from the larvae using entomological needles. Otoliths were embedded in epoxic resin and analyzed using a microscope and computer image analyzer (Optimas® 6.1 software). One measurement of otolith area and three consecutive measurements of otolith diameter were made and the average otolith diameter was calculated for each otolith. Larval otoliths were read at 1000x magnification in immersion oil. Larval lengths were not corrected for shrinkage and it was assumed that otolith increments were deposited daily, as can be observed in several marine fish larvae (Kokita & Omori 1998, Hernández & Castro 2000).

Integrated growth of larvae per survey (2001 and 2002 separately) was estimated from the slope of a linear regression by least squares between body size and age: $L(t) = \alpha + \beta t$, where $L(t)$ = larval length (mm) at age t , t = ring counts, β = slope (growth rate, mm day⁻¹), and α = intercept (larval length at hatch, mm). To establish if significant differences in larval growth occurred between the two surveys, an ANCOVA test was run (multiple-slope test, Zar 1999). To obtain the 95% confidence intervals of the estimated parameters, 5000 randomly generated data sets were utilized to determine the frequency distribution of α and β for each cruise (Table 3), Monte Carlo simulations were used to test differences between the mean values of α and β (Table 4).

The hatching period of larvae collected during the surveys carried out in November 2001 and March 2002 were first estimated by obtaining a larval length-at-age

key for both sampling periods. 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 hatching period was back-calculated. The hatching date distribution for each sampling day from both surveys was weighted according to the standardized abundance of the catch per station, and then summed to obtain the distribution in the population.

RESULTS

DESCRIPTION OF *Normanichthys crockeri* EGGS

Normanichthys crockeri eggs are spherical, measuring 0.75-0.83 mm in diameter (mean \pm standard deviation, 0.78 ± 0.04 mm, N = 122). They have homogeneous yolk, narrow perivitelline space, smooth chorion and a single oil globule (0.21-0.26 mm diameter, 0.22 ± 0.07 mm, N = 122) pigmented in their internal base. Prior to hatch, embryos show puntiform melanophores along the dorsal and caudal region. The proportion between oil globule diameter and egg diameter (oleocapsular ratio, 19-28%) is a unique feature for the identification of eggs from this species. Fish eggs collected in the same area (central Chile) either don't have oil globules (*e.g.*, sardines, *Strangomera bentincki*, *Ethmidium maculatum*, Herrera *et al.* 1987), have smaller oleocapsular ratios (*e.g.*, Chilean hake, *Merluccius gayi*, Pacific sandperch *Prolatilus jugularis*, Fischer 1958, 1959) or have larger egg diameters (*e.g.*, bigeye flounder, *Hippoglossina macrops*, Landaeta *et al.* 2006). Development at 12°C from the morula stage took up to 48 h for hatching. After hatching, yolk-sac larvae fed endogenously for 6 days at 12°C. Preflexion larvae hatched from eggs collected in the field were positively identified for the 1) presence of puntiform melanophores ventrally along the trunk and tail, 2) stellate melanophores in the dorsal zone of the tail, and 3) pigment in the isthmus (Vélez *et al.* 2003).

SPATIAL DISTRIBUTION OF EARLY LIFE STAGES OF *N. crockeri*

During the austral spring of 1996 early life stages of *N. crockeri* were collected over the continental shelf of central Chile (Fig. 2). Eggs were found close to shore (<12 km offshore) and associated to headlands in the north part of the study area, such as Carranza cape and inside Gulf of Arauco. Abundance ranged between 1.1 and 89.4 10 m⁻², with the highest abundance collected south of Carranza cape (Table 1). Pre- and postflexion larvae were concentrated over the Itata terrace, particularly off

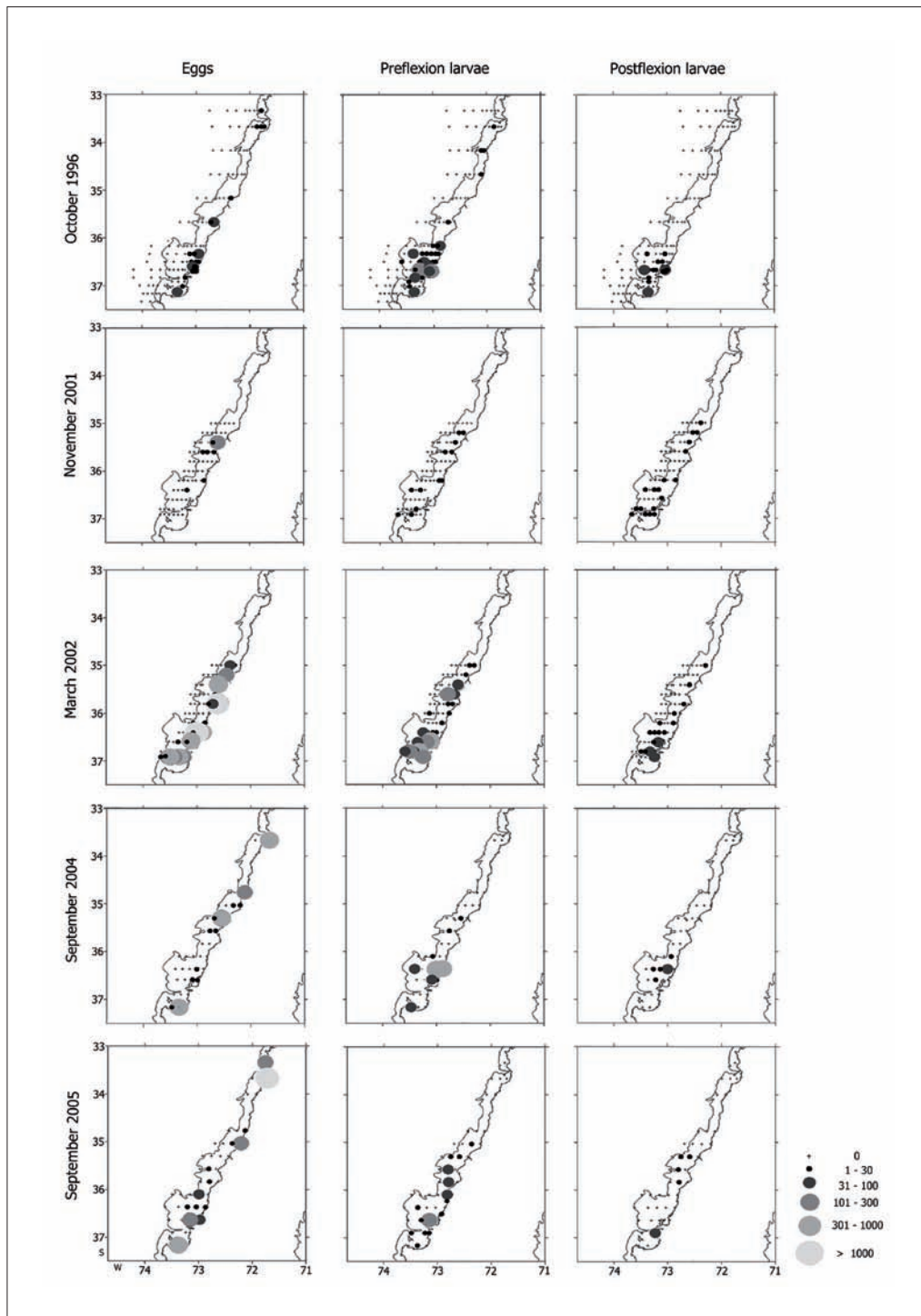


Figure 2. Horizontal distribution of eggs, prefixion larvae and postflexion larvae of *N. crockeri*, off central Chile during October 1996, November 2001, March 2002, September 2004 and 2005. Abundances expressed as individuals 10 m^{-2} / Distribución horizontal de huevos, larvas en prefixión y larvas en postflexión de *N. crockeri*, frente a Chile central durante octubre 1996, noviembre 2001, marzo 2002, septiembre 2004 y 2005. Abundancias expresadas como individuos 10 m^{-2}

Table 1. Mean abundance (individuals 10 m⁻²), median, standard deviation (SD), maximum values and quartiles of eggs and larvae of *N. crockeri* off central Chile / Abundancia promedio (individuos 10 m⁻²), mediana, desviación estándar (SD), valores máximos y cuartiles de huevos y larvas de *N. crockeri* frente a Chile central

Sampling date	Eggs						Preflexion larvae						Postflexion larvae					
	Mean	SD	Max	Median	Lower Quartile	Upper Quartile	Mean	SD	Max	Median	Lower Quartile	Upper Quartile	Mean	SD	Max	Median	Lower Quartile	Upper Quartile
October 1996	16.66	21.17	89.41	6.19	2.62	25.63	24.59	28.94	111.47	14.85	4.25	33.35	14.97	14.98	53.75	8.52	3.17	20.68
November 2001	22.06	37.18	104.64	5.64	3.98	24.48	8.64	8.94	27.24	4.52	3.50	9.58	5.79	3.65	14.13	4.29	2.94	8.06
March 2002	788.02	2163.73	9693.16	35.04	7.86	457.81	50.69	99.52	374.65	32.27	15.37	84.33	13.19	13.82	55.20	8.19	4.78	14.12
September 2004	174.57	311.88	899.00	19.33	11.68	122.82	108.03	158.47	398.45	35.63	9.23	81.10	31.23	36.75	96.32	17.89	11.39	21.80
September 2005	158.77	325.23	1240.88	29.16	11.17	109.51	31.96	52.80	210.59	10.47	6.22	35.72	18.43	17.11	47.15	11.17	8.13	20.78

Talcahuano (maximum value, 111.5 preflexion larvae 10 m⁻², 53.7 postflexion larvae 10 m⁻²), with decreased abundance of larvae (<10 10 m⁻²) in the northern part of the study area.

Few eggs and larvae were collected over the shelf during November 2001 (austral spring). Off Carranza cape egg abundance was 104.6 10 m⁻², but in the rest of the study area egg abundance ranged between 3.9 and 24.5 10 m⁻² (Fig. 2). Larval abundance was low throughout the continental shelf, with mean values (\pm one standard deviation, SD) of 8.6 ± 8.9 10 m⁻² and 5.8 ± 3.6 10 m⁻² for pre- and postflexion larvae, respectively (Table 1).

During the austral late summer of 2002 (March) large numbers of eggs were collected in coastal waters off central Chile (Fig. 2). Mean density of *N. crockeri* eggs was 788 ± 2163.7 10 m⁻², with the highest abundance found south of Carranza cape (9693 10 m⁻²) and off Talcahuano (4628 10 m⁻²) (Table 1). North of Itata canyon, pre- and postflexion larvae were found mainly in nearshore waters, but over the Itata terrace larvae were collected throughout the shelf and inside of the Gulf of Arauco. Larval abundance varied from 1.6 to 607.3 10 m⁻² (preflexion larvae) and from 0.5 to 55.2 10 m⁻² (postflexion larvae) (Fig. 2).

During the late winter of 2004, coastal spawning was patchy (Fig. 2). Large numbers of eggs were collected off San Antonio (899 10 m⁻²), north of Carranza cape (807 10 m⁻²), and inside the Gulf of Arauco (461 10 m⁻²). However, larvae were found almost exclusively over the Itata terrace (Fig. 2). Mean larval abundance was 108.0 ± 158.5 preflexion larvae 10 m⁻² and 31.2 ± 36.8 postflexion larvae 10 m⁻² (Table 1). Similarly, during late winter in 2005, *N. crockeri* spawning was concentrated off San Antonio (1240.9 eggs 10 m⁻²) and inside Gulf of Arauco (496.8 eggs 10 m⁻²) (Fig. 2). Preflexion larvae were located over the shelf, mainly in nearshore waters off Talcahuano (210.6 10 m⁻²). Compared to smaller larvae, postflexion larvae were scarce, ranging between 4.9 and 47.1 10 m⁻² (Fig. 2).

Analysis of vertically stratified samples showed that eggs and larvae were found mainly in the upper 50 m of the water column throughout their early development (Fig. 3). During the austral spring of 1996 two strata were sampled (0-40 and 40-100 m depth) and early stages were more recurrent in the shallower surface stratum. However, significant differences in depth distribution were only detected for preflexion larvae (Mann-Whitney U test, $U = 107$, $P < 0.001$). Eggs and postflexion larvae did not show significant differences between depth strata (eggs: $U = 29$, $P = 0.16$, postflexion larvae: $U = 30$, $P = 0.40$). Although sampling was carried out to 250 m depth during November 2001, eggs were restricted to the top 50 m and larvae were present from 100 m to surface (Fig. 3). The highest densities of pre- and postflexion larvae were obtained in the mixed layer (240 preflexion larvae 1000 m⁻³ at 0-10 m depth; 48 postflexion larvae 1000 m⁻³ at 0-25 m depth).

A similar trend was observed during March 2002, when early life stages were predominantly found in the upper 50 m (Fig. 3). The largest densities of eggs and larvae were collected in surface waters ($\sim 92,000$ eggs 1000 m⁻³ at 0-10 m, 4674 preflexion larvae 1000 m⁻³ at 0-25 m, and 326 postflexion larvae 1000 m⁻³ at 0-25 m).

Table 2 summarizes the results obtained for the estimation of the centroid depth distribution of pre- and postflexion larvae during the cruises carried out in November 2001 and March 2002 off central Chile. During spring 2001, larvae smaller than 7 mm NL were widely distributed in the water column during the day, but were restricted to the shallowest depth strata (mean depth = 13 m) at night; however, no significant differences were detected in the depth distribution ($U = 6$, $P = 0.09$). Postflexion larvae were distributed at similar depths, and their centroid depths were located near the pycnocline with no significant differences in depth distribution detected ($U = 26.5$, $P = 0.50$). During March 2002, pre- and postflexion larvae were homogeneously distributed during day and night, and the centroid depths were located

Table 2. Basic statistics of the centroid depth distribution (CDD, in m) of pre and postflexion larvae of *N. crockeri* during November 2001 and March 2002 off central Chile. SD = standard deviation / Estadísticas básicas de la distribución de profundidad del centroide (CDD, en m) de larvas en pre y postflexión de *N. crockeri* durante noviembre de 2001 y marzo de 2002 frente a Chile central. SD = desviación estándar

	November 2001				March 2002			
	Preflexion		Postflexion		Preflexion		Postflexion	
	Day (n = 8)	Night (n = 4)	Day (n = 11)	Night (n = 6)	Day (n = 27)	Night (n = 16)	Day (n = 14)	Night (n = 9)
Minimum	6.08	13.00	18.00	16.53	13.00	13.00	13.00	13.00
Maximum	75.00	13.00	52.19	63.00	38.00	38.00	38.00	38.92
Mean	34.93	13.00	36.84	43.69	21.43	22.04	24.11	20.67
SD	21.79	-	10.53	22.44	14.05	8.51	11.40	9.97

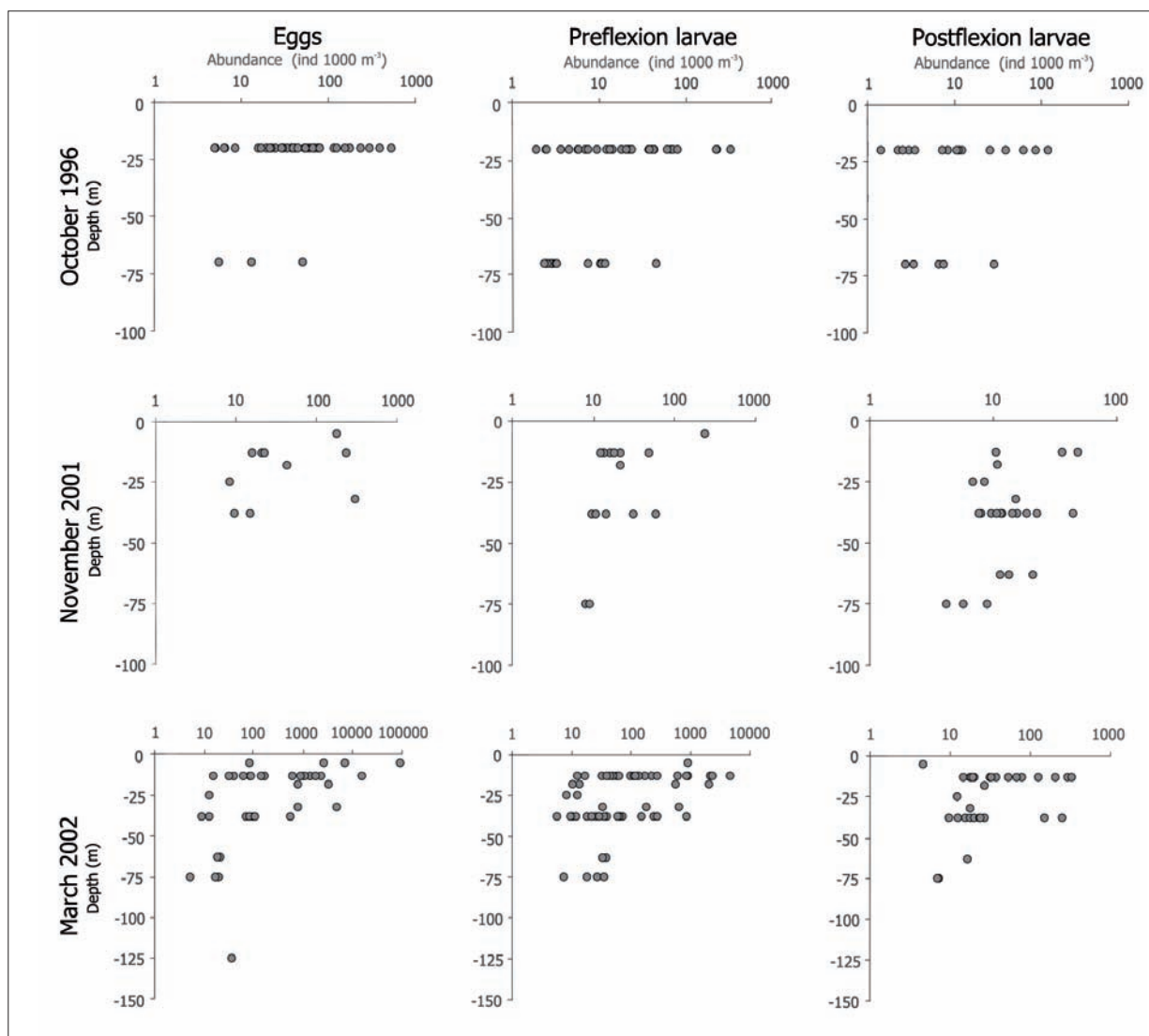


Figure 3. Vertical distribution of eggs and larvae of *N. crockeri* off central Chile during October 1996, November 2001 and March 2002. Abundances expressed as individuals 1000 m⁻³; x-axis in log scale / Distribución vertical de huevos y larvas de *N. crockeri* frente a Chile central durante octubre de 1996, noviembre de 2001 y marzo de 2002. Abundancias expresadas como individuos 1000 m⁻³; eje x en escala logarítmica

Table 3. Linear regression models (LL = $\alpha + \beta \cdot A$) fitted to larval growth of wild-caught *N. crockeri* off central Chile during November 2001 and March 2002. LL = larval length (mm), A = age (number of otolith increments), CI = confidence intervals / Modelos de regresión lineal (LL = $\alpha + \beta \cdot A$) ajustados al crecimiento larval de *N. crockeri* capturados frente a Chile central durante noviembre de 2001 y marzo de 2002. LL = longitud larval (mm), A = edad (número de incrementos de otolitos), CI = intervalos de confianza

Sampling date	N	Parameter	Best-fit value	Standard Error	CI lower	CI upper	P -value	r ²
November 2001	19	α	2.866	0.3118	2.2079	3.5236	< 0.05	0.90
		β	0.201	0.0161	0.1673	0.2354	< 0.05	
March 2002	71	α	3.934	0.2877	3.3607	4.5081	< 0.05	0.89
		β	0.151	0.0061	0.1386	0.1629	< 0.05	

between 20 and 24 m for all cases, with no significant diel differences detected (preflexion larvae: $U = 136.5$, $P = 0.43$; postflexion larvae: $U = 52$, $P = 0.49$).

Figure 4 shows the spatial distribution of eggs, preflexion (larvae < 7 mm NL) and postflexion (larvae > 7 mm SL) larvae during two phases of an upwelling cycle, at relaxation (November 2001) and at the beginning of an upwelling event (March 2002). During relaxation, there was strong stratification across the shelf, with a mixed layer of warmer (>11°C) and less salty (< 34.3) waters to 50 m depth, and a denser deep layer (> 26.4 units of sigma-t). Under this oceanographic setting, eggs and larvae were restricted to nearshore and surface waters of the continental shelf off central Chile (Fig. 4).

In the Gulf of Arauco during March of 2002, there was a coastal ascent of a 12°C isotherm and a 34.4 isohaline (Fig. 4). Eggs and larvae were located throughout the Gulf in the upper 25 m (>300 1000 m⁻³), but they were found in higher abundance in nearshore waters with few collected in deeper and denser waters (<30 1000 m⁻³).

TEMPORAL DISTRIBUTION OF EGGS AND LARVAE OF *Normanichthys crockeri* IN COASTAL WATERS

The coastal time series of eggs and larvae of *N. crockeri* off the Talcahuano area showed peaks of abundance mainly during the mid and late summer months (January, March and April) (Fig. 5). Maximum egg abundances occurred in April 2005 (338.5 ± 289.1 10 m⁻²) and January 2006 (123.9 ± 175.2 10 m⁻²) (Fig. 5a). On the other hand, larvae were collected in higher abundance and frequency almost exclusively between August and November 2004, with a peak during August 2004 (11.2 ± 11.4 10 m⁻²) and August 2005 (20.3 ± 37.2 10 m⁻²). Decreased larval abundances were observed in the following months during the austral spring of 2005 and early autumn of 2006 (Fig. 5b).

LARVAL LENGTH DISTRIBUTION, GROWTH AND HATCHING DATE

Larval length frequency distribution differed between collections carried out during November 2001 and March 2002 (Fig. 6). In spring 2001, larvae collected in the zooplankton samples ranged between 3.38 and 18.83 mm (mean = 8.25 mm, SD = 3.51) with most of the larvae at the postflexion stage. On the other hand, larvae collected during late summer had a shorter length range, varying from 2.00 to 13.24 mm (mean = 5.15 mm, SD = 1.75), with most of them at the preflexion stage (Fig. 6).

Otolith microstructure analysis from larvae collected in the wild showed significant relationships between otolith size and larval length (Fig. 7a, b). Pooling together the data from both cruises, a linear regression described the relationship between otolith diameter (OD, in μm) and larval length (LL, in mm), $OD = 24.2 (LL) - 80.2$ ($r^2 = 0.95$, $n = 90$, $P < 0.001$) (Fig. 7a). Similarly, a power model explain the relationship between otolith area (OA, in μm^2) and larval length, $OA = 5.5 (LL)^{3.5}$ ($r^2 = 0.92$, $n = 90$, $P < 0.001$) (Fig. 7b). These results indicate that otolith growth may be a good predictor of somatic growth.

The number of microincrements in otoliths of ethanol-preserved larvae of *N. crockeri* collected during November 2001 and March 2002 ranged between 7 and 37, and from 14 to 80, respectively. Linear regression models were estimated separately for both surveys (Table 3) and then compared. However, no significant differences were detected between slopes (*i.e.*, growth rates between 0.15 and 0.20 mm day⁻¹) of both regressions (ANCOVA, $F = 0.11$, $P = 0.74$). Therefore, all data were pooled together, and the intercept (a parameter in the linear regression) was fixed at 2.7 mm, the mean larval size at hatch. The linear model yielded a daily growth rate of 0.16 mm day⁻¹ ($N = 90$, $r^2 = 0.93$, $P < 0.01$) (Fig. 7c).

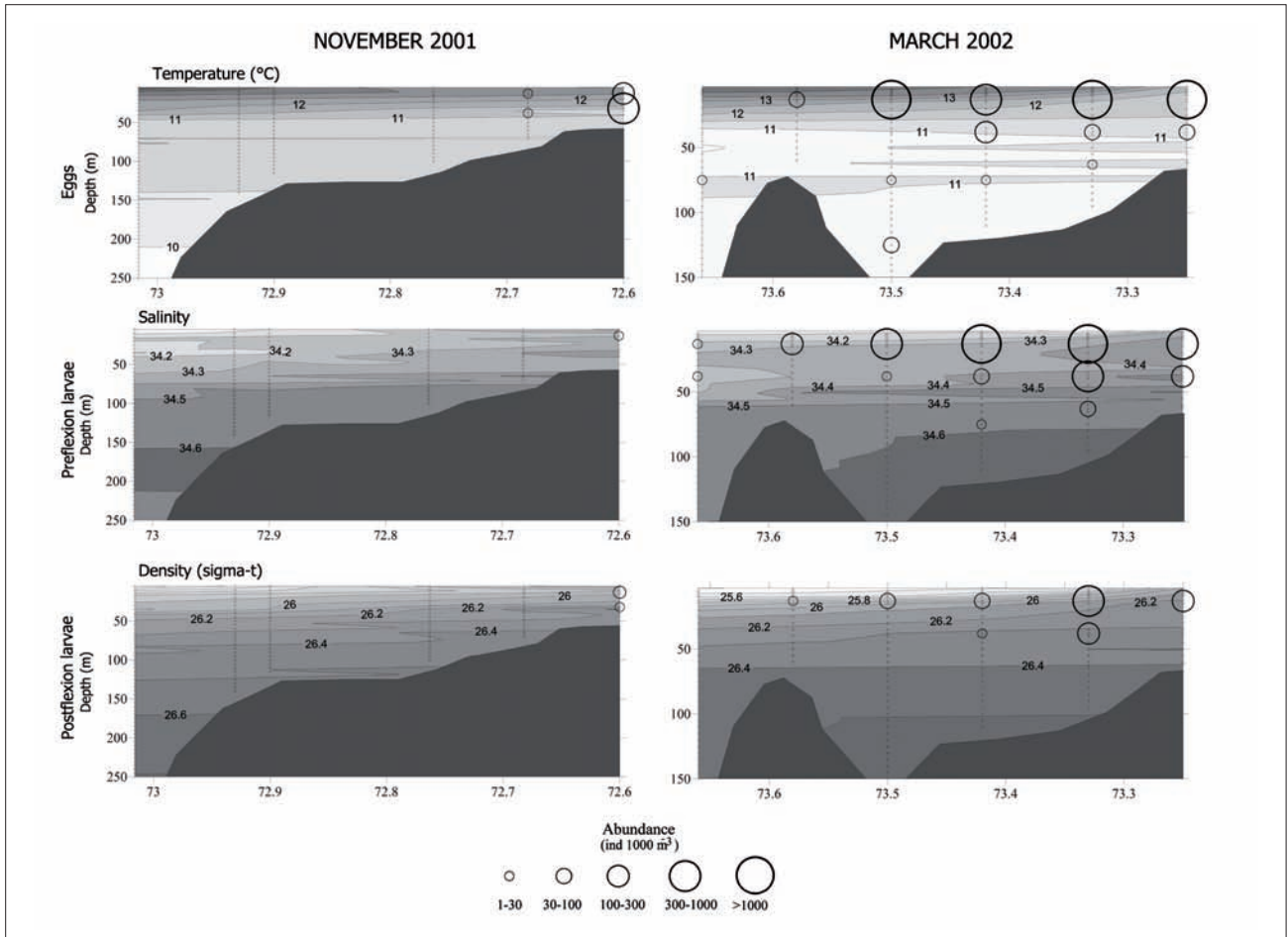


Figure 4. Across-shelf vertical sections of temperature ($^{\circ}\text{C}$), salinity and density (units of sigma-t) showing two phases of an upwelling cycle: relaxation (November 2001) and the start of an upwelling event (March 2002). Crosses indicate the location and depth of CTD casts. Overlaid are the vertical distribution of eggs, pre- and postflexion larvae, with abundances expressed as individuals 1000 m^{-3} . Left section located at $35^{\circ}25'\text{S}$; right section located at 37°S / Secciones verticales a lo ancho de la plataforma continental de temperatura ($^{\circ}\text{C}$), salinidad y densidad (unidades de sigma-t) mostrando dos fases de un ciclo de surgencia: relajación (noviembre de 2001) y el comienzo de un evento de surgencia (marzo de 2002). Las cruces indican la ubicación y profundidad de los lances de CTD. Superpuesta se encuentra la distribución vertical de huevos, larvas en pre y postflexión, con abundancias expresadas como individuos 1000 m^{-3} . La sección de la izquierda está ubicada a $35^{\circ}25'\text{S}$; la sección de la derecha se ubica a 37°S

Hatching period estimated from August 2001 (mid winter) to March 2002 (late summer) (Fig. 8) showed a peak during late austral summer (February and March 2002, 3659 and 2029 1000 m^{-3} , respectively) with few hatching events during late winter and spring 2001 ($<650\text{ }1000\text{ m}^{-3}$) (Fig. 8).

DISCUSSION

There are similarities and differences in the early life history of *N. crockeri* and the reproductive tactics of other small pelagic fishes inhabiting the Humboldt upwelling ecosystem. Like several species of schooling fishes in the area, reproductive events are carried out in protected

shallow waters and eggs and larvae are found in surface nearshore waters where they may benefit from retention and enrichment processes (Bakun 1996, Lett *et al.* 2007). Anchoveta (*Engraulis ringens*) and common sardine (*Strangomera bentincki*) reproduce inside bays, gulfs and near estuaries off central Chile mainly during austral winter season (Castro *et al.* 2000, Cubillos *et al.* 2001, 2007, Vargas *et al.* 2003) and occasionally during summer (Lett *et al.* 2007).

Previous ichthyoplankton studies in the Humboldt ecosystem have collected preflexion larvae of *N. crockeri* inside bays off Perú mainly during austral spring (up to $4700\text{ }1000\text{ m}^{-3}$, Vélez *et al.* 2005) and close to shore off

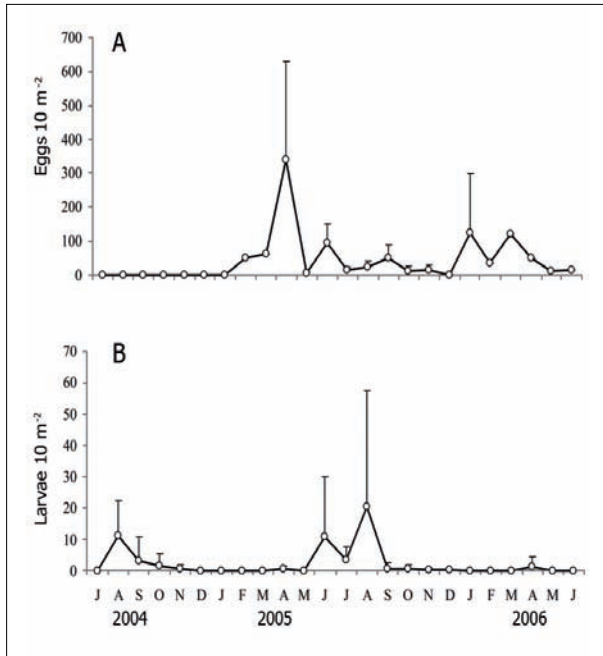


Figure 5. Coastal time series of A) eggs and B) larval abundance (individual 10 m⁻²) of *N. crockeri* off Talcahuano, central Chile between July 2004 and June 2006 / Serie de tiempo costera de abundancia de A) huevos y B) larvas (individuos 10 m²) de *N. crockeri* frente a Talcahuano, Chile central entre julio 2004 y junio 2006

central Chile during late winter, spring and summer (up to 50 1000 m⁻³, Castro *et al.* 2000, Hernández-Miranda *et al.* 2003, Landaeta *et al.* 2008). Our results showed that higher abundances of *N. crockeri* eggs were collected during transitional periods such as late winter and late summer and, in a lesser extent, during spring (Table 1, Fig. 5). The transitional periods (from winter to spring, from summer to autumn) off central Chile are characterized by strong changes in wind speed and direction (Arcos & Navarro 1986, Parada *et al.* 2001), which affect the incidence of relaxation and upwelling events. This variability reduces the offshore Ekman transport of surface waters and there is an increase of the anticlockwise vorticity, increasing the retention of nearshore water parcels (Sobarzo *et al.* 2007) and the zooplankton contained in the surface water column. Since most eggs and larvae of *N. crockeri* are located in the top 50 m of the water column (Fig. 3), where the surface Ekman layer has been estimated (Sobarzo *et al.* 2001), spawning processes occurring during transitional periods may increase the coastal retention of eggs and larvae of *N. crockeri*, especially when the spawning occurs inside bays (Landaeta & Castro 2006b).

On the other hand, during austral spring and summer south-westerly winds lead to the offshore transport of

surface waters resulting in the upwelling of cold, deep water in coastal waters. Spawning near capes during the upwelling season (austral spring and summer) may increase the chance of coastal retention of eggs and larvae that occur between the upwelling front and headlands (*i.e.*, in an upwelling shadow, Graham *et al.* 1992, Wing *et al.* 1998, Marín *et al.* 2003). Such retention has been observed in several marine species with meroplanktonic larvae that settle near the coast in upwelling systems (gastropod *Concholepas concholepas*, Poulin *et al.* 2002, crabs *Emerita analoga* and *Neotrypaea uncinata*, Yannicelli *et al.* 2006a, *Paraxanthus barbiger*, Palma *et al.* 2006, fishes *Sebastes* spp. Wing *et al.* 1998, Bjorkstedt *et al.* 2002). This physical mechanism may explain the horizontal distribution of early stages of the *N. crockeri* off central Chile during austral spring 1996 and 2001 (Fig. 2). In this sense, the coastal geometry may play a role in the maintenance, growth and survival of planktonic stages of *N. crockeri* throughout their early ontogeny in nearshore surface waters (Fig. 3 and 4). At a scale of 100's m to few kilometers, peninsular sites protected from southerly winds (favorable for upwelling) are vertically more stratified and promote the increment

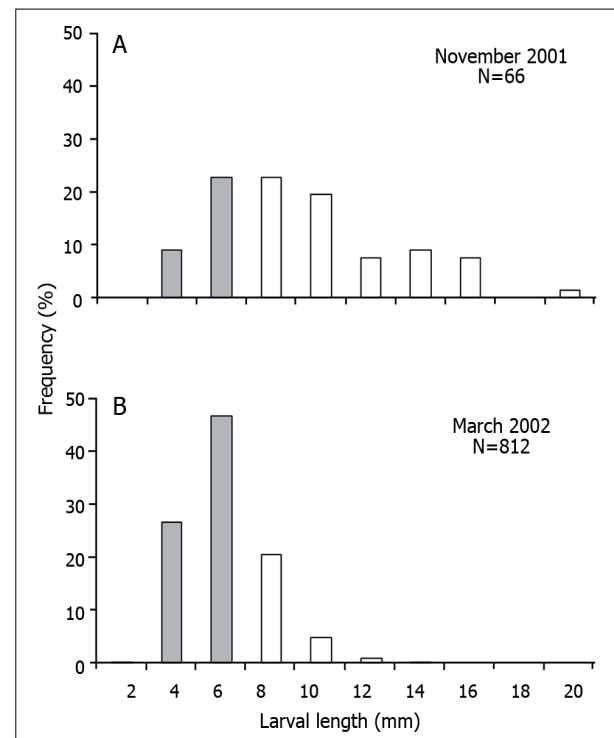


Figure 6. Larval size distribution of *N. crockeri* collected during A) November 2001 and B) March 2002, off central Chile. Grey bars indicate preflexion larvae / Distribución de tamaño de larvas de *N. crockeri* recolectadas durante A) noviembre 2001 y B) marzo 2002, frente a Chile central. Las barras grises indican larvas en preflexión

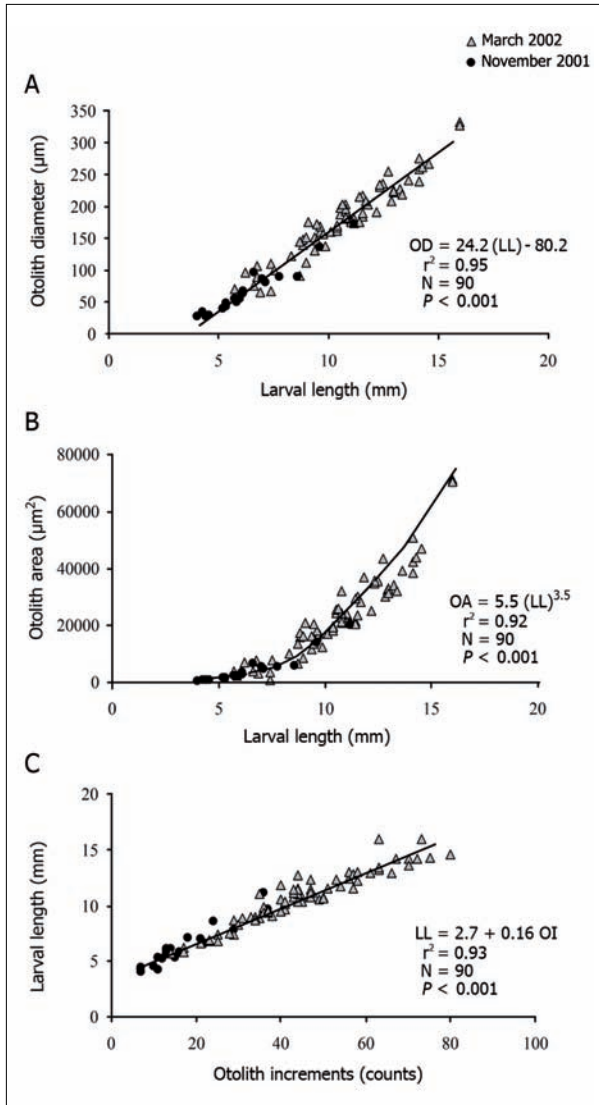


Figure 7. Relationships *N. crockeri* larval length (LL, mm) with A) otolith diameter (OD, μm), B) otolith area (OA, μm^2), and C) number of otolith ring counts (OI). The slope of the least-squares linear regression corresponds to the larval growth rate (mm day^{-1}) / Relaciones entre la longitud larval de *N. crockeri* (LL, mm) con A) diámetro del otolito (OD, μm), B) área del otolito (OA, μm^2) y C) número de conteos de anillos en otolitos (OI). La pendiente de la regresión lineal por mínimos cuadrados corresponde a la tasa de crecimiento larval (mm día^{-1})

of phytoplankton biomass, high concentration of primary production and the retention and settlement/recruitment of meroplankton (Palma *et al.* 2006, Henríquez *et al.* 2007). Although more recently an opposite pattern has been described whereas the weakening of upwelling-favorable winds favors the retention, along exposed sides of small headlands, of phytoplankton and associated primary production (Palma *et al.* 2009). Since larvae of

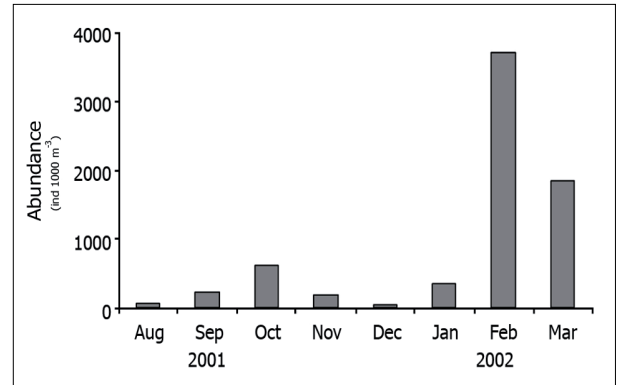


Figure 8. Back-calculated hatching date estimates of *N. crockeri* off central Chile based on otolith ring counts. Abundance of hatched larvae expressed as individuals 1000 m⁻³ / Fechas de eclosión retrocalculadas de *N. crockeri* frente a Chile central basadas en conteo de anillo de otolitos. La abundancia de las larvas eclosionadas se expresa en individuos 1000 m⁻³

N. crockeri are vertically distributed in surface waters and feed on microplankton (mostly copepod eggs, copepods and tintinids, Balbontín *et al.* 1997), protected sites around headlands along central Chile are optimal locations where the feeding success and larval growth of *N. crockeri* can occur.

Although no diel vertical migration of larvae was detected in our analysis (Table 2), this behaviour should not be discarded. Probably the sampled strata in our study were too broad to detect the variability of larval *N. crockeri* in the vertical plane. Some zooplankters, such as the copepods *Calanoides patagoniensis* and *Calanus chilensis*, show vertical oscillations at a fine scale (between 10 and 30 m depth) off central Chile (Castro *et al.* 2007). Therefore, this topic needs to be addressed in the future, particularly in relation to physical processes occurring in coastal waters, such as sea breeze and tidal forcing (Yannicelli *et al.* 2006b).

The lack of recently hatched larvae in the field samples may be due to extrusion from the nets, particularly for the Tucker trawl. Although Vélez *et al.* (2003) collected larvae as small as 1.8 mm LL by using Bongo nets of 0.333 μm mesh size, the towing speed and the lower capture efficiency of the Tucker trawl for larvae smaller than 5 mm (Pepin & Shears 1997) may have affected the estimated abundances of larval *N. crockeri* during November 2001 and March 2002.

In relation to the otolith microstructure and growth, larvae of *N. crockeri* showed lower growth rates than those of other small pelagic fishes with slender larvae inhabiting upwelling ecosystems. Otolith-based estimations of larval

Table 4. Monte Carlo simulations (N = 5000) for the comparison of the mean values of the growth parameters for larval *N. crockeri* / Simulaciones Monte Carlo (N = 5000) para la comparación de los valores promedio de los parámetros de crecimiento en larvas de *N. crockeri*

	<i>A</i>		<i>β</i>	
	2001	2002	2001	2002
N	5000	5000	5000	5000
Estimated mean	2.874	3.93	0.201	0.15
<i>S</i> ² <i>P</i>	0.07568		0.00015	
<i>t</i> _{cal}	-191.86		208.29	
<i>P</i> - value	> 0.05		> 0.05	

growth of anchoveta (*E. ringens*, 0.66 mm day⁻¹, Herrera *et al.* 1985, 0.47 mm day⁻¹, Hernández & Castro 2000, 0.68-0.79 mm day⁻¹ Castro & Hernández 2000), common sardine (*S. bentincki*, 0.38 mm day⁻¹, Castro *et al.* 1997) and sardine (*Sardinops sagax*, 0.40-0.65 mm day⁻¹, Castillo *et al.* 1985) off central Chile where higher than estimates for *N. crockeri* larvae (0.15-0.20 mm day⁻¹). Growth estimates of larval *N. crockeri* were more similar to other fish species with deeper bodied larva such as rockfish (*Sebastes saxicola*, 0.13 mm day⁻¹, Laidig *et al.* 1996; *S. goodie*, 0.14 mm day⁻¹, Sakuma & Laidig 1995; *S. jordani*, 0.17 mm day⁻¹, Laidig *et al.* 1991; *S. oculatus*, 0.15 mm day⁻¹, Landaeta & Castro 2006c) and hake (*Merluccius productus*, 0.16 mm day⁻¹, Bailey 1982; *M. bilinearis*, 0.17-0.18 mm day⁻¹, Jeffrey & Taggart 2000; *M. hubbsi*, 0.16 mm day⁻¹, Brown *et al.* 2004), which also have relatively slow growth rates. The slow growth rate observed in *N. crockeri* larvae seems intriguing considering that is a short-lived species (up to 4 years old, G.A. Aedo, pers. comm.); probably for this species larval length is not the best predictor of body growth. According to Vélez *et al.* (2003), the body depth of *N. crockeri* preflexion larvae is 13% body length (BL), increasing to 19% BL in the transformation stage. Therefore, during postflexion stage, individuals grow more in depth than in length.

In summary, our results indicate that *N. crockeri* off central Chile spawn in coastal protected sites mostly during transitional periods, eggs and larvae are located in the top 50 m of the water column, and larvae grow at a rate of 0.15-0.20 mm day⁻¹.

Finally, it is important to understand the reproduction and larval ecology of *N. crockeri* due to the increase in landings of this species in recent years as part of the by-catch of the anchoveta and common sardine artisan fisheries. Increased early life history knowledge, will assist in the sustainable

management of exploited populations that inhabit the coastal waters of central Chile.

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