

Inter-annual reproductive trait variation and spawning habitat preferences of *Engraulis ringens* off northern Chile

Variaciones interanuales en aspectos reproductivos y preferencias por el sitio de desove en *Engraulis ringens* del norte de Chile

Gabriel Claramunt¹, Leonardo R. Castro², Luis A. Cubillos³, Hans-Jürgen Hirche⁴, Graciela Perez⁵ and Mauricio Braun⁶

¹Departamento Ciencias del Mar, Universidad Arturo Prat, Casilla 121, Iquique, Chile. gclaramu@unap.cl

²Laboratorio de Oceanografía Pesquera y Ecología Larval, Centro FONDAP-COPAS y Departamento de Oceanografía, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Casilla 160-C, Concepción, Chile

³Laboratorio de Evaluación de Poblaciones Marinas (EPOMAR), Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile

⁴Alfred Wegener Institute for Polar and Marine Research, Columbusstrasse D-27568, Bremerhaven, Germany

⁵Instituto de Fomento Pesquero, Barrio Industrial, Sitio Nº 2, Casilla 170, Iquique, Chile

⁶Instituto de Fomento Pesquero, Blanco 839, Casilla 8-V, Valparaíso, Chile

Resumen.- A lo largo del Sistema de la Corriente de Humboldt, la anchoveta (*Engraulis ringens*) se distribuye entre los 4ºS y 42ºS. Las condiciones ambientales difieren notablemente tanto entre las zonas de desove y las estaciones del año. Por lo tanto, diferentes tácticas reproductivas se esperan en respuesta al medio ambiente. En este estudio se utilizó la información proveniente de cruceros para la aplicación del Método de Producción Diaria de Huevos (MPDH) para estudiar la variabilidad latitudinal e interanual de los parámetros reproductivos de las poblaciones de *E. ringens* en la zona norte (18º 20' a 26º00'S) y sur (33º 00' a 41º 30'S) de Chile. El objetivo principal es investigar las potenciales preferencias por ciertos rangos de temperatura y concentración de clorofila-*a* en el hábitat de desove y los cambios en el potencial reproductivo y tamaño de los huevos de anchoveta en respuesta a las condiciones del hábitat, en especial a la temperatura. Los resultados muestran que la temperatura no es una variable relevante del medio ambiente para determinar la posición geográfica de las zonas de desove de *E. ringens*. Altas concentraciones de clorofila sería la variable seleccionada para los cambios en la posición de las áreas de desove. Se postula que en lugar de preferir cierto rango de temperatura, anchoveta acomoda los productos del desove de acuerdo a las condiciones predominantes del medio ambiente (*ej.* tamaño del huevo, fecundidad) y esta respuesta sería en la escala de la frecuencia de desove, es decir, semanas.

Palabras clave: Áreas de desove, producción de huevos, fecundidad, anchoveta

Abstract.- Along the Humboldt Current System, the anchoveta (*Engraulis ringens*) is distributed between 4ºS and 42ºS. Environmental conditions differ markedly both between spawning areas and seasonally. Hence, different reproductive tactics are expected in response to the environment. Here we used information from Daily Egg Production Method surveys to study latitudinal and interannual variability of the reproductive parameters in stocks of *E. ringens* from the northern (18º 20' to 26º 00'S) and southern (33º 00' to 41º 30'S) Chilean coast. The main goal was to investigate potential preferences for temperature and chlorophyll concentration in the spawning habitat and changes in the reproductive potential and egg size of anchoveta in response to the prevalent habitat conditions, mainly temperature. Temperature was not a relevant environmental variable to determine geographical position of the spawning areas in *E. ringens*. High chlorophyll-*a* concentration appears as the selected variable for spawning habitat. According to our results, the interannual changes in the body weight-fecundity relationship are related to the temperature of the environment, which affects the egg size. We postulate, therefore, that instead of searching for certain temperatures, anchoveta accommodate their offspring characteristics according to the prevalent environment (*e.g.*, egg size, fecundity). The response of the reproductive system to temperature might be in the scale of spawning frequency, *i.e.*, weeks.

Key words: Spawning areas, egg production, fecundity, anchoveta

INTRODUCTION

Along the Humboldt Current System, the anchoveta, *Engraulis ringens* Jenyns, 1842, is distributed mainly between 4° S and 42° S (Serra 1986). Castro *et al.* (2009) distinguished three major stocks: the largest off northern-center Peru, a mid-sized one off southern Peru–northern Chile, and the smallest off central Chile (see also Valdivia *et al.* 2007). The occurrence of upwelling changes from mostly continuous in northern Chile to a more seasonal pattern in central Chile (Thiel *et al.* 2007, Sobarzo *et al.* 2007). Off central Chile, the spawning season is in wintertime, when temperatures are lower, upwelling events are scarce and wind induced turbulence in the water column is higher than in northern Chile (Castro *et al.* 2009). On an interannual scale, the physical forcing is associated with the El Niño Southern Oscillation (ENSO) cycle (Yañez *et al.* 2008). The persistence of *Engraulis ringens* in these highly variable environments is probably a result of a complex set of behavioral and biological traits that form part of the adult reproductive strategy. Therefore, different reproductive tactics are expected in response to the differences in environmental conditions along the species range and in an interannual scale.

Wright & Trippel (2009) report that unlike many other branches of evolutionary ecology, fishery science theory has tended to consider offspring survival (recruitment) in relation to a population's peak or duration of egg production rather than the reproductive success of individual parents. As such, fishery science has tended to focus on the role of the environment in influencing year-class variation rather than the life history traits that fish have evolved to reproduce successfully under these varying conditions. In the case of *Engraulis ringens* from the Chilean coast, studies during recent years have determined how the early life stages of this species cope with variations in environmental conditions (Castro *et al.* 2000, 2009, Hernández & Castro 2000, Llanos-Rivera & Castro 2004, 2006). In particular, it has been shown that egg size, larval length at hatching and yolk sac volume of recently hatched larvae increase with latitude and instantaneous yolk sac larval growth rates vary between populations (Llanos-Rivera & Castro 2006). Leal *et al.* (2009) found that the oocyte size is smaller and fecundity is higher in northern population as compared with the population off central Chile, concluding that the environmental temperature could play an important role in oocyte number and size regulation.

Most of the recent studies assessing potential reproductive trait variations of anchoveta have focused

on either seasonal or latitudinal variations along the species range. Less attention has received the study of the potential relationship between these traits and environmental fluctuations within each population distribution range at the inter-annual time scale. Along the Chilean coast, the Daily Egg Production Method (DEPM) has been utilized for several years to estimate spawning biomass in the northern and central Chile *E. ringens* populations. One of the great advantages of this method is that in addition to abundance estimates it provides valuable information about the reproductive biology of the stocks through intensive sampling of the ichthyoplankton and adult females. This information may be utilized to study maternal effects as it includes datasets of large sample size, large spatial coverage and almost unchanged repetitive sampling design over several years that allow interannual and inter population comparisons.

In the present study, we analyzed the interannual variability in the reproductive parameters of *E. ringens* from the population located in northern Chile, to determine potential changes in the characteristics of the reproductive output (spawning habitat preferences, egg size, fecundity and daily spawning fraction) in response to the prevalent habitat conditions. As indicators of habitat condition we utilized sea surface temperature and phytoplankton biomass (satellite derive chlorophyll-a). Temperature is usually used as a proxy for habitat condition in coastal upwelling areas, it is a common variable available from all surveys carried out in the different spawning areas, and also it is an environmental variable known to affect reproductive parameters. Phytoplankton biomass (chlorophyll-a concentration) distribution is here utilized to explore whether it might have a relationship with the selection of the main female spawning sites (as depicted by the largest egg abundances) within the spawning area. Temperature and phytoplankton biomass abundance may co-vary in some environments (depending on the time and space scales explored). However, this potential relationship may not always hold in upwelling areas since the highest chlorophyll values are usually reached not at the lowest temperature zones (*i.e.*, in recently upwelled water) but in nearby areas where the upwelled waters rich in nutrients have reached some stability after few days at the photic zone. When reproductive and environmental data was available, we expanded our analyses to the southern *E. ringens* population located in central Chile. These complementary analyses in some cases allowed to broadening the range of environmental values over with

the reproductive traits were assessed and, in other cases were utilized for inter-population comparisons in traits response to different conditions.

We use the term selection or habitat preference as usual in the related literature of characterization of the spawning habitats. According to SPACC Meeting (Castro *et al.* 2005): small pelagic fish are indeterminate spawners that spawn repeatedly over a protracted reproductive season, and often in a variety of environments. The number of eggs produced per spawning season depends both on energy (lipid) reserves and the quantity and quality of food available during the season, and hence is not fixed at the beginning of the reproductive season. Additionally, small pelagic fish can cease spawning and reabsorb their eggs if conditions become unfavourable, a process known as atresia. Given the above, weak or no selection for temperature/salinity optima or for other environmental proxies could perhaps be expected. A disadvantage of this approach is that temperature/salinity or other variable may not necessarily be important *per se* for spawning habitat selection, but may be proxies for other variables (*e.g.*, productivity) that may be more relevant to spawning habitat selection (Castro *et al.* 2005).

MATERIALS AND METHODS

In Chile, spawning stock biomass estimates for *Engraulis ringens* have been obtained by conventional application of DEPM in the two main spawning areas. In northern Chile (18°20'S-26°S), DEPM was applied in 1995, 1996 and from 1999 to 2007¹. In central Chile (33°00'S-41°30'S), DEPM was applied from 2002 to 2007¹. Plankton stations were distributed regularly in a sampling grid where eggs were collected in vertical hauls of Paironet nets (0.05 m² and 0.150 mm mesh size). The sampling scheme was based on transects spaced approximately ten nautical miles apart and stations located at five-nautical-mile intervals on each transect. In addition, purse-seine boats were used for annual adult surveys, which sampled a minimum of 30 females in each of 32 hauls (Table 1).

SPAWNING AREA

A single factor quotient analysis was utilized as an exploratory data analysis tool to describe the potential relationship between egg abundance and temperature (Van der Lingen *et al.* 2001, Drapeau 2004). First, the seawater temperature data set (temperature at 10 m depth) collected

Table 1. Number of hauls and total number of females sampled in the DEPM surveys and used for histological analysis. All surveys are centered in August / Número de lances y número de hembras muestreadas en los cruceros y las utilizadas para análisis histológico. Todos los cruceros están centrados en agosto

Year	Northern Chile		Southern Chile	
	Hauls	Females	Hauls	Females
1992	48	1440	-	-
1995	40	1177	-	-
1996	32	927	-	-
1997	60	1800	-	-
1999	51	1530	-	-
2000	92	1800	-	-
2001	60	1800	-	-
2002	60	1800	32	1384
2003	60	1800	78	2620
2004	55	1651	45	1456
2005	60	1799	40	1147
2006	42	1260	-	-
2007	55	1645	50	1991

over the entire region each year was divided in equally temperature ranges classes and the percentage frequency of occurrence (p_i) of each class (i) within the entire area was determined as:

$$p = \frac{p_i}{\sum_{i=1}^j p_i} * 100$$

The same procedure was applied to egg abundance data, with the number of eggs associated with each temperature class (h_i), expressed as a percentage of the total number of eggs collected during the survey:

$$h = \frac{h_i}{\sum_{i=1}^j h_i} * 100$$

Finally the quotient was estimated as

$$Q = \frac{h}{p}$$

Confidence intervals of the null hypothesis of even distribution were computed by a resampling procedure

¹Final reports are available online at <<http://www.fip.cl>>

(999 times) in order to test for the significance of quotient values larger or smaller than one according to Bernal *et al.* (2007), through an implementation of a routine in Visual Basic (Macro in Microsoft Excel). If the quotient value is significantly > 1 or above the upper confidence interval, fish are assumed to select that variable range for spawning, and if it is significantly < 1 or below the lower confidence interval the variable range is assumed to be avoided (Van der Lingen *et al.* 2001, Bernal *et al.* 2007). For the northern and southern zone intervals of 0.2 and 0.5°C were used respectively, because of the range of temperatures on the surveys.

A quotient analysis was also carried out in the northern area utilizing chlorophyll-a satellite derived data. In this area, monthly chlorophyll (Chl-a) data (years 2002 to 2011) were obtained from the MODIS-Aqua sensor, produced and distributed by Ocean Color Data Processing System², with a resolution of 10x10 nm in a hierarchical data file and represent a global coverage for each month. Due to the high asymmetry, Chl-a data were transformed by using natural logarithm. The quotient analyses with chlorophyll-a were carried out following the same procedures utilized for the temperature analyses.

Egg density (number by 0.05 m²), latitude, longitude, temperature (10 m depth) and satellite Chl-a (ln transformed) data were used to fit a GAM model as a complement of the quotient analysis in order to assess the potential influence of this set of parameters on the selection of spawning sites by *E. ringens* females in northern Chile. For the selection of the GAMs smoothing predictors we applied the methodology proposed by Wood & Augustin (2002), using the 'mgcv' library in the R statistical software (R Development Core Team 2004). GAMs produced smoothed fits for each environmental predictor.

BATCH FECUNDITY

From both spawning areas, the number of eggs spawned per batch (batch fecundity; *F*) was estimated by applying the gravimetric method on hydrated females (Hunter *et al.* 1985), which excludes females with new postovulatory follicles as determined from histology. The oocyte countings were carried out on three ovary sections (front, medium and posterior) of about 0.2 g each, from which at least 100 hydrated oocytes were observed. Batch fecundity was estimated as the average of these three

subsamples. The same procedures were utilized in the southern spawning zone.

OOCYTE AND EGG SIZE

From 2000 to 2003 and in 2007, anchoveta eggs collected in northern Chile were measured (major and minor axis) utilizing an image analysis software ImageJ³. The volume was estimated assuming the egg to be of ellipsoid shape ($V = 4/3 \pi \cdot a \cdot b \cdot c$, being a, b and c the radius of the ellipsoid).

SPAWNING FRACTION

The daily spawning fraction (*S*) of *E. ringens* (*i.e.*, proportion of female fish that reproduce daily) in each DEPM application was estimated from the histological preparation of the female ovaries by identifying and classifying postovulatory follicles (POF) into daily cohorts. POFs were classified in 0-, 1- and 2-days, where POF 0- day means that spawning occurred less than 9 h, POF 1- day from 9 to 33 h and POF 2- day from 33 to 56 h from the spawning peak (we used 23:00 h), according to the criteria of Hunter & Macewicz (1985). The mean of *S* was estimated using females with POF 1- day and 2- day (POF 1+2), thus increasing the sample size and reducing the variance (Alheit *et al.* 1984). These same procedures were utilized for the southern spawning population.

RESULTS

SPAWNING AREA

In the northern zone a high variability in both location (geographical position) and extent (area covered by positive stations) of the spawning area was observed (Fig. 1). In terms of locations, changes occurred in latitude and coast-ocean directions. In some years the eggs were distributed near the coast (*e.g.*, 2001, 2003 and 2004), in contrast to years with a more oceanic distribution (2000, 2002, 2005). Latitudinally within the spawning area in northern Chile, in some years the main spawning zones were north of 20°S (*e.g.*, 2007), while in others years they were south of 21°S (*e.g.*, 2001, 2005).

In the northern spawning area off Chile, the mean temperature at 10 m depth throughout the years studied was 15.9°C (SD = 0.997) (Fig. 2). In 1997 the influence of a strong El Niño event was clearly observed as revealed by

²<http://oceancolor.gsfc.nasa.gov>

³<http://rsb.info.nih.gov/ij/>

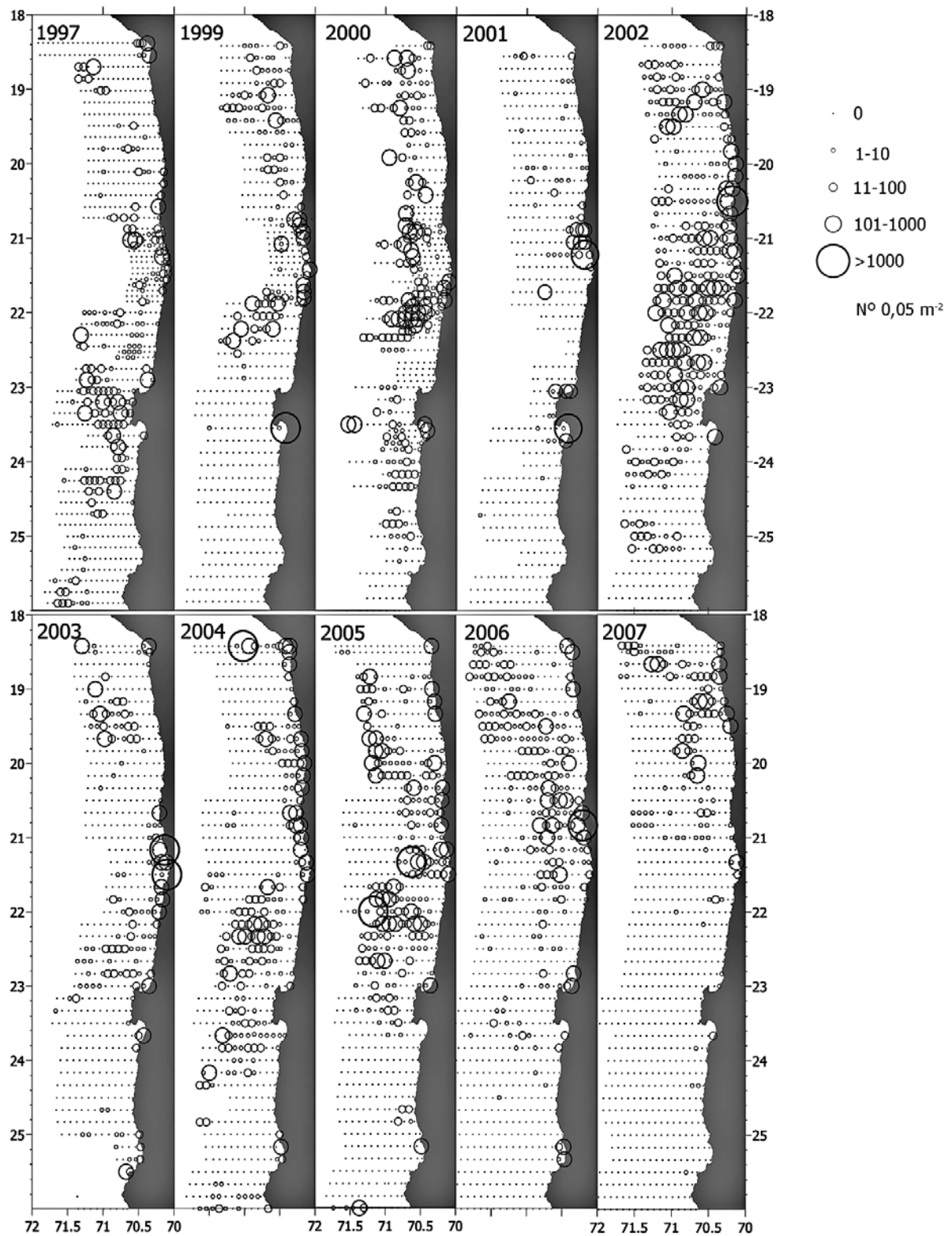


Figure 1. Spawning areas of anchoveta from northern Chile. Size of the circles represents eggs density / Áreas de desove de anchoveta en el norte de Chile. Tamaño de los círculos representan la densidad de huevos

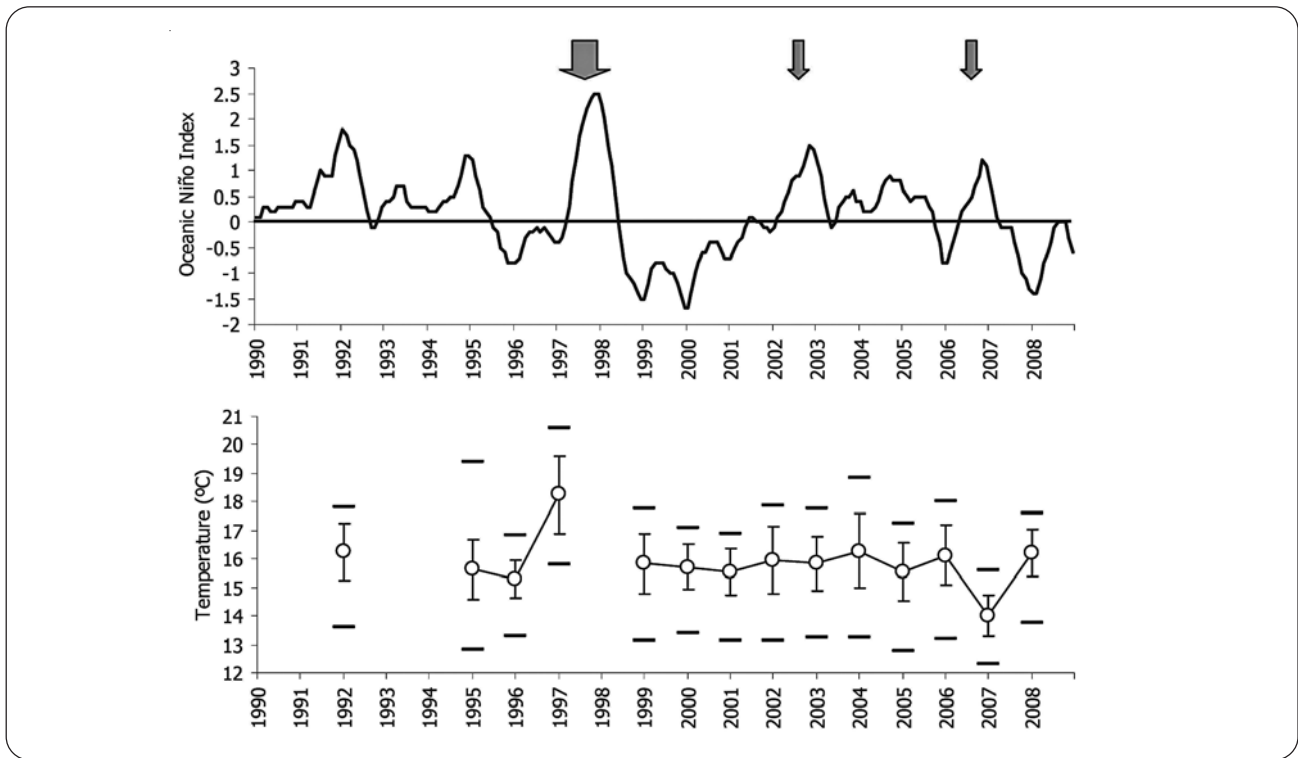


Figure 2. Up: Warm and cold episodes based on the Oceanic Niño Index (ONI) anomalies in the Niño 3.4 region (5°N-5°S; 120°-170°W), based on the 1971-2000 base period (*). Arrows indicate El Niño events (1997, 2002 and 2006). Bottom: Mean temperature (10 m depth) of each survey in northern Chile. Vertical lines: standard deviation. Horizontal lines: Minimum and maximum / Arriba: Episodios cálidos y fríos basados en las anomalías del Índice Oceánico de El Niño (ONI) en la región Niño 3.4 (5°N-5°S; 120°-170°W), con período base de 1971-2000(*). Flechas indican eventos El Niño (1997, 2002 y 2006). Abajo: Temperaturas medias (10 m profundidad) de cada crucero en el norte de Chile. Líneas verticales: Desviación estándar. Líneas horizontales: Mínimo y máximo
 (*): <http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml>

a temperature mean of 18.3°C (SD = 1.36) during the survey. In contrast, the year 2007 was under La Niña influence with a mean survey temperature of 14°C (SD = 0.73).

The quotient analysis shows different situations for every year. In Figure 3 only three years of contrasting environmental conditions (El Niño; La Niña; Neutral ENSO) are presented (for graphic simplicity) for the northern and southern spawning areas. A shift in the frequency of observed temperatures of the water column over the area were observed among years in both areas (from higher temperatures in El Niño to mid temperatures in Neutral ENSO and to lower temperatures during La Niña), more particularly evident in the northern spawning area. The quotient analyses for the northern area (intervals of 0.2°C) indicate that under the influence of El Niño (1997) a significant preference for a narrow range of temperatures of 19.0-19.2°C, while in normal years (Neutral ENSO, 2002) significant association are found at 15.0-15.2 and 16.6-16.8°C. In colder years (2007, La Niña) a

significant relationship for 14.8 to 15.2°C was observed. Accordingly, potential temperature associations during these very contrasting years changed also following the variations in environmental conditions. All years grouped (1992 to 2007) shows significant peaks at 15.0-15.2, 16-16.2 and 19-19.2°C (Fig. 3, bottom panels). For southern zone the quotient analysis (every 0.5°C) shows a significant peak at 11.0-11.5°C in 2002 and 11.5-12.0 in 2005. There are no significant preferences in 2007 (Fig. 3). All years grouped for the southern zone shows a significant preference between 9.5-11°C due to the influence of the colder year of 2007.

A summary of the quotient analysis for the time series in northern zone (Fig. 4) show different significant peaks of the quotient (preferences) for every year. The years 2000, 2001, 2003 and 2006 do not shows any significant preferences. There is not a clear pattern for avoidance (quotient significantly <1).

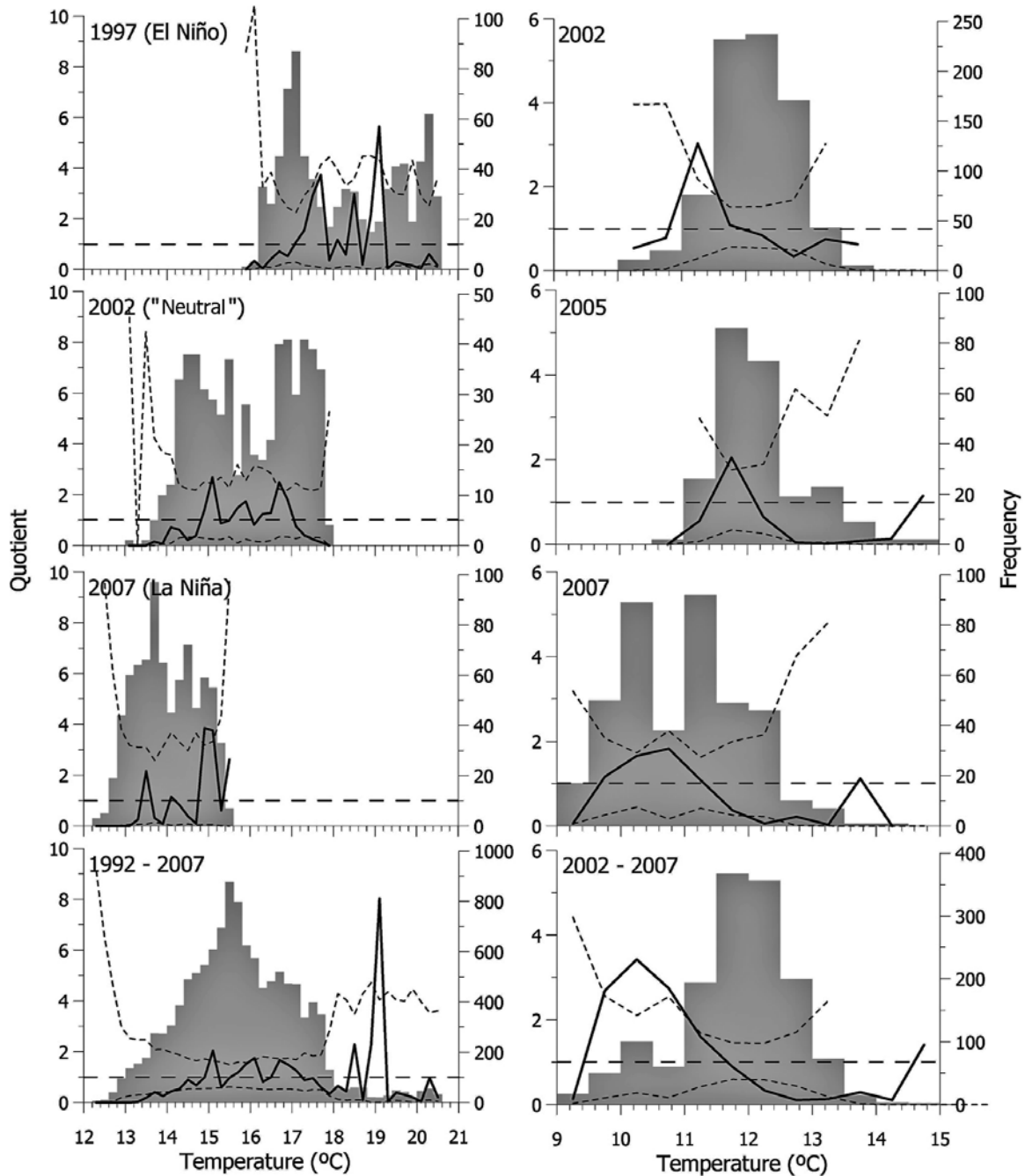


Figure 3. Quotient analysis for anchoveta egg distribution according to temperature in northern (left panels) and southern Chile (right panels) for three years of contrasting environmental conditions and the entire period analyzed (bottom). Grey areas show the number of observation (frequency) within each interval of temperature. The continuous line represents the egg concentration quotient value. Dashed lines represent its upper and lower confidence interval. The horizontal lines represents the null hypothesis of evenly distributed eggs (Quotient = 1) / Análisis del cociente para la distribución de huevos de anchoveta en relación a la temperatura en el norte (paneles a la izquierda) y sur (paneles a la derecha) de Chile para tres años de condiciones ambientales contrastantes y para el período total analizado (abajo). Áreas grises muestran el número de observaciones (frecuencia) dentro de cada intervalo de temperatura. La línea continua representa el cociente de la densidad de huevos. Líneas discontinuas representan el límite de confianza superior e inferior. La línea horizontal representa la hipótesis nula de huevos igualmente distribuidos (Cuociente = 1)

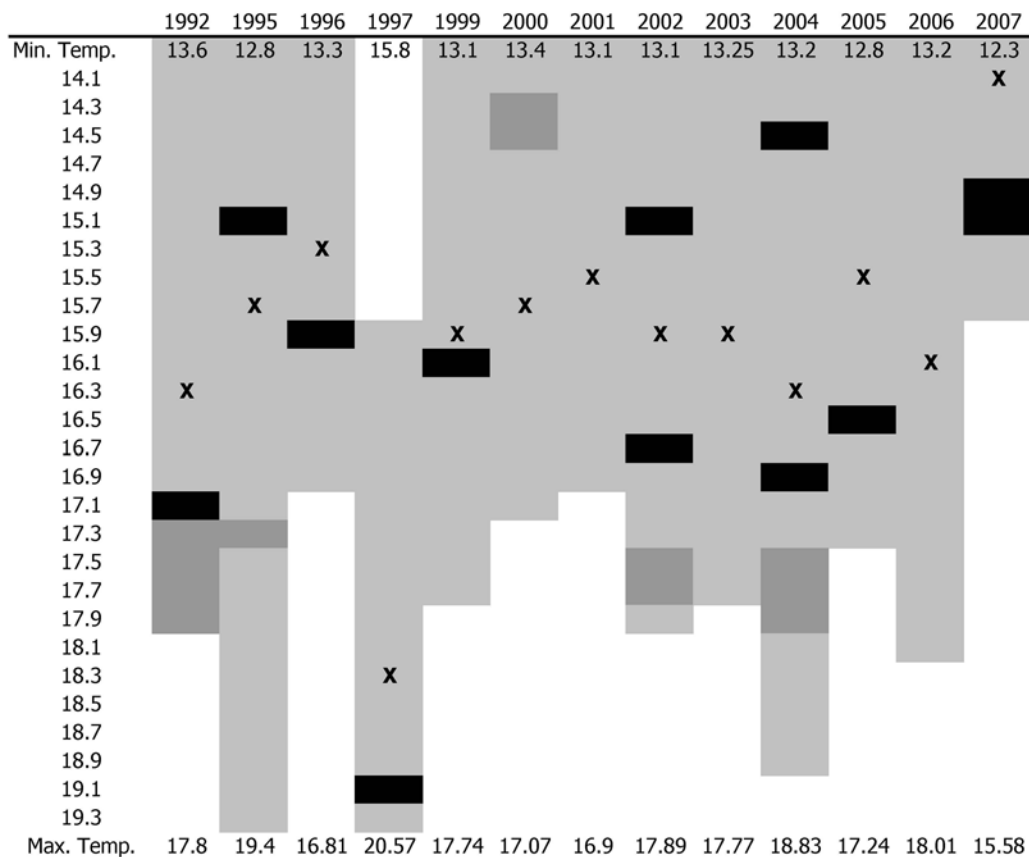


Figure 4. Results of the Quotient analysis for anchoveta egg distribution according to temperature in every survey in northern Chile. Black square represents significant preferences (Quotient > 1). Dark grey rectangles represent significant avoidance (Quotient < 1). Light grey shadow represent the temperature range (minimum and maximum temperature are showed). X represents mean temperature of the survey / Resultados del análisis del cociente para la distribución de huevos de anchoveta en relación a la temperatura en cada crucero en el norte de Chile. Cuadrados negros representan preferencias significativas (Cuociente > 1). Rectángulos grises oscuros representan rechazos significativos (Cuociente < 1). Gris claro muestra el rango de temperaturas (Se muestran la temperatura mínima y máxima). X representa la temperatura media del crucero

Thus, according to the results of quotient analyses for temperature, there is an inconsistency in the preferences for a temperature range by anchoveta females on an interannual scale.

The quotient analysis for chlorophyll-*a* in the northern zone for the period 2004-2009 shows significant peaks at high levels of chlorophyll-*a* (Fig. 5a). Because of the high asymmetry in the data, we carried out the same analysis but with the logarithm of the chlorophyll-*a* data. The results shows a persistent preference for values higher than 0.6-0.8 mg m⁻³ (-0.25 to -0.5 in ln) (Fig. 5b).

The best GAM models applied to analyze the preferences, according to the deviance explained was

Eggs number = s(Latitude) + s(Longitude) + s(logarithm of Chl-*a*) (Table 2) with Poisson distribution and a link function log. Adding the Year and Temperature there is an increase of 0.2 and 4.2% of the explained deviance, respectively (Table 2). The plot of the smooth for Chl-*a* effect on eggs number shows similar result as quotient plot, a preference for higher concentration of Chl-*a* (Fig. 6).

BATCH FECUNDITY

The linear regression between body weight (*W*) and batch fecundity (*F*; Table 3) showed that in the 12 years analyzed in northern Chile, only in three years the intercept was

Figure 5. Quotient analysis for anchoveta egg distribution according to chlorophyll-*a* concentration (satellite) in northern Chile (a) and with log transformed chlorophyll-*a* concentration (b). Grey areas show the number of observation (frequency) within each interval of chlorophyll. The continuous line represents the egg concentration quotient value. Dashed lines represent its upper and lower confidence interval. The horizontal lines represents the null hypothesis of evenly distributed eggs (Quotient = 1) / Análisis del cociente para la distribución de huevos de anchoveta en relación a la concentración de clorofila-*a* (satelital) en el norte de Chile (a) y con los valores de clorofila-*a* transformados a logaritmo (b). Áreas grises muestran el número de observaciones (frecuencia) dentro de cada intervalo de clorofila-*a*. La línea continua es el valor del cociente de la concentración de huevos. Líneas discontinuas representen el intervalo de confianza superior e inferior. La línea horizontal representa la hipótesis nula de huevos igualmente distribuidos (Cuociente = 1)

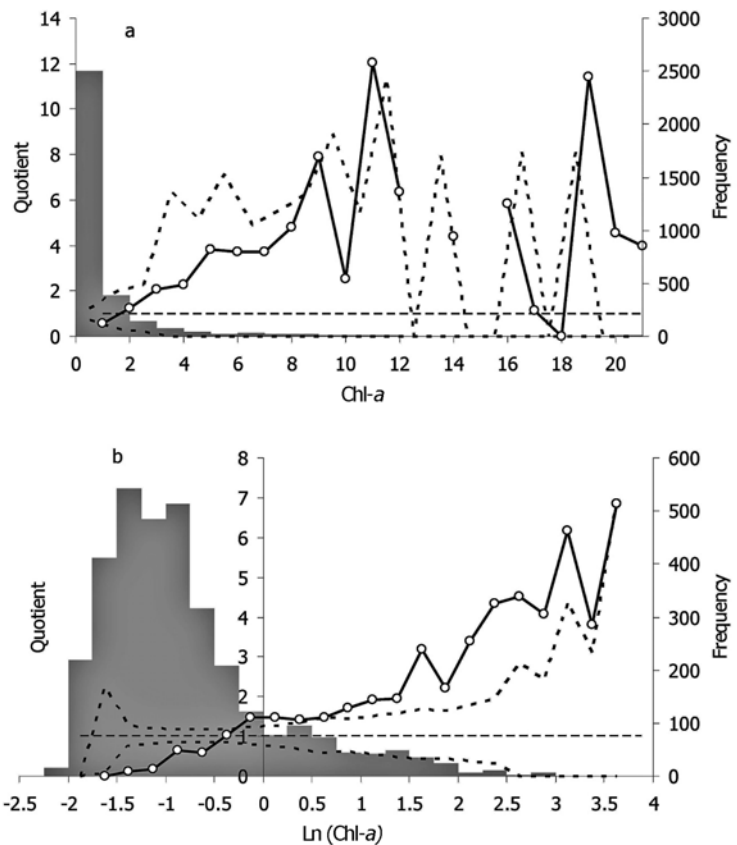


Figure 6. Plots of the smoothing response of the Generalized Additive Model for anchoveta spawning against chlorophyll-*a* concentration (satellite). Black thick line indicates the value of the GAM smoothing response and dotted lines represent the 95% confidence intervals / Respuesta suavizada del modelo aditivo generalizado para el desove de anchoveta en función de la concentración de clorofila-*a* (satélite). Línea gruesa negra indica el valor de la respuesta del modelo (GAM) y líneas segmentadas representan el intervalo de confianza al 95%

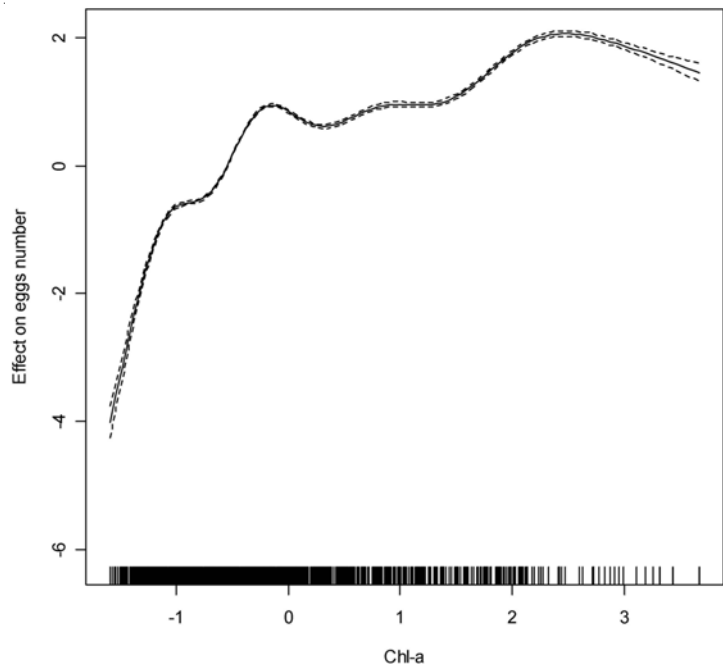


Table 2. Results of the generalized additive models (GAM). Intercept represents the overall mean, and s(Parameter) is the tensor product smoother. The standard error is shown in parenthesis. All parameters are significant. First column: Eggs number = s(Latitude) + s(Longitude) + s(logarithm of Chl-a). Second column: Same model more year. Third column: same model more temperature / Resultados del modelo aditivo generalizado (GAM). Intercepto representa la media y s(Parámetro) es el suavizador. El error estándar es mostrado en paréntesis. Todos los parámetros son significativos. Primera columna: Número de huevos = s(Latitud) + s(Longitud) + s(logaritmo de Chl-a). Segunda columna es el mismo modelo más año. Tercera columna: mismo modelo más temperatura

	1	2	3
Intercept	1.97 (0.0099)	147.91 (5.42)	185.36 (5.68)
Year		-0.073 (0.0027)	-0.091 (0.0028)
s(Latitude)	8.912	8.912	8.884
s(Longitude)	8.784	8.784	8.714
s(log(Chl-a))	8.942	8.942	8.926
s(Temperature)	---	---	8.901
R ² (adj)	0.057	0.054	0.0674
UBRE score	71.875	71.654	67.788
Deviance explained	25.2%	25.4%	29.4%

Table 3. Parameters of the regression between body weight (W) and batch fecundity (F) for each year in northern and southern Chile. Sa and Sb: Standard error of parameter. F = b*W: Regression forced to the origin (a = 0). (*): Intercept not significant different from zero (P > 0.05) / Parámetros de la regresión entre peso corporal (W) y fecundidad parcial (F) para cada año en el norte y sur de Chile. Sa y Sb: Errores estándar de los parámetros. F = b*W: Regresión forzada al origen (a = 0). (*): Intercepto no significativamente distinto de cero (P > 0,05)

Year	Northern Chile						F = b*W		
	Intercept(a)	S _a	F = a + b*W Slope (b)	S _b	r ²	n	Slope (b)	S _b	
1995	671.77 (*)	1916.66	534.57	65.12	0.30	156	557.18	8.93	
1996	337.46 (*)	1514.08	690.51	55.68	0.59	107	702.69	10.63	
1997	6950.80	1923.85	262.61	78.30	0.05	210	543.16	10.35	
1999	105.44 (*)	816.02	498.60	34.12	0.54	187	502.85	8.90	
2000	-5127.08 (*)	3285.50	740.45	116.16	0.28	109	560.55	14.35	
2001	2205.21 (*)	2097.95	465.10	69.02	0.26	133	536.77	10.70	
2002	11341.20	2719.11	259.56	121.04	0.06	69	761.07	15.52	
2003	-1237.67 (*)	1388.04	615.84	57.52	0.54	99	565.24	9.36	
2004	-4164.12 (*)	2944.92	584.18	120.27	0.20	96	414.75	10.38	
2005	1152.76 (*)	2582.87	431.29	86.79	0.24	79	469.74	10.61	
2006	-4476.16 (*)	2326.28	788.63	87.82	0.54	72	622.63	16.76	
2007	-4212.84	1688.05	726.94	74.06	0.57	76	544.00	10.93	
				Southern Chile					
2002	-613.40 (*)	824.67	422.38	44.29	0.37	158	390.16	9.20	
2003	121.00 (*)	580.50	395.12	34.07	0.58	100	401.89	10.97	
2004	600.21 (*)	864.32	360.86	39.08	0.56	68	387.13	9.76	
2005	-311.16 (*)	677.80	331.17	40.18	0.76	23	313.89	13.82	
2007	-574.21 (*)	734.85	445.11	33.36	0.66	92	419.91	8.54	

significantly different from zero (1997, 2002 and 2007; t test; $P < 0.05$). For central Chile population Chile in all years the intercept was not different from zero (t test; $P > 0.05$; Table 3). If the relationship between body weight and batch fecundity has intercept equal to zero, therefore the model is: $F = b \cdot W$, which the slope is relative fecundity (N° oocytes per gram of body weight) and is independent of the female body weight. The confidence interval (95%) of the slope (relative fecundity) for the central Chile population zone does not overlap with the northern population except 2004, indicating a significant lower relative fecundity in the central Chile population. When all years are pooled the slope of the relationship is

significantly higher in the northern than in the central population ($t_{\text{calc}}: 3.76, P < 0.05$) (Fig. 7), indicating a higher fecundity at the same female body weight. However, there is no significant difference ($t_{\text{calc}} = 1.38; P > 0.05$) in the slope of the relationship between body weight and ovary weight between populations (Fig. 7). A small difference was found between intercepts ($P < 0.05$), but for the northern zone these results have the risk of extrapolation of the regression lines far beyond the range of body weight (below 20 g). Therefore, a female with the same body weight has the same ovary weight in both populations.

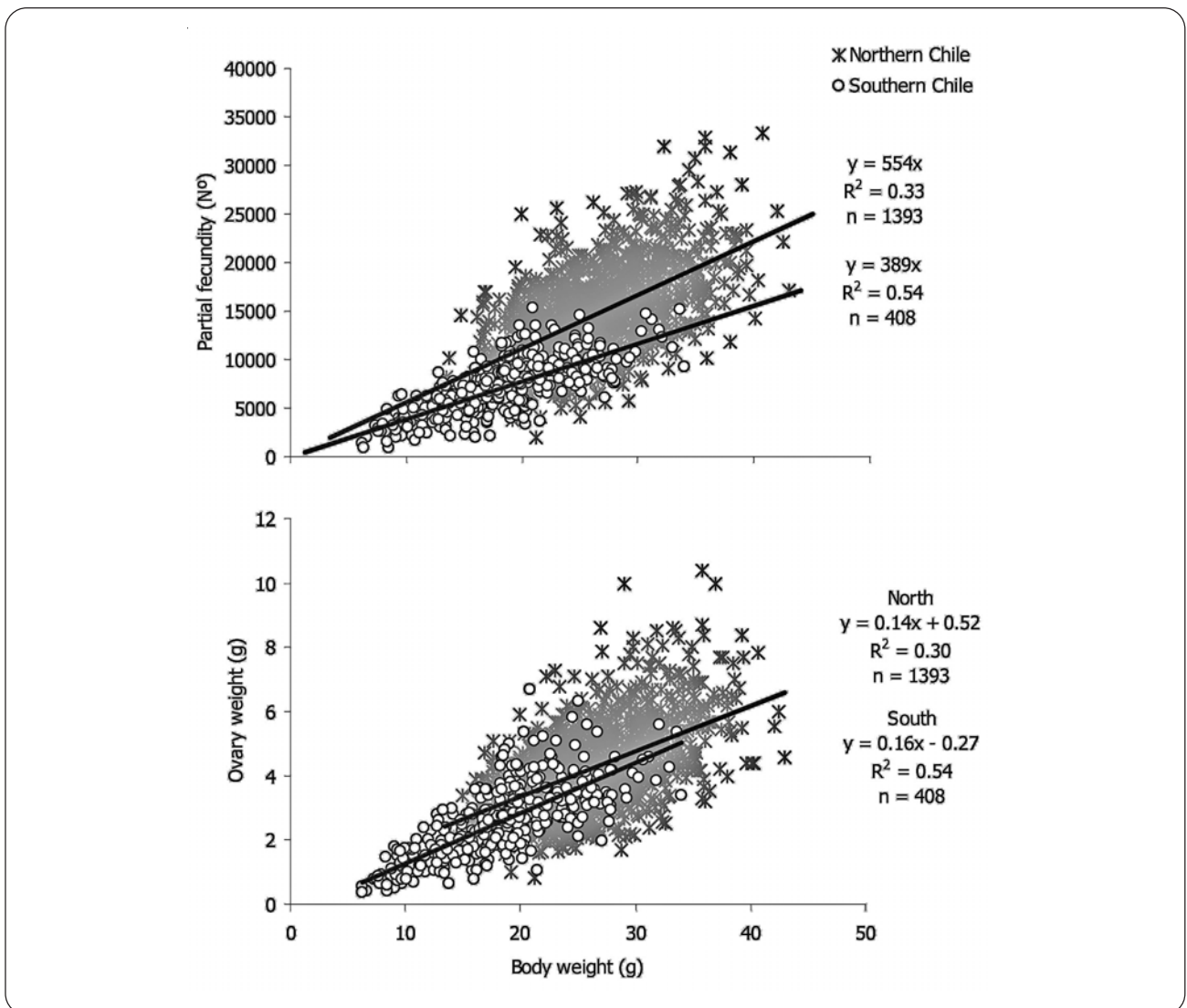


Figure 7. Relationships between body weight and batch fecundity (Top) and ovary weight (Bottom) for anchoveta of northern and southern Chile. All year pooled / Relación entre el peso corporal y la fecundidad parcial (Arriba) y con el peso del ovario (Abajo) para anchoveta del norte y sur de Chile. Todos los años agrupados

EGG SIZE

In the northern zone, the volume of eggs collected in the plankton surveys showed a significantly negative relationship with temperature on the stations (10 m depth) in all years analyzed (Table 4). The mean egg volume at temperature intervals (0.5°C) pooled for all years showed a clear negative relationship (Fig. 8).

Interannually, the mean egg volume of the survey conducted in 2007 (La Niña) was higher in comparison to the other years analyzed, as a product of the colder temperatures (Fig. 9) and there is a significant effect of the mean temperatures on the mean diameter of the eggs collected in the surveys.

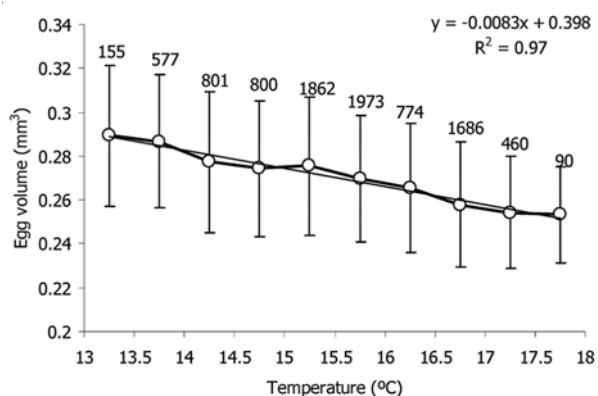


Figure 8. Mean of the egg volume (mm^3) at temperature intervals (0.5°C) for all year pooled (2000, 2001, 2002, 2003 and 2007). Number of samples in each interval is indicated. Vertical lines: standard deviation / Volumen medio de los huevos (mm^3) a intervalos de temperatura (0,5°C) para todos los años agrupados (2000, 2001, 2002, 2003 y 2007). Se indica el número de muestras en cada intervalo. Líneas verticales: Desviación estándar

SPAWNING FRACTION

There is no evidence of a relationship between the mean temperature and daily spawning fraction (slope = 0.0037; $t_{\text{calc}} = 0.906$; $P = 0.38$) (Fig. 10).

DISCUSSION

Our study shows that temperature is not a selected environmental variable to determine spawning sites in anchoveta. We postulate therefore, that instead of searching for certain temperatures, anchoveta accommodate their offspring characteristics (*e.g.*, egg size, fecundity) according to the prevalent environment. The response of the reproductive system to temperature might be in the scale of spawning frequency, *i.e.*, weeks. The selected environmental variable and that explains the changes in the localization and extension of the spawning sites would be the high chlorophyll concentrations.

REGIONAL DISTRIBUTION OF SPAWNING AREAS

According to Castillo-Jordán *et al.* (2007), the main spawning area in the southern zone is restricted to the more coastal zone. Usually, it occurs in waters with < 75 m water depth and peaks at around 50 m water depth. GAM models (Castillo-Jordán *et al.* 2007) indicate that in southern Chile egg density distribution was better explained by a bivariate function of longitude and latitude together with bottom depth. However, since in this case egg densities depend exclusively on parameters that are not directly sensitive for fish, the results are not satisfactory from a biological point of view (Castillo-Jordán *et al.* 2007). These authors attribute the fact that sea surface temperature was not significantly related to

Table 4. Parameters of the regression between temperature (10 m depth) and the egg volume of each station for 5 years. Sa and Sb: Standard error of parameter. Ho: b = 0: Probability that slope = 0 / Parámetros de la regresión entre temperatura (10 m de profundidad) y el volumen de los huevos en cada estación para 5 años. Sa y Sb: Errores estándar de los parámetros. Ho: b = 0: Probabilidad que la pendiente = 0

	2000	2001	2002	2003	2007
Intercept(a)	0.46	0.34	0.31	0.35	0.40
Sa	0.021	0.011	0.010	0.011	0.015
Slope (b)* 10^{-3}	-12.13	-4.19	-3.39	-5.73	-7.67
Sb* 10^{-3}	1.345	0.718	0.645	0.711	1.018
Ho: b = 0	$8.05*10^{-19}$	$6.10*10^{-9}$	$1.57*10^{-7}$	$2.92*10^{-15}$	$7.16*10^{-14}$
r^2	0.066	0.013	0.010	0.080	0.026
n	1148	2496	2693	747	2094

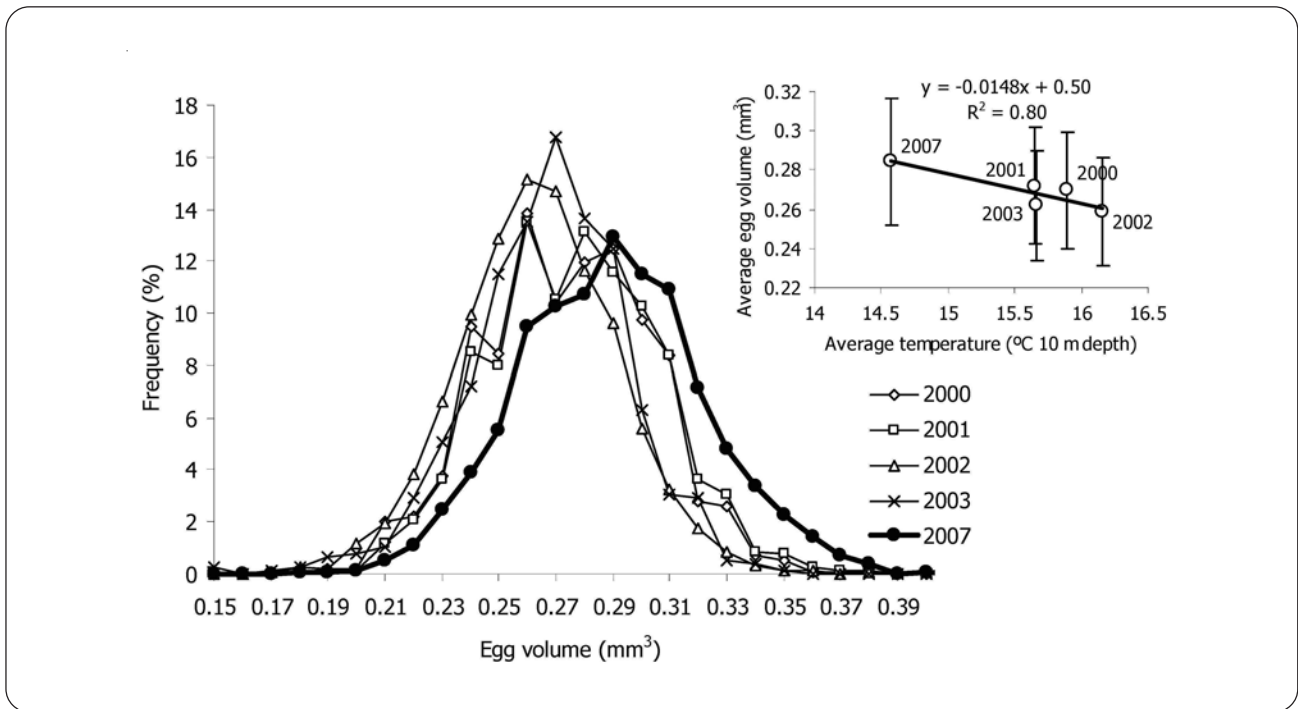


Figure 9. Eggs volume frequency distribution for surveys from 2000 to 2003 and 2007. Small figure is the relationship between survey average of temperature and egg volume (Vertical lines: standard deviation; year is indicated for each point) / Distribución de frecuencia del volumen de los huevos para los cruceros del 2000 al 2003 y 2007. Figura pequeña es la relación entre el promedio de la temperatura y del volumen de los huevos (Línea vertical: Desviación estándar; Se indica el año para cada punto)

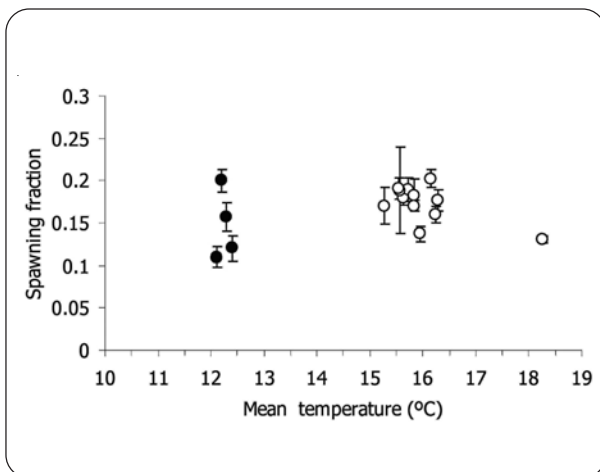


Figure 10. Relationship between mean temperature of the survey and daily spawning fraction in anchoveta of northern (Open circles) and southern (Solid circles) Chile / Relación entre la temperatura media del crucero y la fracción diaria de hembras desovantes en anchoveta del norte (círculos blancos) y sur (círculos negros) de Chile

the egg distribution of anchoveta to the narrow temperature range during their survey (11° to 13°C) and speculate that this temperature range may represent the optimum for spawning. Bustos *et al.* (2008) found for *Engraulis ringens* inhabiting fjords in the most southern region of Chile, the presence of spawning associated to zones with highly stratified waters, which may increase the vertical aggregation of the plankters and promote feeding success of larvae. But, fjord zone of Chile has an ocean dynamics quite different from the coastal area of northern and central Chile, where upwelling events dominate the coastal ecosystem. For northern populations there is no explanation yet for the changes in the location of their spawning areas. As they are located in oceanic regions with thousands of meters water depth, they cannot be used as explanatory variable in models as in the southern zone.

Chlorophyll-*a* appears as a selected environmental variable for spawning habitat, similar as founded by Schismenou *et al.* (2008) for *Engraulis encrasicolus*, probably because chlorophyll concentration is generally accepted as a good indicator of primary production (Longhurst *et al.* 1995) and food availability (Basilone *et*

al. 2004), and it is related with fish biomass production (Iverson 1990). Yañez-Rubio *et al.* (2011) indicates for anchoveta larvae a high feeding incidence with a mixed diet initially dominated by phytoplankton (small larvae) and later switching to zooplankton preys (older larvae). Basilone *et al.* (2004) observed a significant relationship between chlorophyll concentration derived from satellite images and anchovy growth in the Mediterranean Sea, indicating that sea surface estimates of chlorophyll concentration are good indicators of food availability for anchovy, and Basilone *et al.* (2006) show that anchovy spawning intensity and condition factor were affected by chlorophyll concentration.

One restriction of this study and the GAM modeling is that chlorophyll satellite estimations were not validated with *in situ* information. Silva *et al.* (2000) showed that SeaWiFS chlorophyll estimations were overestimated in the Chilean coastal upwelling, in comparison with *in situ* data (approximately 2.3 times higher). The real values can therefore be considerably different from those derived from satellite images, but the latter are still useful for comparative studies of intra- and inter-annual chlorophyll concentration (Basilone *et al.* 2006) and for modeling the spawning in relation to easily accessible environmental information (Schismenou *et al.* 2008).

Other aspect to consider, is that the delineation of spawning habitat based on the abundance of spawning products, identifies realized spawning habitat (*i.e.*, habitat where spawning actually occurs), and can be used to demarcate potential spawning habitat (*i.e.*, where the hydrological and/or physical conditions are suitable for spawn), but cannot identify successful spawning habitat (*i.e.*, from where successful recruitment has resulted) (Castro *et al.* 2005).

BATCH FECUNDITY

The relationships between body weight and batch fecundity have intercepts significantly different from zero only in years under the influence of ENSO events like the El Niño 1997 and 2002, or the La Niña 2007. The differences in the intercepts indicate higher or lower relative fecundity (number of oocytes per gram of body weight) as compared with 'normal' years (Neutral ENSO), when the intercept is zero and variations in the relative fecundity between years appear much smaller. Thus, relative fecundity is constant over the range of female weights in 'neutral' years. For *Engraulis encrasicolus*, Motos (1996) found that years with negative intercept coincided with high levels of recruitment and consequently high number of small 1 year

old individuals at sea. According to our results, the interannual changes in the body weight-fecundity relationship are related to the temperature of the environment, which affects the egg size. The effect of female size is discarded according to the work of Leal *et al.* (2009) who demonstrated that oocyte volume in *E. ringens* was not significantly correlated with female length or weight from northern and southern Chile. Therefore, at the same size and ovary weight, females produce larger eggs in a cold rather than in a warm environment, but with a lower fecundity.

EGG SIZE

Variations in egg size among populations located along a latitudinal gradient or during the spawning season have been reported for a number of demersal and pelagic fishes (Blaxter & Hempel 1963, Bagenal 1971, Blaxter & Hunter 1982, Chambers 1997, Castro *et al.* 2002, Bustos *et al.* 2008, Castro *et al.* 2009). In general, larger eggs are spawned at higher latitudes, egg size tends to decrease as the spawning season progresses, and eggs produced in winter are larger than those spawned in summer (Ciechomski 1973, Clarke 1989, Claramunt *et al.* 1994, Rijnsdorp & Vingerhoed 1994, Chambers & Waiwood 1996, Plaza *et al.* 2002, Llanos-Rivera & Castro 2004, Rideout *et al.* 2005, Bustos *et al.* 2008, Leal *et al.* 2009). It has long been documented that larger eggs usually produce larger and more robust larvae capable of searching larger volumes of water for food, evading predators more successfully, or growing faster. All these characteristics should reduce mortality under adverse environmental conditions (Marteinsdottir & Steinarsson 1998). Whereas most authors have proposed egg size variability to be an adaptive trait to enhance offspring survival under different environmental conditions, others have suggested that egg size variation may result from changing environmental temperature and hence, not necessarily represent an adaptive genetic response to facilitate offspring survival in different environments (Daoulas & Economou 1986). Our results of an increase in egg size in the cold year 2007 as compared with 'neutral' years with neutral ENSO, indicates that the temperature regime (along with its associated factors such as the food quality, see below; Castro *et al.* 2009) induces changes in the reproductive system which determines egg size (phenotypic plasticity), probably to enhance offspring survival. Furthermore, if schools of anchoveta are moving around the environment, our results of a significant relationship between the temperature at a station and egg

volume in the plankton in all years analyzed, means that females are responding to the prevalent temperature on the temporal scale of their spawning frequency (each 5 to 10 days), *i.e.*, in the scale of weeks. Previous reports indicated that the environmental temperature during the 90 to 60 days before spawning might have an important effect on fish fecundity and egg size (Tanasichuk & Ware 1987, Leal *et al.* 2009). Also, the differences in the yolked mode between northern and southern populations indicate that the oocyte size is determined during early vitellogenesis, as found by Plaza *et al.* (2002) in *Sardinops sagax* from northern Chile. For this species, reports also show that the initial differences in egg size between the northern and southern populations off Chile propagate to the following exogenous-feeding larval stage (post yolk sac larvae) (Llanos-Rivera & Castro 2006). In both populations, initial winter egg sizes were highly correlated with larval length at hatching, yolk sac volume at hatching, and larval length at yolk absorption; all these traits may positively affect the survival chances of the young larvae. Castro *et al.* (2009) also show that hatching success is higher in the southern than northern population, associated with the size of the eggs and higher lipid content. According to these authors, in periods during the reproductive season when egg quality is high (*i.e.*, larger and high lipid contents), hatching success is also high, independent of the geographic distribution of the population. Larger sized eggs have also been observed to have different fatty acids proportions, indicative of better quality and of variations in the female's feeding environment (Castro *et al.* 2010). These results are particularly interesting when considering inter-annual variations, and they might explain the abrupt changes in recruitment observed from one year to another despite large reductions in biomass (Castro *et al.* 2009).

SPAWNING FRACTION

Claramunt *et al.* (2007) report a relationship between female size and spawning fraction in *E. ringens* from northern and southern Chile, but did not find a clear influence of temperature. In the present study, no relationship was observed between temperature and spawning fraction. Fitzhugh & Hettler (1995) report a reduction of postovulatory follicle duration of approximately 24 h with an increase of temperature by 4°C. Accordingly, some of the observations at higher temperatures might be indicative of potential problems in the aging of postovulatory follicles (*i.e.*, during El Niño) rather than the spawning fraction (Claramunt *et al.* 2007). Alday *et*

al. (2008) report a minimal influence of temperature on the degeneration of POFs for *Engraulis encrasicolus* at the range of temperatures covered, basically between 13 and 19°C. Therefore, more research is needed to understand the effect of temperature on the degeneration of the postovulatory follicle stages (Claramunt *et al.* 2007, Alday *et al.* 2008).

ACKNOWLEDGMENTS

Funding for the present study was provided by the 'Fondo de Investigación Pesquera' and FONDECYT (Grants 1100534) to Leonardo Castro and Gabriel Claramunt.

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Received 17 January 2012 and accepted 28 May 2012

Associate Editor: Mauricio Landaeta D.