

Variability in oocyte size and batch fecundity in anchoveta (*Engraulis ringens*, Jenyns 1842) from two spawning areas off the Chilean coast

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SUMMARY: Utilising histological preparations of ovaries from *Engraulis ringens* females collected in two contrasting spawning habitats along the Chilean coast, we assess the variability in oocyte size and batch fecundity during the peak spawning seasons in three years. The effects of female size (length and weight), batch fecundity and mean sea surface temperature on oocyte size were also examined. Results showed larger oocytes and lower batch fecundity in females from the southern area. Oocyte volume differences persisted inter-annually and were not explained by differences in female sizes. Since ovary weight was similar between areas, the cost of producing larger oocytes in the south population seems to be a fecundity reduction. The latitudinal variations in oocyte number and size seem to be determined by the predominant environmental conditions in each habitat. Hence, female *E. ringens* seem to adapt their reproductive tactics by producing eggs sizes and quantities that favour survival of their offspring under the environmental conditions in which they are to develop.

Keywords: oocyte size, inter-population variations, Humboldt Current, small pelagic, egg size, latitudinal variations.

RESUMEN: VARIABILIDAD EN EL TAMAÑO DE OVOCITOS Y FECUNDIDAD PARCIAL DE ANCHOVETA (*ENGRAULIS RINGENS*, JENYNS 1842) EN DOS ÁREAS DE DESOVE DE LA COSTA DE CHILE. – Utilizando preparaciones histológicas de ovarios de anchovetas (*Engraulis ringens*) colectadas en dos hábitats contrastantes a lo largo de la costa de Chile, se estudia la variabilidad en tamaño de ovocitos y fecundidad parcial en la estación de máximo desove durante tres años. Los efectos de tamaño de hembra (longitud total y peso total), fecundidad parcial y temperatura superficial del mar sobre el tamaño de los ovocitos, también fueron investigados. Los resultados mostraron ovocitos más grandes y menor fecundidad en hembras de la zona sur. Las diferencias en volumen de ovocitos persistieron inter-anualmente y no fueron explicadas por diferencias en el tamaño de las hembras. Dado que los pesos de los ovarios fueron similares entre zonas, el coste de producir ovocitos más grandes en la población del sur sería la reducción en la fecundidad. Las variaciones latitudinales en número y tamaño de ovocitos parecen ser determinadas por las condiciones ambientales predominantes en cada hábitat de desove. De este modo, las hembras de *E. ringens* adaptarían sus tácticas reproductivas produciendo tamaño y cantidades de huevos que favorezcan la supervivencia de sus descendientes a las condiciones ambientales en las que se desarrollarán.

Palabras clave: tamaño de ovocitos, variaciones inter-poblacionales, corriente de Humboldt, peces pelágicos pequeños, tamaño de huevo, variaciones latitudinales.

INTRODUCTION

Egg size is a key factor in fish reproductive strategies and its variability is modulated by the trade-off

between offspring quantity and quality (Fleming and Gross, 1990). A latitudinal trend in egg size has been observed in natural populations, which are distributed over a wide geographic range (De Ciechowski,

1973; Funamoto and Aoki, 2002; Llanos-Rivera and Castro, 2004). Hypotheses proposed to explain this variability include environmental factors such as temperature, oxygen and food availability (Tanasichuk and Ware, 1987; Beacham and Murray, 1993), and biological factors such as size and endocrine state of the female during oocyte growth in the ovary (Hay and Brett, 1988; Ojanguren *et al.*, 1996; Laine and Rajasilta, 1999). Because the initial egg size determines many features of the offspring and has an important effect on early life stage growth and survival (Bagenal, 1971; Wootton, 1994; Ojanguren *et al.*, 1996; Brooks *et al.*, 1997), some of these hypotheses propose that egg size constitutes an adaptation to local environmental conditions.

The anchoveta *Engraulis ringens* is a partial spawner in the Humboldt Current with a marked winter (July-September) reproductive season along its wide geographic range (4°-42°S). The species distribution and parasitic fauna (Valdivia *et al.*, 2007) indicate the existence of two main spawning areas off Chile: one to the north (18°-23°S) and one to the south (35°-38°S). Separated by over 15 degrees of latitude, these spawning habitats show strong environmental differences.

Castro *et al.* (2002) and Llanos-Rivera and Castro (2004, 2006) reported a latitudinal gradient in egg size and other early life history traits of *E. ringens* along the Chilean coast. Unfortunately, due to the planktonic origin of the eggs analysed, it was not possible to determine any relationship between female size (length and weight) and egg size in the plankton. Also, it is not known whether these differences in egg size were the result of processes occurring inside the ovary (i.e. during the early oocyte stages, or later during hydration) or later when the eggs were released into the environment.

In this study, we consider whether intra-species variability in *E. ringens* egg number and oocyte size might be adaptive traits in individuals from the two spawning areas, where important differences in habitat conditions are observed.

MATERIAL AND METHODS

Data for the analyses come from studies in which female size (length and weight), oocyte size, and sea surface temperature were measured simultaneously for a large set of female individuals. Oocyte size (volume, mm³) was measured from histological

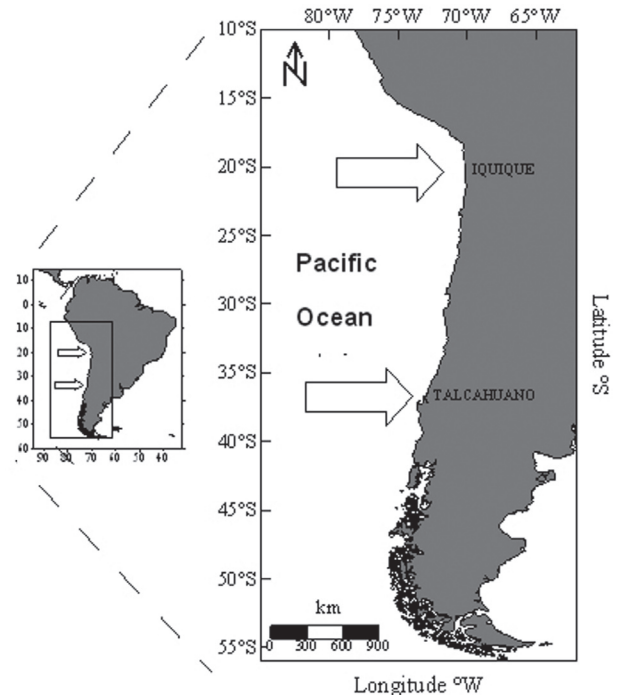


FIG. 1. – Spawning areas from which females *E. ringens* were collected during the reproductive season (arrows).

preparations of *E. ringens* ovaries obtained during fisheries assessment surveys in which the daily egg production method (DEPM) was used to estimate anchovy spawning biomass off northern (18-23°S and 70-72°W) and southern Chile (35-38°S and 72-73°W) (Fig. 1) in 2002, 2003 and 2004. The samples were collected during the peak spawning period (August-September) of each year. The females' ($n > 3000$ in each year and area) total length (TL), total weight (Tw) and ovary-free weight (Ofw) were measured in both areas.

Based on an ovarian development scale modified for *E. ringens* (Hunter and Macewicz, 1985), ovaries in the mature stage (with full yolk-stage oocytes) were selected under an optical microscope. Since the techniques used for histological preparations deteriorate and deform the oocytes, only histological preparations that presented oocytes appropriate for measurement (oval form, oocyte and follicular cover integrity, central position and integrity of the nucleus) were selected.

Measurements and estimates

The selected histological preparations were digitally photographed at a screen resolution of 624 x 480 pixels with a Sony CCD-Iris video camera mounted

on a microscope at 40x magnification. Based on previous calibrations (120 pixels/1 mm), measurements done with digital oocyte images used Image J software. The width and length of the oocyte and the nucleus were measured.

Oocyte volume (Ov) was estimated assuming an ellipsoid shape of the *E. ringens* oocytes (Llanos-Rivera and Castro, 2004), $V = \pi * MaA * MiA^2 / 6$ (Maruyama *et al.*, 2003), where MaA and MiA are the major and minor axes, respectively. To ensure that the analysed oocytes included only those cut on a longitudinal and central plane by the microtom, we only used oocytes whose nucleus size was within the standard deviation range estimated for each year and area. Oocytes were at the same stage in both populations (full yolk-stage oocytes). Based on these criteria, the number of oocytes measured per female ranged between 3 and 5.

Batch fecundity (Bf) (number of oocytes liberated by a female in one spawning event) was estimated for each female from a linear fecundity model based on ovary-free female weight (Ofw) (Hunter and Macewicz, 1985) as $PF_{(w)} = a + b * Ofw$; the parameters (a,b) were previously estimated for each year and area in the DEPM studies. The relationship between mean oocyte volume and batch fecundity was then estimated in each area.

The potential effect of female size (Tl, Tw) on oocyte volume was evaluated in females from each year and area. The possible differences in the female size among areas that could explain the variability in oocyte size was also analysed. Moreover, data on female length and weight in both areas were transformed to their natural logarithms, as proposed by Jonsson and Jonsson (1999), prior to comparing the regressions.

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 and Ware, 1987). Accordingly, in this study we assessed the effect of the mean sea surface temperature 2 and 3 months (May, June) before the main spawning month (August) on the annual mean oocyte volume. The temperature value corresponded to the average between May and June and the standard deviation was the monthly variability each year. The mean monthly sea surface temperature in the coastal zone in 2002, 2003 and 2004 were taken from the Hydrographic and Oceanographic Service of the Chilean Navy (SHOA) database.

Statistical analyses

Previous to all parametric analyses, the data were first tested for normal distribution (Kolmogorov-Smirnov one-sample test ($P > 0.05$)) and homoscedasticity of variance (Levene test, $P > 0.05$).

One-way analysis of variance (ANOVA) was used to evaluate differences in oocyte volume among years within each population (Power *et al.*, 2005) and *t*-tests to determine whether differences in the mean oocyte volume occurred each year between areas. The *t*-tests were also used to assess whether differences in mean fecundity occur between stocks based on the three years of data.

The relationship between oocyte volume and batch fecundity was evaluated within each area through a Pearson's correlation coefficient. This analysis was also used to estimate the correlation between the females' size (Tl, Tw) and the oocyte volume for all the females measured in each area. To test the hypotheses about equality in regression coefficients of length-weight data of two populations, a *t*-test was used (Zar, 1984).

A simple regression analysis was used to determine the correlation between mean sea surface temperature 2 and 3 months before the main spawning month on the annual mean oocyte volume within each area.

Finally, we carried out a two-way ANOVA with interaction using area and year as factors to examine their effects on oocyte size in the areas included in the present study.

RESULTS

The mean length and weight of the females sampled differed between populations (*t*-test, $P < 0.001$), probably because too few small individuals (< 13 cm Tl) were included in the northern area (Fig. 2). The mean length and weight values were higher in the northern Chile population. The differences in the average Tw persisted (*t*-test; $P < 0.001$) when females were compared within the same length range (i.e. 13-17.5 cm,) between populations. Additionally, the regression analysis (Fig. 3) showed that northern females exhibited a higher mean weight than the southern ones for fish of the same length (*t*-test, $P < 0.001$).

Statistical analyses showed significantly different oocyte volumes (mm^3) between the northern and

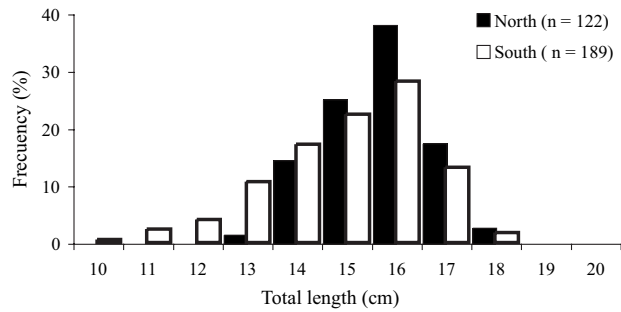


FIG. 2. – Length frequency distribution of *E. ringens* females from the northern and southern Chile spawning areas used for oocyte volume and batch fecundity analyses.

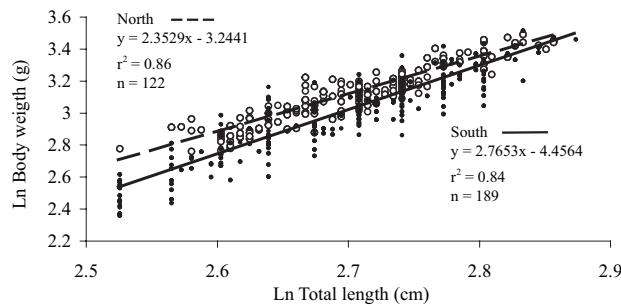


FIG. 3. – Relationship between female total length and total weight (natural logarithm) *E. ringens* of northern (empty circles) and southern Chile (solid circles).

southern *E. ringens* populations (*t*-test, $P < 0.001$). While in the northern area the oocyte sizes ranged between 0.005 and 0.045 mm³, in the south they ranged between 0.010 and 0.055 mm³ (Fig. 4). In 2002, the mean oocyte volume was 95% larger in south Chile females (Table 1); this difference decreased to 66% in 2003 and 30% in 2004 (Fig. 5). Significant dif-

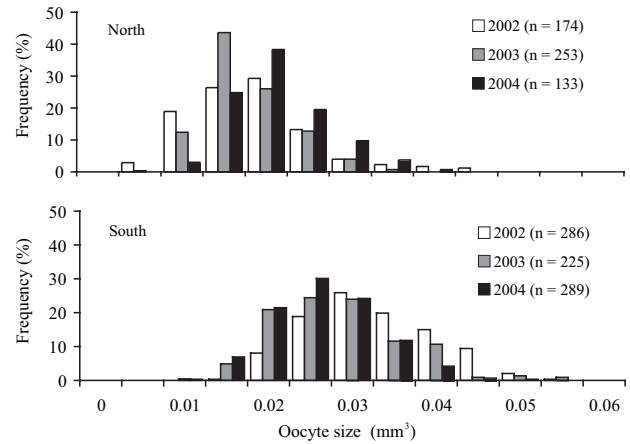


FIG. 4. – Size frequency distribution of *E. ringens* oocytes in northern and southern Chile spawning areas, obtained during the peak month of spawning 2002, 2003 and 2004.

ferences in mean oocyte volume were also detected among years within each area (ANOVA, $P < 0.001$) (Table 2).

Batch fecundity was also significantly different between areas. The mean batch fecundity (estimated from the ovary-free female weight) was higher (*t*-test; $P < 0.001$) during the entire period for the northern females (12788 oocytes; std = 2175) than for the southern females (8197 oocytes, std = 2326). The differences in mean batch fecundity persisted among areas (*t*-test; $P < 0.001$) when females were compared within the same length range (i.e. 13-17.5 cm,) between populations.

The trends between ovary weight and ovary-free female weight were similar between females (Fig.

TABLE 1. – Results of a *t*-test to assess whether differences in oocyte volume occurred between the northern and south Chilean *E. ringens* spawning areas during the winters 2002, 2003 and 2004.

	2002		2003		2004	
	North	South	North	South	North	South
Oocyte volume (mm ³)	0.016	0.030	0.015	0.026	0.019	0.024
Standard deviation	0.0055	0.0054	0.0039	0.0056	0.0045	0.0050
n	38	67	50	53	34	69
<i>t</i> _{crit}		1.96		1.96		1.96
<i>T</i> _{crit}		13.4		10.6		5.5
P		<0.001		<0.001		<0.001

TABLE 2. – One way ANOVA to test differences in oocyte volume among years within each spawning area.

	North			South		
	2002	2003	2004	2002	2003	2004
Oocyte volume (mm ³)	0.016	0.015	0.019	0.030	0.026	0.024
F crit		3.07			3.04	
F		5.84			24.63	
P		<0.01			<0.001	

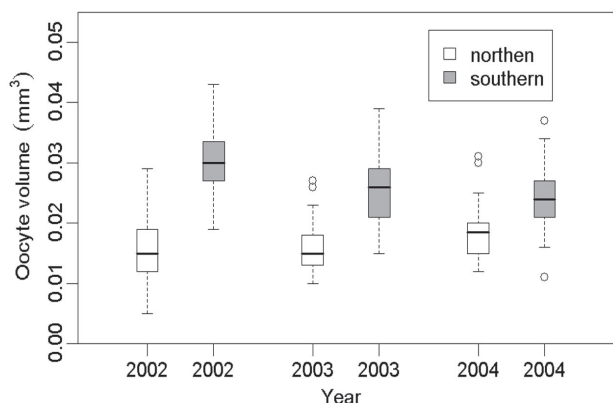


FIG. 5. – Median *E. ringens* oocyte volume (horizontal lines inside the box) in females collected from northern (1) and southern Chile (2) spawning areas in the winters of 2002, 2003 and 2004. Range observed value (vertical dotted lines on box) and outliers (points on graphs) are also given.

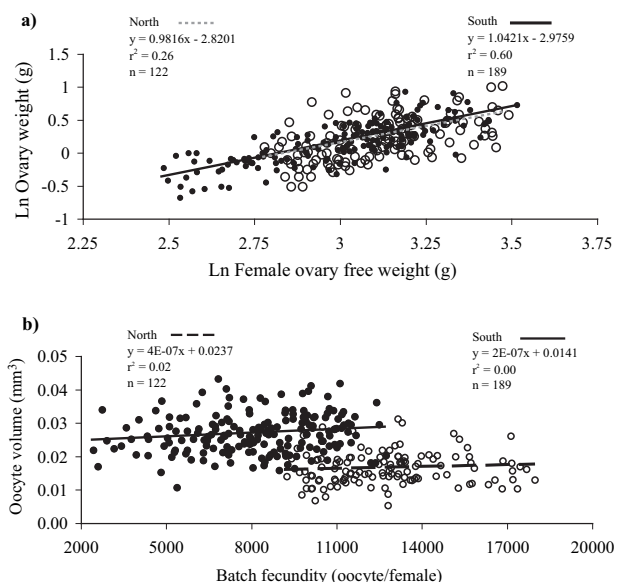


FIG. 6. – a) Relationship between female ovary free weight and ovary weight (natural logarithm) from northern (empty circles) and southern Chile (solid circles) *E. ringens*. b) Relationship between batch fecundity and oocyte volume for northern (empty circles) and southern (solid circles) Chile.

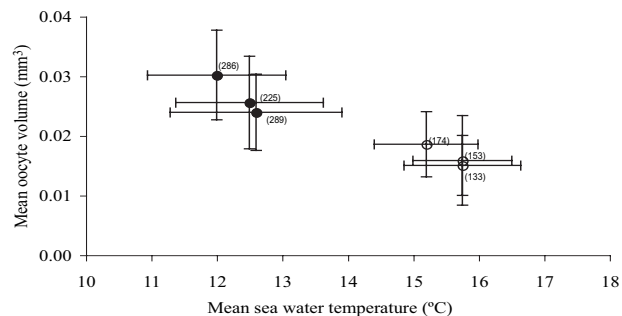


FIG. 7. – Relationship between mean sea surface temperature of the two months (May-June) prior to the spawning peak and mean oocyte volume in northern (empty circles) and southern Chile (solid circles). Lines on circles are oocyte volume standard deviations (vertical) and temperature standard deviations (horizontal). Among parenthesis () is the number used to estimate mean oocyte volume.

TABLE 3. – Result of a two-way ANOVA to test effect of population and year on oocyte size *E. ringens*.

Source of variation	df	Variance explain (%)	F	P
Area	1	46.1	315	<0.001
Year	2	3.7	12	<0.001
Area x Year	2	5.6	19	<0.001
Total	5	55.3		
Error	305	44.7		

6a) from both areas. Pearson’s correlation coefficient showed that oocyte volume was not significantly correlated ($P>0.13$) with fecundity in each area (Fig. 6b). Also, oocyte volume was not significantly correlated with female length or weight ($P>0.08$). Nevertheless, a trade off between oocyte volume and fecundity may be observed in the comparison of areas.

Sea surface temperature was the only environmental variable compared between the two spawning areas. The mean sea surface temperatures in May and June (two and three months prior to August, the peak spawning month) were lower (average 4°C every year) in the southern area than in the northern area and were not correlated with the mean oocyte volume ($P>0.05$) within each location (Fig. 7). The ANOVA showed that area was the most important factor to explain the oocyte size variability (46%). The year effect and area x year interactions explained less variance (3.7 y 5.6%, respectively) but were also significant predictors of oocyte size variability in the geographical range and years included in this study (Table 3).

DISCUSSION

The general objective of this study was to determine whether differences in reproductive parameters and oocyte sizes occurred between *E. ringens* populations located along the Chilean coast and whether such intra-specific differences might be adaptive given the strong differences in spawning habitat conditions. The results of the present study show smaller oocyte volume and higher fecundity for the northern female anchoveta than for the southern ones. These differences were significant and persisted throughout the three-year study period. The results of this study agree with those obtained by Llanos-Rivera and Castro (2004), who analysed eggs obtained from plankton samples, reporting an increase in *E. ringens* egg volume with

latitude; the volumes were 55% smaller off Iquique (northern Chile) than off Talcahuano (southern Chile). The differences in oocyte size between populations found in the present study were 95% (2002), 66% (2003), and 30% (2004), and were thus in the middle of the range reported by Llanos-Rivera and Castro (2004) for planktonic eggs. Variability in egg size has been described by several authors for diverse fish species that are distributed over wide geographic ranges or are exposed to divergent environmental conditions (De Ciechowski, 1973; Tanasichuk and Ware, 1987; Beacham and Murray, 1993; Duponchelle *et al.*, 2000; Funamoto and Aoki, 2002; Kokita, 2003).

Batch fecundity, estimated from all female sizes sampled, was also significantly different between areas, with higher values for the northern females than for the southern ones. Among females within the same body length range between populations, the differences in mean batch fecundity persisted among areas, indicating that the observed differences in Bf cannot be attributed to differences in body sizes between populations. Interestingly, when we compared our results with others from northern Peru (years 1981, 1985, 1990, 1994, 1995 and 1996) (Ayon, 2000) a latitudinal trend seemed to emerge as batch fecundities in northern Peru seem to be higher (12701-18495 oocytes) than those we found in northern Chile (12788 oocytes, std = 2175) and much higher than those from southern Chile (8197 oocytes, std = 2326).

Egg size is affected by female body size in some fish (Chambers, 1997). However, in this case the oocyte volume was not correlated with female size within each population. These results, according to Kokita (2003), indicate that the effect of female size difference between populations can be ignored as a covariate to explain oocyte size variability between the two areas. In the literature, the relationship between female size and oocyte size in other small pelagic fish is not clear cut. Some authors report this relationship for some species but not for others. For example, Hay and Brett (1988) found a positive correlation between female length and/or age and egg weight in *Clupea arengus*, but Claramunt *et al.* (1994) reported that oocyte size in *Sardinops sagax* is independent of female body size. West (1990) indicated that, for small fish with a short life history, the narrow size range of the adults and their eggs could explain the lack of relationship between female size and egg size.

In our study, oocyte volume was larger in southern females. Since the ovary weight was similar between females from the two areas, the cost for spawning larger eggs in the southern females is a decrease in batch fecundity. A trade-off between fecundity and egg size has been reported before for other *Engraulis* species (Funamoto and Aoki, 2002), suggesting that this trend may be a common feature but not extensively reported. In our study, though, we were unable to detect this inverse relationship within each population, and this could have been because Bf were estimated from randomly selected females within the population and not based on direct measurements from the same females whose Ov were measured. However, when we consider both populations combined (i.e. entire female batch fecundity range in Figure 6b) a negative relationship between Ov and Bf is strongly suggested.

Oocyte size and environmental conditions

The results of our study agree with the idea that environmental temperature could play an important role in oocyte number and size regulation in fish populations. In this study the smaller oocyte size and higher batch fecundity in females from the northern area coincided with higher mean sea surface temperatures (4°C) than in the southern area. Examples of such relationships have been provided for different Clupeiform species. De Ciechowski (1973), for instance, found a positive latitudinal gradient in the size of *Engraulis anchoita* eggs collected from the plankton along the west coast of the South Atlantic; this gradient was largely attributed to the decreasing temperatures at higher latitudes. Tanasichuk and Ware (1987), alternatively, reported positive correlations between *Clupea harengus* egg size and temperature anomalies observed from 90 to 60 days before spawning along the northwest coast of North America. Tascheri and Claramunt (1996) suggested that temperature is the main regulating factor in the inter-seasonal variations in oocyte size observed in *Sardinops sagax* off northern Chile. Along the Japanese coast, temperature was also reported to be positively correlated with fecundity and negatively correlated with egg size for *Engraulis japonicus* (Funamoto and Aoki, 2002), indicating the existence of a trade-off between fecundity and egg size, and that temperature probably modifies the energy levels dedicated to reproduction. This phenomenon was also seen in a different type of fish species: three

Pomacentrus coelestis populations distributed in reefs along Japan's Pacific coast showed increased egg numbers and decreased egg sizes with higher sea temperatures (Kokita, 2003).

Along with potential temperature effects, food availability for adults and larvae may also play a role in determining differences in oocyte number and size. In this study the females in the northern area showed a higher mean weight than females from the southern area at a same fish length, suggesting that northern females had been exposed to better feeding or growth conditions. Also, compared to northern Chile, the possibilities for first feeding larvae to find food are lower in the southern spawning area because of lower concentrations of microplankton and higher turbulence in the water column resulting from winter storms (Castro *et al.*, 2002; Llanos-Rivera and Castro, 2004). Temperature is also lower and, hence, the duration of the larval stages is longer in the south (Tarifeño *et al.*, 2008). Therefore, in this area, larger eggs from which larger larvae hatch with a larger amount of yolk should be favoured (Llanos-Rivera and Castro, 2006). Consequently, the differences in egg size between the northern and southern Chilean anchoveta populations could result from local adaptations to the environmental conditions in each area and may be part of a reproductive strategy to produce an optimal number of eggs and egg sizes in order to maximize young offspring survival in each spawning habitat (Johnston and Leggett, 2002; Kokita, 2003).

Ferrada *et al.* (2002) used molecular genetic analyses to determine that *E. ringens* belongs to a pure panmictic stock along the Chilean coast, although the presence of some morphs in low frequency could represent variations at a genetic level. A recent work (Valdivia *et al.*, 2007) used studies of the parasitic fauna of *E. ringens* to show marked differences in the parasitic loads in individuals off northern and southern Chile, suggesting that some degree of separation should exist, at least on an ecological level. Thus, the cumulative information to date suggests that evidence of a potential genetic divergence able to explain differences in reproductive characteristics such as oocyte or egg size are not clear. Consequently, the differences observed seem to be a result of the high phenotypic plasticity of the anchoveta in different reproductive environments.

In summary, our results from this study suggest that some reproductive parameters differ between *Engraulis ringens* females from northern and southern

Chile, and also that differences previously observed in the free planktonic egg stage originated inside the females prior to oocyte hydration. The differences in reproductive traits agree with adaptive points of view that suggest these result from local adaptations to the dominant conditions in each habitat, favouring the survival of young offspring. The presence of this variability in the reproductive characteristics suggests that the anchoveta is capable of a marked phenotypic plasticity (hence, the characteristics are not fixed for each population or stock) and that, for now, it is not possible to conclude that these differences are the result of any degree of genetic isolation conducive to genetic differentiation.

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