Latitudinal and seasonal egg-size variation of the anchoveta (*Engraulis ringens*) off the Chilean coast

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The anchoveta *Engraulis ringens* is widely distributed along the eastern South Pacific (from 4° to 42°S; Serra et al., 1979) and it has also supported one of the largest fisheries of the world over the last four decades. However, there are few interpopulation comparisons for either the adult or the younger stages. Reproductive traits, such as fecundity or spawning season length, are known to vary with latitude for some fish species (Blaxter and Hunter, 1982; Conover, 1990; Fleming and Gross, 1990; Castro and Cowen, 1991), and latitudinal trends for some early life history traits, such as egg size and larval growth rates, have been reported for others clupeiforms and other fishes (Blaxter and Hempel, 1963; Ciechomski, 1973; Imai and Tanaka, 1987, Conover 1990, Houde 1989). However, there is no published information on potential latitudinal trends during the adult or the early life history of the anchoveta, even though this type of information may help in understanding recruitment variability, especially during recurring large scale events (such as El Niño or La Niña) that affect the entire species range.

Egg volume has been found to vary widely among species and among populations of the same species. For fish that broadcast planktonic or benthic eggs, egg size often varies as the spawning season progresses (Bagenal, 1971), and the magnitude of this variation depends on the species. For instance, the egg volume of the pelagic spawners *Engraulis anchoita* and *Solea solea* decreases 23% and 38%, respectively, throughout the spawning season (Ciechomski, 1973; Rijnsdorp and Vingerhoed, 1994). Maternal and environmental factors may also affect egg volume (Bagenal, 1971; Thresher, 1984; Rijnsdorp and Vingerhoed, 1994; Chambers and Waiwood, 1996; Chambers, 1997). Variations in size of the spawning females and shifts in energy allocation from reproduction to growth as the spawning season progresses may influence the egg volume (Wootton, 1990). Alternatively, seasonal variations in photoperiod, seawater temperature, and food supply during the spawning season may affect the reproductive output (Wootton, 1990).

Scarce information exists on the variability of egg sizes for fishes in the Humboldt Current. In this extensive area, the heavily exploited anchoveta *Engraulis ringens* is the dominant small pelagic species. Throughout this range, three major stocks are recognized: the northern stock off northern Peru (the largest); the central stock off southern Peru and northern Chile (midsize), and the southern stock off central Chile (the smallest of the three). For the entire distribution of anchoveta, the main spawning season is from July through September, but may extend to December or January (Cubillos et al., 1999). The wide latitudinal range and prolonged spawning period suggest the possibility of egg-size variation, as observed in other clupeifoms (Blaxter and Hempel, 1963; Ciechomski, 1973; Imai and Tanaka, 1987). Egg size correlates with larval characteristics such as larval length at hatching, the time to first feeding, and time before irreversible starvation (Shirota, 1970; Ware, 1975; Hunter, 1981; Marteinsdottir and Able, 1992). To explore whether differences in potential early-life-stage survival would exist among populations and (or seasons), the objective of our research was to determine whether variations in some early-life-stage characteristics occur among populations of *E. ringens* along its distribution. In this study, we 1) report changes in egg size throughout the anchoveta spawning season as well as for the peak months of the spawning season, 2) evaluate whether egg size varies with respect to latitude, and 3) evaluate whether differences in larval length and yolksac volume occur in hatching larvae from the two major spawning stocks along Chile (central and southern stocks).

Materials and methods

We collected anchovy eggs from four locations along the coastal zone (<20 nmi offshore) off northern and central Chile during the austral winter and spring spawning seasons 1995–97 (Fig. 1). Eggs were collected with a Calvet net (150 μm mesh) in Iquique and Antofagasta (northern Chile), with a standard conical net (330 μm) in Valparaíso and with either a Tucker trawl (250 μm mesh) or a standard bongo net (500 μm) in Talcahuano. The shorter axis of the anchovy eggs varied from 0.563 mm (SD=0.032) in Iquique to 0.657 mm (SD=0.027) in Talcahuano. Consequently, egg extrusion from the nets was ruled out as a potential source of variation in our collections. Egg size (length and width) was measured with an ocular micrometer on a dissecting microscope at 25× magnification. Upon collection, all eggs were preserved in 5% buffered formalin. Previous studies on anchoveta eggs have reported no egg size shrinkage or shape changes with formalin preservation (Fisher, 1958). Similarly, reports on this species and other anchovies show that egg-size variations throughout their development do not occur (*Engraulis ringens,* Fisher, 1958; *Engraulis japonica,* Imai and Tanaka, 1987). We tested this hypothesis using eggs that we collected in northern Chile and found no size differences among different egg stages (ANOVA, n=535, P=0.1176).

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Egg volume was calculated considering the anchovy egg as an ellipsoid ($V=4\pi \times a \times b \times c/3$, where a, b and c are the ellipse radii).

Statistical analyses included one-way ANOVA tests for volume differences among eggs spawned in three subperiods during the spawning season (initial, middle, and final) in Valparaíso and Talcahuano (1996–97). We did not have samples from the start of the spawning season in 1996 for Valparaíso; thus, we used samples collected in late June 1995 for this subperiod (Table 1). Variations in the egg-size frequency distributions between contiguous subperiods were also tested with nonparametric tests (Kolmogorov-Smirnov test). Changes in egg volume with latitude were tested by using egg sizes measured at four localities (20°, 23°, 33°, and 36°S) during the peak spawning months (initial subperiod). The same statistical tests were used as in the previous objective (ANOVA, Kolmogorov-Smirnov test).

To evaluate the relationship between egg size and larval length at hatching, live eggs from ichthyoplankton samples from the field in August 2000 were transported to the laboratory and reared at the normal mixed-layer temperature off Antofagasta and Talcahuano (15°C and 12°C, respectively) (Escribano et al., 1995; Castro et al., 2000). A subsample of the incubated egg batch was preserved in 5% formalin and measured at the beginning of the experiments. The rest of the eggs were placed in 1-L flasks and incubated until hatching under 12h/12h photoperiod. This procedure was repeated twice (4 days apart) in each zone. From each rearing experiment, 30 just-hatched larvae (max. 30 min from hatch) were anesthetized and measured (notochord length) under a dissecting microscope with the aid of an ocular micrometer. Additionally, yolksac sizes of recently hatched larvae were measured and volume estimated as one half of an ellipsoid by using the algorithms given above.

Results

A total of 7196 anchovy eggs were measured. The egg size tended to decrease as the spawning season progressed (Fig. 2). From late June through January the mean volume decreased by about 20% in Valparaíso and by about 10% in Talcahuano (ANOVA, $P<0.05$)(Table 1). The size-frequency distribution between consecutive subperiods (initial, middle, and final) also differed in both areas (Kolmogorov-Smirnov test, $P<0.05$). The mean size of the eggs in Valparaíso was smaller than in Talcahuano during all subperiods (Table 1), and the largest difference between areas was at the end of the spawning season (15%).

During the spawning peak (spawning commencement), when the eggs were larger, the mean anchoveta egg size increased with latitude (ANOVA, $P<0.01$; Fig. 3). At Iquique (20°S), the mean egg volume was 21% smaller than at Antofagasta (23°S), 49% smaller than at Valparaíso (33°S), and 56% smaller than the eggs from Talcahuano (36°S), the southernmost location (Table 2). The egg-size frequency distribution differed between adjacent areas (Kolmogorov-Smirnov test, $P<0.05$). Interestingly, the smallest egg sizes measured in Iquique (<0.19 mm^3) did not occur in Talcahuano. Similarly, the largest sizes determined in Talcahuano (>0.30 mm^3) did not occur in Iquique, at the lowest latitude.

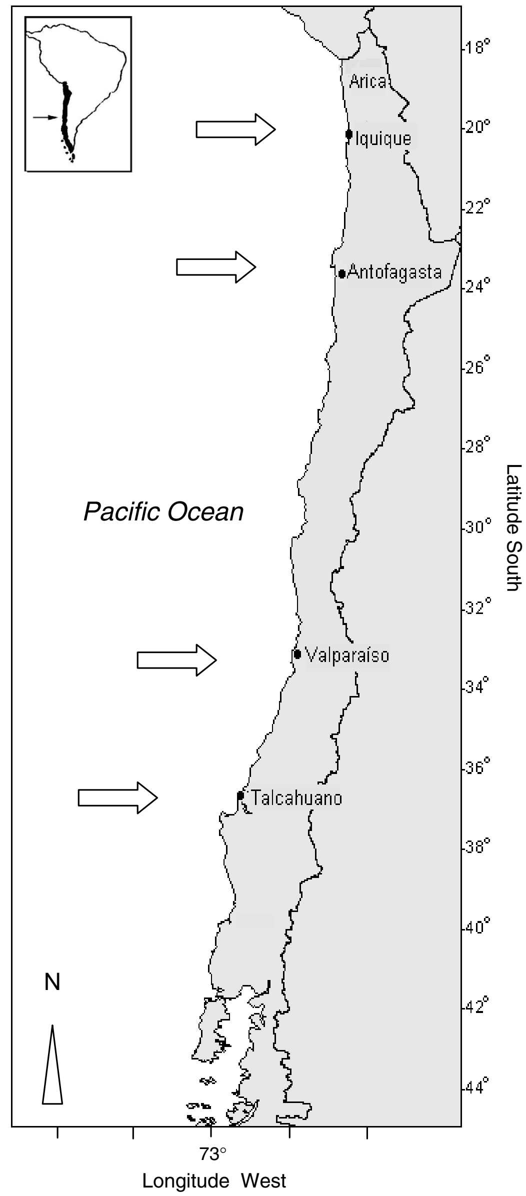

Figure 1

Areas where anchoveta eggs were collected to determine egg-size variations along the Chilean coast. Arrows show the locations depicted in Table 2.

Larval length at hatching determined in the rearing experiments at normal field temperatures was greater for the southernmost population (Talcahuano) (Table 3). The mean larval size for the southern location (2.70 mm notochord length) was 8.2% greater than the larvae hatched from eggs collected at the northern experimental location (Antofagasta, 2.50 mm). Furthermore, the yolksac volume in the recently hatched larvae in Talcahuano (0.130 mm^3)

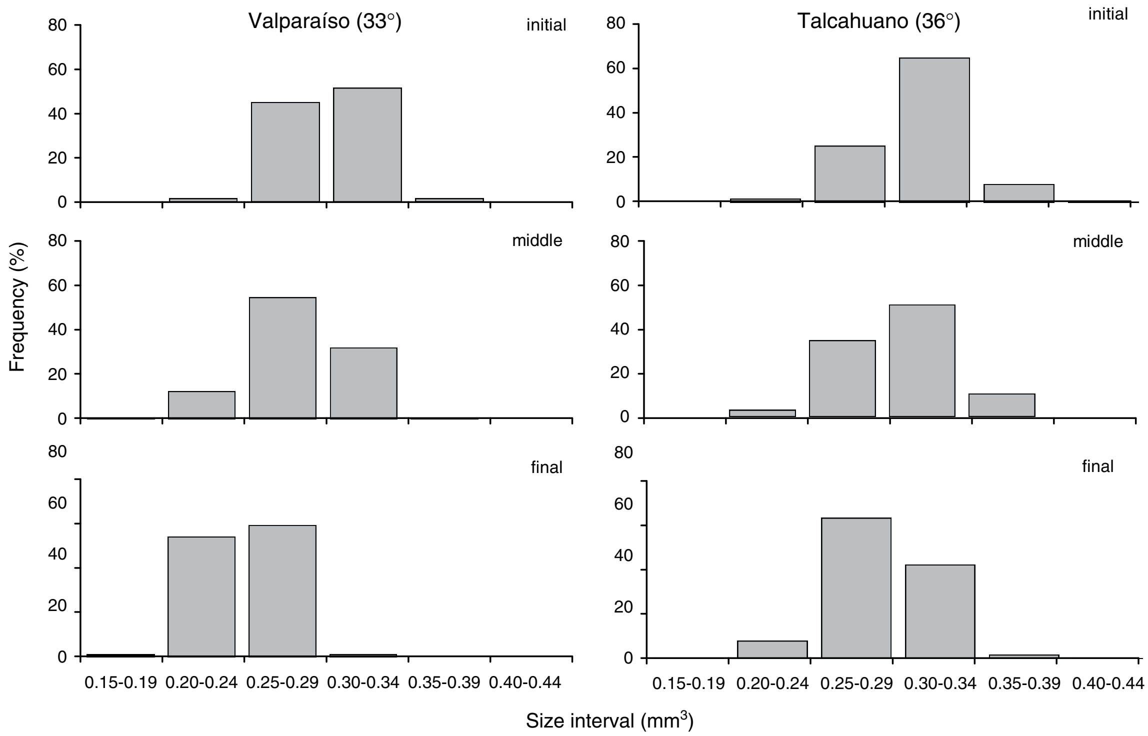

Figure 2

Seasonal variation in egg size of the anchoveta (*E. ringens*) off Valparaíso and Talcahuano. *Y*-axis is frequency over the total number of eggs measured at each locality. Initial, middle, and final are subperiods within the spawning season (see Table 2).

Table 1

Mean volume of *Engraulis ringens* eggs at the beginning, middle, and end of the spawning season off Valparaíso and Talcahuano, central Chile. SD = standard deviations. n = number of eggs measured.

	Valparaíso			Talcahuano		
	June 1995	October 1996	December 1996	August 1996	October 1996	January 1997
Volume (mm^3)	0.298	0.281	0.247	0.312	0.308	0.286
SD	0.026	0.029	0.022	0.030	0.034	0.029
n	62	759	630	1833	718	1099

was much larger (33% larger) than the yolk volume of the larvae hatched in Antofagasta (0.098 mm^3).

Discussion

The results of this study identified several trends that are related to egg-size variation. First, egg size tends to decrease with the progression of the spawning season. Second, egg size increases with latitude during the peak spawning period. Third, larval size at hatching is smaller in the northern latitude populations. Fourth, the yolk sac of recently hatched larvae is much larger than expected (based on the larval size at hatching) in the southern population.

A number of hypotheses have been proposed to explain egg-size variations in fish that spawn at multiple times as the reproductive season progresses. It has been proposed that in clupeiforms, the decrease in egg size may result from maternal reduction of energy reserves over the spawning season, a switch in the stored energy from reproduction to growth, seasonal changes in the age structure of the spawning population, or changes during ovogenesis that are correlated with temperature (Blaxter and Hunter, 1982; Chambers, 1997, for a recent review). In the anchoveta *E. ringens*, published data suggest that some

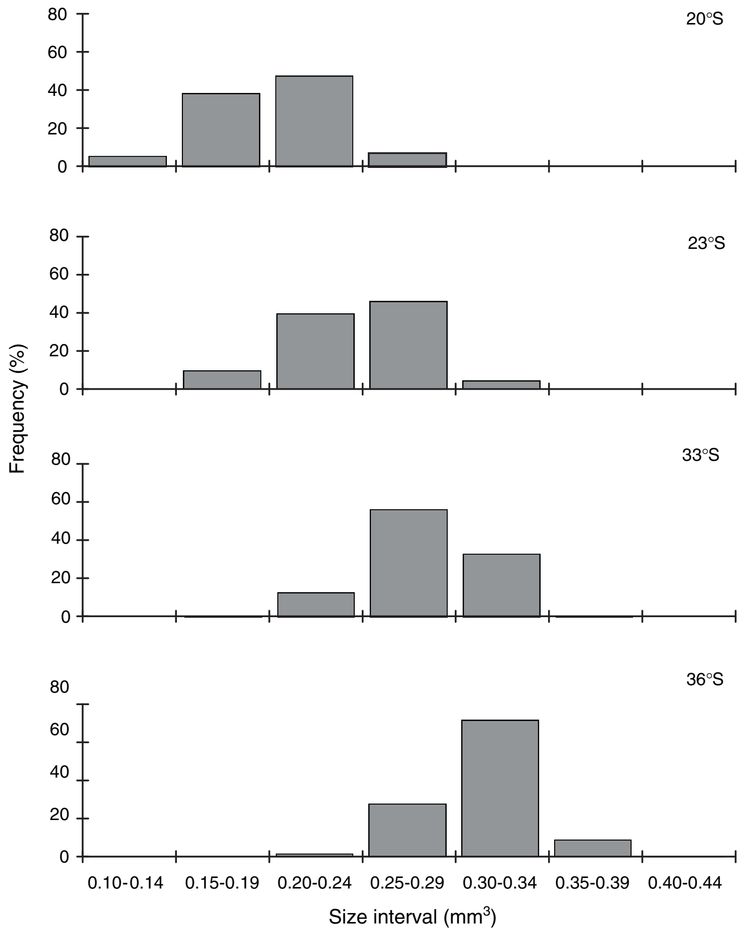

Figure 3

Latitudinal variation in egg size of the anchoveta (*E. ringens*) along northern and central Chile during the peak months of the spawning season. *Y*-axis is frequency over the total number of eggs measured at each locality.

of these factors co-occur. For instance, changes in growth rates for yearly cohorts during the spawning season (low at the beginning, fast at the end) have been documented for the southernmost population (Cubillos et al., 2001). Alternatively, variations in the population age structure during the spawning season have also been reported as the 1.5 year-old new recruits begin to spawn in early summer (late December–January, Cubillos et al., 1999, 2001). Changes in environmental factors affecting the spawning adults also correlate with the egg-size variations. The photoperiod and nearsurface temperatures increase as the spawning season progresses from mid-winter to late spring.

Larger egg size at the beginning of the spawning season in winter may be advantageous for these offspring because the chances of survival increase with the larger sizes of the hatching larvae. According to Cushing (1967), larger size larvae should be favored over smaller larvae in seasons with variable environmental conditions. In the Talcahuano area, strong fluctuations in the hydrographic regime occur during winter as strong north wind storms alternate with short periods of south winds, and also because of the increased river flow to the coastal zone (Castro et al., 2000). Larval food, although variable, seems to be sufficient to support most of the larval growth demands for larger exogenous feeding larvae during winter (Hernandez and Castro, 2000). For recently hatched larvae, however, the picture might be slightly different because, in addition to food supply variability, the strong turbulent environmental conditions may jeopardize first feeding success. In these highly variable areas, therefore, larger larval size at hatching and larger yolk reserves may be even more important than in other less hydrographically variable areas and seasons.

A remarkable increase in egg size at the peak spawning season occurred with respect to latitude. Egg from the northernmost (20°S) latitude were at a maximum 55% larger than eggs from the southernmost (36°S) latitude. Latitudinal variations in egg size have been previously reported for other anchovies (i.e. *Engraulis anchoita*; Ciechomski, 1973). However, egg-size variations for fishes

Table 2

Width, length, and volume of anchoveta eggs collected at different latitudes along the Chilean coast during the peak months of the spawning season. SD = standard deviations. *n* = number of eggs measured.

	Width (mm)		Length (mm)		Volume (mm^3)		
Latitude and area	mean	SD	mean	SD	mean	SD	*n*
20° Iquique	0.563	0.032	1.201	0.076	0.201	0.031	1670
23° Antofagasta	0.597	0.030	1.293	0.083	0.243	0.034	425
33° Valparaíso	0.643	0.023	1.373	0.064	0.298	0.026	62
36° Talcahuano	0.657	0.027	1.377	0.063	0.312	0.030	1833

Table 3

Morphological characteristics of recently hatched *Engraulis ringens* larvae from rearing experiments at normal field temperatures in Antofagasta (15°C) and Talcahuano (12°C). SD = standard deviations. *N* = number of eggs measured. Exp. = experiment.

		Egg volume (mm^3)		Larval length at hatching (mm)		Yolksac size at hatching (mm^3)	
		Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2
Antofagasta							
15°C	Mean	0.264	0.260	2.49	2.50	0.099	0.096
	SD	(0.023)	(0.023)	(0.170)	(0.104)	(0.012)	(0.012)
	n	358	325	30	30	30	30
Talcahuano							
12°C	Mean	0.302	0.292	2.71	2.69	0.126	0.134
	SD	(0.023)	(0.026)	(0.111)	(0.103)	(0.016)	(0.017)
	n	254	66	30	30	30	30

are not necessarily always associated with latitude (i.e. north Atlantic herring stocks) because local environmental conditions that trigger spawning (i.e. specific temperature or others) may have a stronger effect in some species (Chambers, 1997). Because of the extremely wide distribution range of the anchoveta (4–42°S) and its residence along an almost linear coast oriented exactly north–south, we proposed that any potential differences in egg size due to specific local conditions is probably over-driven by the larger scale changes in environmental conditions associated with latitude.

The strong latitudinal gradient in egg size of the anchoveta may be an adaptive measure if different egg sizes are favored at different latitudes or if there is a correlation between egg size and adult life history traits that maximize net reproductive output. Unfortunately, an analysis of the anchoveta in which fecundity, age of first reproduction, longevity, or other adult traits are compared in relation to latitude has not yet been carried out. The timing and length of the spawning season seem to be similar for the northern (Iquique, 20°S) and southern (Talcahuano, 36°S) stocks along Chile, despite the different temperatures at which anchoveta spawn (Castro et al., 2001). The decrease in egg size coincides with known temperature effects on physiological rates (Houde, 1989) and on ecological factors related to the need of anchoveta at early life stages to remain in nearshore environments (Bakun, 1996). At lower latitudes, the sea temperature is higher and the seaward surface Ekman transport is stronger and therefore eggs and larvae in such conditions would likely develop rapidly. Alternatively, anchovy egg and larvae at higher latitudes are retained nearshore in winter (because the Ekman transport is negative, Castro et al., 2000) but are exposed to lower temperatures and to strong turbulence that may not facilitate the first feeding of recently hatched larvae and subsequent rapid larval development. Larger eggs, larger larvae at hatching, and more energy reserves may be the favored early life history strategy in southern populations. How the latitudinal variations in environmental characteristics affect the rest of the life history traits of the different populations of *Engraulis ringens*, one of the most important fish species in the world in terms of catches, remains to be assessed.

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