Inter-population differences in temperature effects on *Engraulis ringens* yolk-sac larvae

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ABSTRACT: Early life stages of *Engraulis ringens* were reared from hatch until yolk exhaustion. We evaluated the effect of temperature on characteristics such as larval length and yolk volume at hatch, larval length at yolk absorption, duration of yolk-sac stage, yolk consumption rate and larval growth rate. Further, we determined the potential differences in these traits between populations located 13° of latitude apart (Antofagasta 23° S, Talcahuano 36° S). The results showed that egg size had an effect on the larval length at hatch, initial yolk volume and larval length at yolk absorption, since the values obtained were always larger in larvae hatched from Talcahuano (from larger eggs) than from Antofagasta (smaller eggs). These characteristics were also modified by the rearing temperature. Duration of yolk-sac phase, yolk consumption rate and larval growth rate until yolk exhaustion showed high thermic dependence in both populations. However, these traits showed no difference between populations when larvae were reared at the same temperature in the range between 12 and 20°C, despite their initial difference in egg size. When extrapolated from the environmental conditions in each nursery area (i.e. 15°C Antofagasta and 12°C Talcahuano), our results suggest that the anchoveta populations from Talcahuano compensate for their lower larval growth rates by increasing their initial egg and hatch sizes, as they are larger than Antofagasta larvae at the end of the yolk-sac stage. This increased larval length should enhance their chances of survival under adverse environmental conditions, such as high turbulence, lower temperature and lower food availability during winter, which is typical of the anchoveta southern spawning area.

KEY WORDS: Anchoveta · Early life-history traits · Egg size · Growth · Latitudinal differences · Temperature effects

INTRODUCTION

A number of environmental parameters that may directly affect the chances of early larval survival vary with latitude. Among them, temperature and day length, especially during winter, have been widely studied (Houde 1989, Conover 1990). The early life stages of species that are distributed across a wide latitudinal range, therefore, are likely to have either behavioral or physiological mechanisms to cope with variations in environmental characteristics.

The anchoveta *Engraulis ringens* is a coastal pelagic species found from northern Peru (4° 30′ S) to southern Chile (42° 30′ S; Serra et al. 1979). Three major spawn-

ing areas have been identified: north (northern Peru), central (southern Peru to northern Chile) and south (central Chile). Environmental characteristics, such as temperature, turbulence index and upwelling index, vary widely within this range (Castro et al. 2001). Egg size of the anchoveta during the peak spawning season also varies with latitude (e.g. 0.20 mm^3 at 20° S and 0.31 mm^3 at 36° S; Llanos-Rivera & Castro 2004). Whether these differences are reflected in variations among yolk-sac larval characteristics is unknown and is a main objective of this study.

Temperature has a strong effect on development and physiological rates of larval fishes (Blaxter 1992). A change in temperature can influence larval size at

hatching and accelerate the development of larval attributes, such as the pigmentation of the eye and the formation of the jaw (Lasker 1964). Generally, larvae incubated at higher temperatures are shorter at the time of hatching. However, in a wider temperature range, length at hatch is maximal at intermediate temperatures and smallest at extremes of low and high temperatures (Chambers 1997). Interestingly, small differences in size at this stage may confer large differences in survival. Larvae that are larger at hatch are more resistant to starvation, and show a greater flexibility in prey selection at the time of first feeding (Miller et al. 1988). Differences in the size at hatch may be an adaptive response to local geographical conditions (Miller et al. 1988).

Temperature also affects early larval growth and yolk consumption rates (Koumoundouros et al. 2001). The effect of temperature, however, may vary among stages, as each developmental stage may have different growth rates. Embryos grow slowly from fertilization to hatching; yolk-sac larvae grow more quickly until they reach the maximum size that their endogenous reserves allow; feeding larvae exhibit relatively slow growth rates at the beginning of exogenous feeding (Kamler 1992).

Abundant information exists on egg development rates for many marine species, especially those of commercial value for stock assessment purposes (Lo 1985). There is an increasing amount of information on larval growth rates, either collected from the field (i.e. based on daily increments on otoliths, Hernández & Castro 2000, Gaughan et al. 2001) or from rearing experiments (tanks and mesocosms, Brown et al. 1998, Otterlei et al. 1999, Van der Meeren & Jorstad 2001). Few studies have addressed the effects of temperature on yolk-sac larvae, probably because of their short duration, fragility and the paucity of easily scored morphological characteristics. In this intermediate stage, it is possible to evaluate direct parental effects on the survival of new larvae (i.e. yolk quality and quantity). The assessment of the parental input may be of great value, for instance, for determining whether characters at this stage are susceptible to selection, especially for populations exposed to contrasting environmental conditions (Chambers 1997), such as in species located over a wide latitudinal range.

During the past decade, we have conducted a series of studies on how different populations of anchoveta cope with latitudinal variations in their environment. We previously described latitudinal variations in anchoveta egg size during the peak spawning season along the Chilean coast (Llanos-Rivera & Castro 2004) and identified several environmental characteristics that might possibly affect the chances of survival of the young life stages (Castro & Hernández 2000, Castro et

al. 2001). Here, we evaluated the effect of temperature on several yolk-sac characteristics of anchoveta hatched from eggs of different sizes collected from 2 areas separated by 13° latitude. The characteristics evaluated were length at hatch, yolk volume at hatch, length at yolk absorption, duration of the yolk-sac phase, yolk consumption rate and growth prior to yolk absorption. With this type of information, we finally assessed whether potential differences between populations in the larval size at hatch are compensated for prior to yolk absorption by means of variations in larval growth rates during the yolk-sac larval stage.

MATERIALS AND METHODS

In 2001, a series of oceanographic cruises to the coastal areas of Antofagasta (23° 05′ S, 70° 30′ W) and Talcahuano (36° 32′ S, 72° 56′ W) (Fig. 1) were carried out during the winter peak spawning of the anchoveta *Engraulis ringens.* During this season (July to September, Cubillos et al. 1999) the sea surface temperatures decrease with increasing latitude. Surface temperature in the northern spawning area (23° S, Antofagasta) varies from 15 to 20°C, and in the southern spawning area (Talcahuano, 36° S) it varies from 11 to 15°C (Fig. 1).

Gently oblique hauls were carried out at 1.5 knots (conical net, 300 µm mesh), and the plankton was deposited in black plastic buckets (30 l) with seawater from the same sampling area. The anchovy eggs were separated from the plankton in <2 h from the time of collection, using a stereomicroscope.

Eggs from early development stages (Phases I and II following Fisher 1958) were utilized for rearing experiments. Sets of 50 eggs were placed in 1 l flasks with 0.5 µm filtered, UV-sterilized seawater. Flasks were placed in 5 temperature-controlled baths set at 10, 12, 15, 18 and 20°C and held under a 12 h light:12 h dark photoperiod.

Two trials (4 d apart) were conducted in each area following this protocol. All rearing temperatures were used except in the second series for Talcahuano, where the 20°C temperature was not evaluated. Close to the time of hatching, the rearing containers were checked every hour for newly hatched larvae. A total of 28 or 30 recently hatched larvae (max. 30 min from hatch) were anesthetized and measured live. Notochord length and yolk-sac size (length and maximum width) were measured under a stereomicroscope equipped with an ocular micrometer (20×). Larval yolk-sac volume was estimated assuming a half-ellipsoid shape ($4\pi abc/6$, where *a*, *b* and *c* correspond to ellipse radii). To avoid underestimating the larval measurements due to shrinkage, the larvae were anesthetized (Bz-20, benzocaine Veterquimica, Chile). Over the course of the experiment,
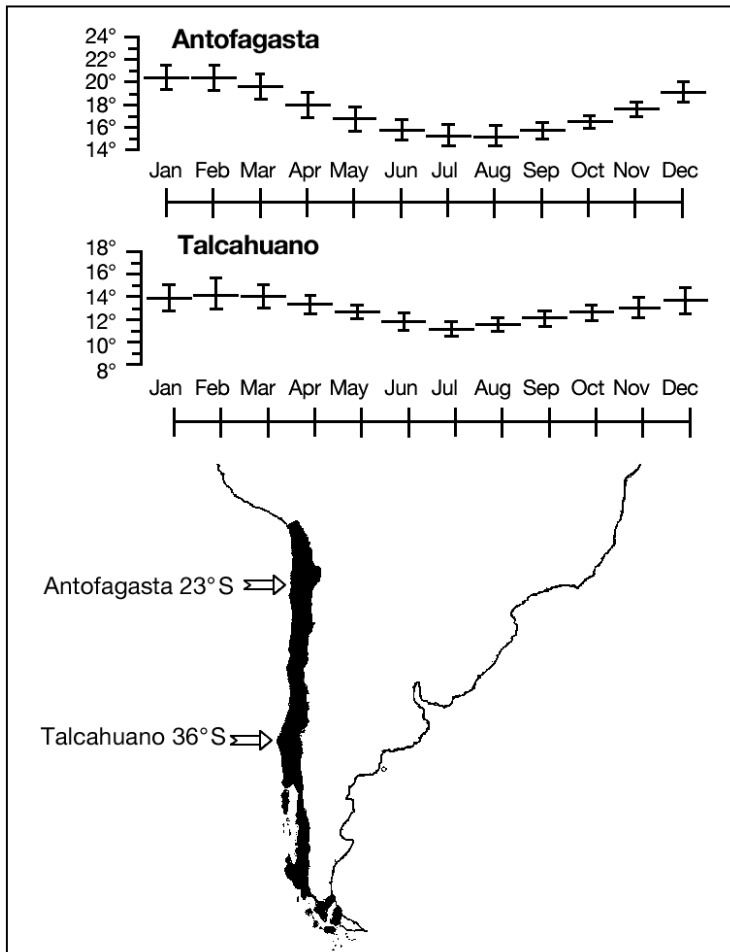
Fig. 1. Time series from 1970 to 1999 of mean (±SD) sea surface temperature (°C) measured at tidal gauge stations along the Chilean coast

area and comparing the parameter estimates with a covariance analysis between them (ANCOVA, Zar 1984). Similarly, the rate of yolk consumption was estimated as the slope of linear regression of Ln yolk volume (mm³) versus time (h) in each area at each temperature. Then, with covariance analyses, we compared their slopes between temperatures within areas and then between areas.

We fit both a non-linear (Gompertz model: $L = L_o \exp\{G[1 - \exp(-gt)]\}$) and simple linear model (linear model: $L = L_o + Bt$) to the growth data from hatch to yolk absorption, where L = length at age t; L_o = length at hatch; G = a dimensionless parameter; g = instantaneous growth rate at age t_o; t_o = an inflection point of the curve and the age at which absolute growth begins to decline; and B = growth rate (STATISTICA 5.0 for Windows, 1996, Stat-Soft). The best model was selected under the Akaike information criterion (AIC, Quinn & Deriso 1999). Differences in growth rates between areas and for the different temperatures were determined by estimating the confidence intervals (95% CI) obtained by means of bootstrap analysis based on 1000 iterations (Manly 1997). Differences in growth rate were considered significant if the confidence intervals were distinct and non-overlapping.

Finally, we checked if differences in egg size between areas occurred as previously reported in studies along the Humboldt Current (Llanos-Rivera & Castro 2004), by collecting and measuring a sub-sample of eggs (preserved in 5% formalin) from all experimental trials. Egg volume was estimated from $4\pi abc/3$, where a, b and c correspond to ellipse radii. We utilized a nested ANOVA, in which trials were nested in egg origin.

RESULTS

Length at hatch, yolk-sac volume and length at yolk absorption

The results of an ANOVA that considered temperature, area and trials as sources of variance revealed that temperature had an effect on the length at hatch, yolk-sac volume and length at yolk absorption in larvae from both areas (Table 1). These larval characteristics reached smaller values at the highest temperatures (Tukey test: length at hatch, df = 495, p < 0.001; yolk-sac volume, df = 495, p < 0.05; length at yolk absorption, df = 300, p < 0.001, Fig. 2). However, a second ANOVA carried out by area assessed the effect of temperature

from the larvae remaining in the experimental flasks, about 10 larvae were collected from each temperature treatment at different time intervals and measured live. Because the rate of yolk absorption is accelerated at higher temperatures (Kamler et al. 1994), measurements were repeated at time intervals from 12 (20°C) to 28 h (10°C), to include the entire process until the event of yolk exhaustion and eye pigmentation.

The effects of rearing temperatures and area on length at hatch, initial yolk volume, length at yolk absorption and time of yolk absorption were tested in a nested ANOVA (analysis of variance), in which trials were nested in areas. Differences in these variables among temperatures were tested with a Tukey *a posteriori* multiple comparison (Zar 1984). To evaluate the effect of temperature within each area, we utilized an ANOVA with trials and temperatures as factors and the same Tukey *a posteriori* multiple comparison.

The temperature effect on yolk-sac stage duration for each egg source (area) was evaluated by applying a linear model of Ln time (h) over temperature (°C) for each
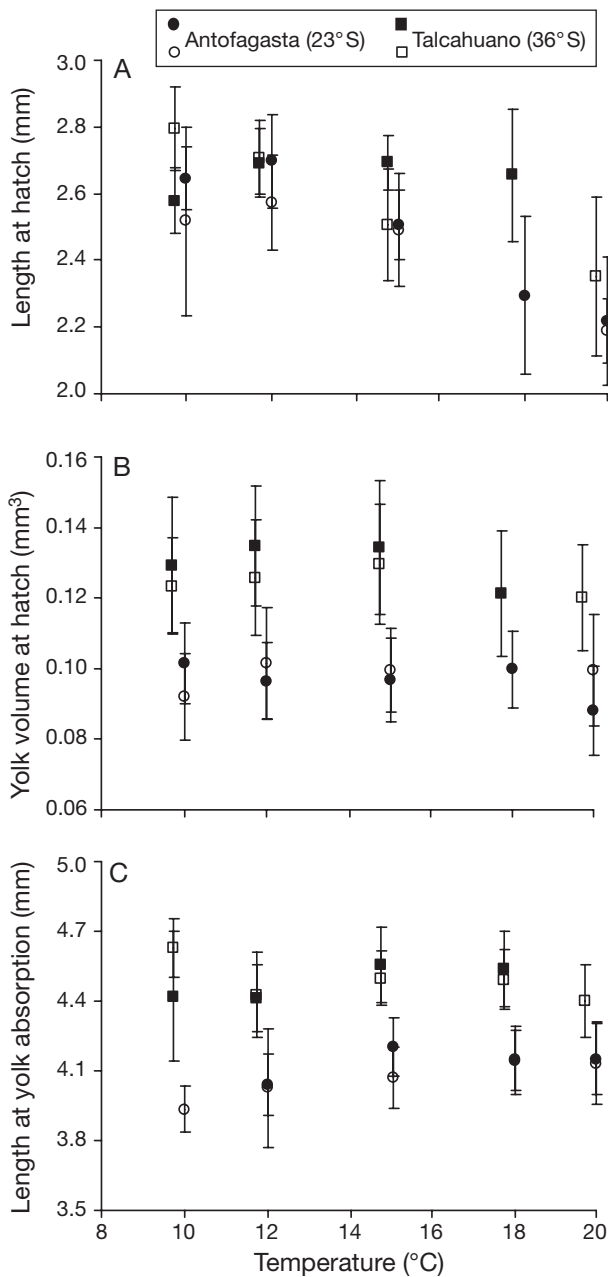
Fig. 2. *Engraulis ringens.* Effect of temperature on mean (±SD) of size characteristics for larvae: (A) length at hatch, (B) yolk volume at hatch and (C) length at yolk absorption. Each mean corresponds to 1 experimental trial (2 trials per area) in Antofagasta and Talcahuano

Table 1. *Engraulis ringens.* Results of ANOVA to test for effects of temperature, area and trial on early larval traits. Values in **bold**: significant values

Source of variation	df	F	p
Length at hatch (mm)			
Temperature	4	78.68	**0.000000**
Area	1	30.66	**0.034139**
Trial (area)	2	2.29	0.101972
Error	495		
Yolk volume at hatch (mm³)			
Temperature	4	3.59	**0.006709**
Area	1	115.53	**0.009300**
Trial (area)	2	3.91	**0.020582**
Error	495		
Length at yolk absorption (mm)			
Temperature	4	5.41	**0.000320**
Area	1	100.99	**0.008630**
Trial (area)	2	3.94	**0.020393**
Error	300		

$p < 0.05$) (Table 2, Fig. 2A). In Talcahuano, differences in the length at hatch were determined only among temperatures (ANOVA: temperature $F_{(4,229)} = 28.68$, p = 0.0001), with the smallest larvae being those hatched at the highest temperatures (Tukey test: df = 229, $p < 0.05$).

Only in Talcahuano did differences exist in yolk-sac volume of recently hatched larvae among temperatures (ANOVA: $F_{(4,229)} = 3.95$, p = 0.0040) and trials (ANOVA: $F_{(1,229)} = 7.426$, p = 0.0069). The differences in yolk-sac volume (highest and lowest volumes) occurred at temperatures between 15 and 20°C (Tukey test: df = 227, $p < 0.05$) (Fig. 2B, Table 2). Between trials, the differences were due to the lowest value of yolk-sac volume, which was observed at 20°C (Tukey test: 15°C (Trial 2) vs. 20 and 12°C (Trial 2) vs. 20°C, df = 227, $p < 0.05$).

Finally, while no differences in length at yolk absorption occurred between trials in Talcahuano, temperature did have an effect (ANOVA: $F_{(4,179)} = 7.46$, p = 0.00014). Larvae maintained at 12, 18 and 20°C absorbed their yolk at a smaller size than those reared at 10°C (Tukey test: df = 179, $p < 0.05$) (Fig. 2C, Table 2). In Antofagasta, in turn, no differences were observed in the length at yolk absorption either among temperatures or trials (ANOVA: temperature, $F_{(4,117)} = 2.29$, p = 0.063; trials, $F_{(1,117)} = 3.05$, p = 0.083). In both areas yolk absorption occurred coincidently with eye pigmentation.

Yolk-sac period duration, yolk consumption and larval growth

Temperature had an inverse effect on yolk-sac stage duration. The inverse power model between temperature and yolk stage duration (YSD) (Fig. 3A) predicts a 2-fold increase of yolk duration with a decrease of 5°C

on larvae from each population and showed that slight differences occurred between areas.

In Antofagasta, a difference was observed in the length at hatch among temperatures and between trials (ANOVA: temperature $F_{(4,262)} = 66.62$, p = 0.0001; trials $F_{(1,262)} = 10.46$, p = 0.001371). An *a posteriori* test revealed that the main difference was due to shorter larvae occurring at 18 and 20°C (Tukey test: df= 259,

Table 2. *Engraulis ringens*. Early traits of larvae reared at different temperatures in Antofagasta and Talcahuano. Values correspond to the mean (±SD, in parentheses) of 2 experimental trials carried out in each area

| | Antofagasta (23° S) | | | | | Talcahuano (36° S) | | | | |
	10°C	12°C	15°C	18°C	20°C	10°C	12°C	15°C	18°C	20°C
Length at hatch (mm)	2.58	2.64	2.50	2.29	2.20	2.69	2.70	2.60	2.66	2.35
	(0.22)	(0.15)	(0.14)	(0.24)	(0.15)	(0.16)	(0.11)	(0.08)	(0.20)	(0.24)
Yolk sac volume at hatch (mm^3)	0.097	0.099	0.098	0.096	0.094	0.126	0.130	0.132	0.121	0.120
	(0.013)	(0.014)	(0.012)	(0.015)	(0.015)	(0.016)	(0.017)	(0.018)	(0.016)	(0.015)
Length at yolk-absorption (mm)	3.97	4.04	4.16	4.14	4.14	4.60	4.42	4.54	4.52	4.40
	(0.15)	(0.27)	(0.14)	(0.14)	(0.16)	(0.17)	(0.16)	(0.15)	(0.15)	(0.16)

(YSD$_{Antofagasta}$ = 6316 × $T^{-1.55}$; YSD$_{Talcahuano}$ = 13 069 × $T^{-1.86}$). In both populations, the strongest difference in YSD among temperatures was observed at the lowest temperature range (10 to 12°C). For instance, a decrease in 2°C in this range increased the YSD by 2 d, while a decrease between 20 and 18°C increased the yolk duration by 0.4 d. Accordingly, yolk consumption rate (mm^3 h^{-1}) increased significantly with temperature in both populations (Table 3; ANCOVA: Antofagasta, n = 982, p < 0.001; Talcahuano, n = 968, p < 0.001) (Fig. 3B). When comparing between areas, no differences in yolk-sac phase duration (Table 3; ANCOVA: n = 17, p > 0.05) or yolk exhaustion rate were observed (ANCOVA: n = 1950, p > 0.05).

Growth in length of yolk-sac larvae was best described by a non-linear Gompertz model at all temperatures (Table 4). Growth rates of yolk-sac larvae increased with temperature for larvae from both areas (Fig. 3C). A trend was observed in which at the highest temperatures (18 to 20°C) northern larvae grew faster than southern larvae. Alternatively, at the lowest temperatures (10 to 12°C) larvae from the southern population grew faster than larvae from the northern location. However, differences in the growth rate of larvae between areas were only statistically significant at the lowest temperature (10°C).

In larvae from Antofagasta, changes in a few degrees of temperature resulted in different variations in growth rates between the lowest and highest temperature ranges (Fig. 3C, Table 3). For instance, while a change in 2°C (between 10 and 12°C) resulted in a 0.10 mm d^{-1} increase in growth rate (58.8%), in the highest temperature range (18 to 20°C) the 2°C change resulted in a growth rate increase of 0.27 mm d^{-1} (45.8%). The growth rate of yolk-sac larvae from Talcahuano did not change in the lower temperature range (between 10 and 12°C), but did change in the highest temperature range (from 18 to 20°C), increasing by 35.2%.

Interpopulation differences in larval sizes and egg volumes

Egg size (volume) differed between source areas (ANOVA: $F_{(2,819)}$ = 5532, p = 0.0001) and also between trials (ANOVA: $F_{(2,819)}$ = 8.576, p = 0.0002), but the difference between trials was much smaller than between areas (Table 2). Eggs from the southern population were, on average, larger than those from the north (23° S) (Table 5, Fig. 4). Thus, egg size, length at hatch, initial yolk volume and length at yolk absorption are characteristics of the early life stages that differ between populations, being larger in individuals originating from the southern population (Talcahuano) (Fig. 4).

Table 3. *Engraulis ringens*. Early rates of larvae reared at different temperatures in Antofagasta and Talcahuano. Values correspond to the mean (±SD, in parentheses) of 2 experimental trials carried out in each area

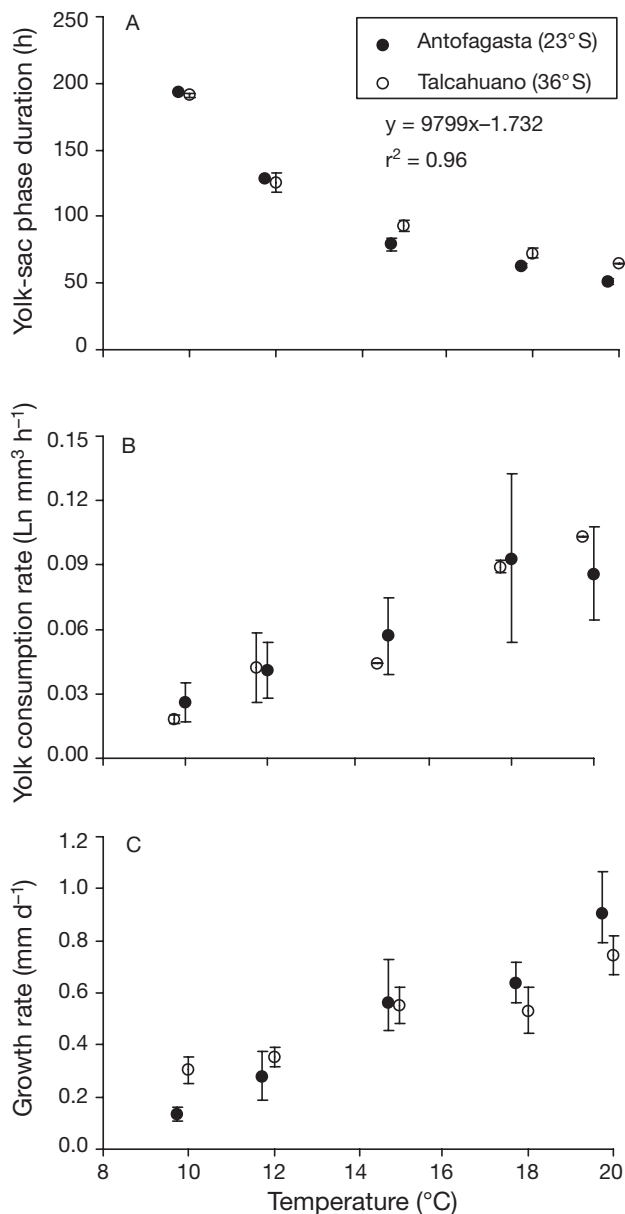| | Antofagasta (23° S) | | | | | Talcahuano (36° S) | | | | |
	10°C	12°C	15°C	18°C	20°C	10°C	12°C	15°C	18°C	20°C
Growth rate (mm d^{-1})	0.17	0.27	0.48	0.59	0.86	0.22	0.33	0.47	0.54	0.73
	(0.019)	(0.022)	(0.022)	(0.121)	(0.047)	(0.004)	(0.042)	(0.031)	(0.06)	
Yolk consumption rate (Ln mm^3 h^{-1})	0.026	0.041	0.057	0.093	0.086	0.018	0.042	0.044	0.0892	0.103
	(0.009)	(0.013)	(0.018)	(0.039)	(0.022)	(0.002)	(0.016)	(0.00007)	(0.003)	0
Duration yolk-sac phase (d)	8.08	5.38	3.29	2.62	2.14	7.96	5.22	3.88	3.02	2.7
			(0.177)	(0.059)	(0.088)	(0.059)	(0.309)	(0.177)	(0.147)	

Fig. 3. *Engraulis ringens*. Effect of temperature on developmental rates of yolk-sac larvae. (A) Yolk-sac duration (mean ± SD) of 2 experimental trials carried out in Antofagasta and Talcahuano. (B) Yolk consumption rate (mean ± SD) of 2 experimental trials carried out in Antofagasta and Talcahuano latitudes. (C) Growth rate (mean ± 95 CI) obtained by bootstrapping. Parameters utilized were obtained from a Gompertz model fitted to the Antofagasta and Talcahuano pooled experimental data

DISCUSSION

The purpose of this study was to evaluate the effect of temperature in characteristics of anchoveta *Engraulis ringens* early life stages and, secondly, to determine potential differences in these traits between populations of this species separated by 13° of latitude.

Previous reports have shown that environmental conditions during the spawning season differ markedly between latitudes and also that differences existed in egg size spawned in both populations. Our results show a similar strong dependence on temperature of all rates measured in yolk-sac larvae from both populations, but also show that strong differences occurred in all larval size characters between populations.

Temperature dependence

Duration of yolk-sac phase, yolk consumption rate and larval growth rate until yolk exhaustion showed high thermic dependence in both populations. These traits showed no difference between populations when their larvae were reared in the temperature range between 12 and 20°C, despite the differences in egg size. In other species, such as cod *Gadus morhua* and yellowtail flounder *Pleuronectes ferrogineus*, temperature also proved to have a greater influence than egg size on egg development rates and the duration of yolk-sac larvae (Pepin et al. 1996, Benoit & Pepin 1999). As a consequence of the temperature dependence of biochemical reactions that drive metabolism, Pepin et al. (1996) proposed temperature as the dominant factor governing early development in cod. The overall results from our observations, therefore, suggest that: (1) temperature is the main factor driving these rate variations in both populations, except at the lowest temperatures; (2) there are no differences between areas in yolk-sac larval growth rates over most of the temperature range naturally experienced by these populations; and (3) some local adaptations might be occur, as evidenced by the higher growth rates at 10°C in the higher latitude population (Talcahuano), which is normally exposed to colder waters.

Larval length at hatch and initial yolk volume were modified by the rearing temperature to some extent. For instance, at the highest temperatures the length at hatch was smaller, as observed in other species. The size reduction has been explained as an effect of the temperature on the relative timing of phases of growth and differentiation (Blaxter 1992). In gadids, a dome-shaped type of response has been observed, with smaller sizes achieved at lower and higher temperatures (Chambers 1997). This dome pattern did not occur in the anchoveta. Similarly, in other clupeiformes species (e.g. *Clupea harengus*) the length at hatch and larval length at yolk absorption have also been reported not to vary over a wide range of temperatures (3.5°C at 17°C, Overnell 1997). Whether there is a relationship between larval forms (elongated in clupeiforms vs. deeper in gadids) and the type of response to temperature (dome-shaped or other), should be dealt with in future studies.

Table 4. *Engraulis ringens*. Parameters of Gompertz and linear models fit to growth of *E. ringens* yolk-sac larvae. r^2 = determination coefficient; L_o = length at hatch; G = dimensionless parameter; g = instantaneous growth rate at age t_o; B = growth rate (slope mm^{-1}); AIC: Akaike information criterion; N: number

	Antofagasta (Trial 1)					Talcahuano (Trial 2)				
	10°C	12°C	15°C	18°C	20°C	10°C	12°C	15°C	18°C	20°C
Gompertz										
r^2	86.37	88.61	95.28	93.52	97.57	94.17	92.27	95.90	95.40	96.16
L_o	2.52	2.57	2.49	2.82	2.20	2.64	2.70	2.52	2.30	2.23
G	0.43	0.44	0.50	0.39	0.61	0.44	0.41	0.50	0.58	0.61
g	0.03	0.06	0.07	0.06	0.10	0.04	0.06	0.05	0.11	0.08
AIC	11.04	13.94	11.08	8.18	9.32	10.24	12.48	10.06	12.18	10.94
Linear										
r^2	60.92	60.83	60.70	73.72	70.24	73.57	65.21	74.53	68.77	73.03
L_o	2.73	2.83	3.02	3.06	2.67	2.97	3.03	2.88	2.77	2.62
B	0.01	0.01	0.01	0.02	0.03	0.01	0.01	0.02	0.02	0.03
AIC	19.82	30.98	46.08	12.72	44.50	23.06	32.96	29.08	45.64	38.64
N	58	78	141	54	126	114	120	123	121	106
	Talcahuano (Trial 1)					Talcahuano (Trial 2)				
	10°C	12°C	15°C	18°C	20°C	10°C	12°C	15°C	18°C	
Gompertz										
r^2	92.12	94.28	95.04	92.50	93.01	93.68	96.10	94.93	94.90	
L_o	2.79	2.70	2.52	3.00	2.37	2.58	2.69	2.72	2.66	
G	0.50	0.52	0.55	0.40	0.61	0.51	0.49	0.51	0.53	
g	0.03	0.04	0.07	0.07	0.08	0.04	0.05	0.05	0.06	
AIC	16.00	14.34	13.08	11.44	18.32	11.16	10.10	14.10	12.00	
Linear										
r^2	69.46	68.14	69.43	70.39	73.89	76.70	69.51	76.62	76.64	
L_o	3.22	3.19	3.03	3.46	2.83	2.79	3.09	3.14	3.04	
B	0.01	0.01	0.02	0.02	0.03	0.01	0.01	0.02	0.02	
AIC	42.48	50.08	47.24	25.34	49.72	23.34	35.74	41.16	31.16	
N	129	138	121	138	157	61	104	165	103	

Inter-population differences in egg-size-derived traits

Larval length at hatch, initial yolk volume and larval length at yolk absorption were larger in individuals originated from Talcahuano eggs than in those hatched from Antofagasta (smaller eggs) (Fig. 4). In our study these larval traits varied among populations and were consistent with the initial differences in egg size spawned in both areas; thus, they could be the result of a maternal effect on the egg volume. The relation between egg size and morphological larval characteristics has been broadly discussed, and a direct relationship between egg size and larval size at hatch has been documented in several species (i.e. *Gadus morhua*, Pepin et al. 1996; *Clupea harengus*, *Solea solea*, Panagiotaki & Geffen 1992).

Maternal effects on early life-history traits probably depend largely on the environmental conditions (i.e temperature, feeding conditions) experienced by females when energy is being acquired and converted during oogenesis (Chambers et al. 1989). In species such as capelin *Mallotus villosus* the initial mean yolk

Table 5. *Engraulis ringens*. Size (mm^3) of eggs used in experiments from Antofagasta and Talcahuano during 2001

	Antofagasta (23° S)		Talcahuano (36° S)	
	Trial 1	Trial 2	Trial 1	Trial 2
Date	4 Aug	7 Aug	5 Sep	12 Sep
Mean egg volume	0.266	0.259	0.302	0.292
SD	0.021	0.023	0.023	0.026
n	180	325	254	66

volume of the eggs has been directly related to the condition and lipid indices of the female (Chambers et al. 1989). In other anchovies (*Engraulis japonicus*), fecundity and egg diameter have been related to environmental temperature. In the latter species, an increase in 3°C produced a decrease in 5.5% of the egg diameter; therefore, temperature probably modified the proportion of energy destined for reproduction (Funamoto & Aoki 2002). Temperatures prior and during the anchoveta reproductive season differ by at least 3°C between the southern Talcahuano and Antofagasta spawning areas. Thus, differences in egg size between
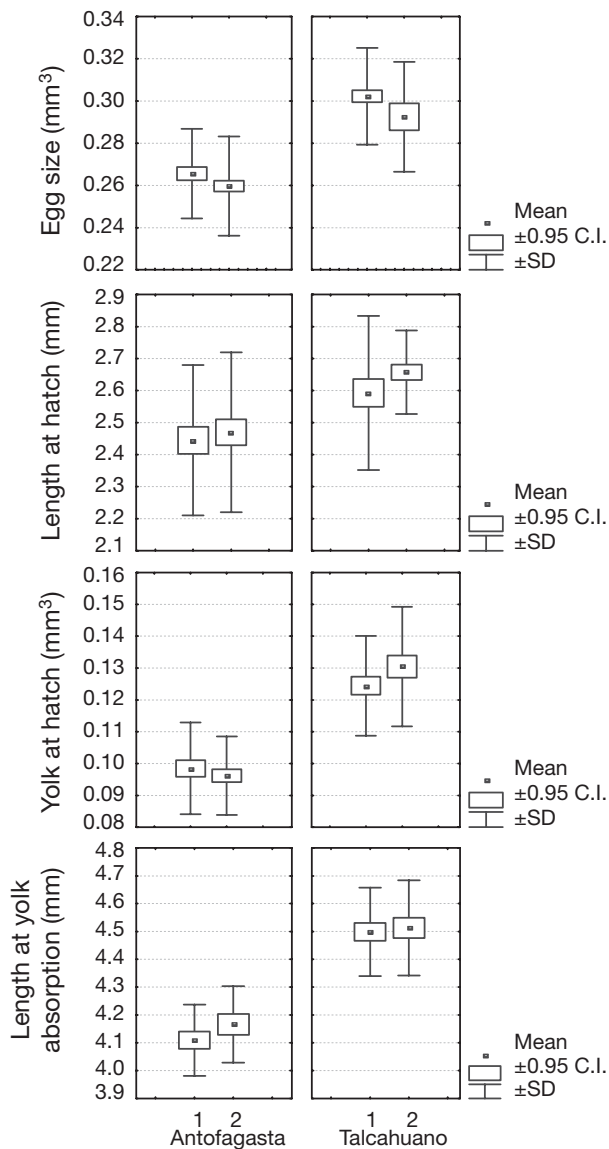
Fig. 4. *Engraulis ringens.* Box plots of each experimental trial (1 and 2) for egg size and larval characteristics from Antofagasta and Talcahuano during the winter spawning season 2000

populations of anchoveta are probably the result of dissimilar environmental conditions experienced by the adults during oogenesis in both geographical areas.

Implications for populations located in different environments

The results of this study are relevant when extrapolated from the environmental conditions prevailing in each nursery area (i.e. 15°C Antofagasta and 11 to 12°C Talcahuano). Anchoveta larvae hatching at Talcahuano are larger and have a larger amount of yolk

than larvae from Antofagasta. The rate of yolk utilization for transformation towards new larval tissue is slower, and the duration of the yolk-sac phase is longer in larvae from Talcahuano (5 d compared with 3 d for larvae from Antofagasta). The larval length differences observed at the end of the yolk-sac phase correspond to the length differences at hatching, and both factors (larval length at hatch and larval length at yolk absorption) are maternal effects originally expressed in the eggs (i.e. egg volume in the southern population is >15% that in the northern population; Table 5). The higher growth rates of the Antofagasta yolk-sac larvae and the resulting sizes at yolk absorption do not compensate for the initial differences in sizes at hatch (i.e. length at yolk absorption Antofagasta: 4.15 mm at 15°C; Talcahuano: 4.42 mm at 12°C; see Table 2). As a final result, at the end of the yolk-sac stage, larvae from Talcahuano begin their exogenous feeding at a larger size. This increased length at yolk-sac absorption means larger mouth sizes, which might result in enhanced capture abilities, increased resistance to starvation (Shirota 1970, Hunter 1981, Fukuhara 1990) and enhanced chances of survival under adverse environmental conditions, such as increased turbulence, lower temperature and lower food availability during winter. These are the normal conditions experienced by the young anchoveta larvae in the southern spawning area (Castro et al. 2001). Therefore, the maternal effect of larger egg size and, moreover, of increased yolk volume in recently hatched larvae in the southern individuals seem advantageous results of the reproductive process during oogenesis to the comparatively more adverse austral environmental conditions faced by the young larvae.

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