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FULL PAPER

Temperature effects on the anchoveta *Engraulis ringens* egg development: do latitudinal differences occur?

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Abstract We assessed differences in the development rates among anchoveta, *E. ringens* populations from the extremes of its range under different temperatures. Time to hatch decreased with increasing temperature but there was no difference in the temperature–development time relationship between eggs from different localities. These results and observations of hatching success differences between populations at lower temperatures support the hypothesis that inter-population differences in the earlier life stages occur along the distribution range of anchoveta, although the current genetic evidence suggests substantial gene flow between localities.

Keywords Anchoveta · Temperature · Incubation · Q_{10}

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Introduction

Predictions of global warming have captured the interest of physiologists and fishery biologists trying to predict the overall consequences of ocean warming on fishery stocks (Blaxter 1992). Davenport and Sayer (1993) pointed out the difficulty in determining whether the distributions of fish species were under thermal constraints arising from the physiological capability of fishes to adapt to changes in ambient temperature. Lasker (1964) found that incubation time (t) of sardine embryos, *Sardinops caerulea* Girard, did not decrease with increasing temperature (T). He proposed the general formula $T = at^b$ to fit experimental data and suggested that data from other fish species were required to test its applicability. Blaxter (1992) suggested that the most significant influence of temperature on physiological parameters of fish would be on development time. Lo (1985) had earlier proposed that fish development rates are a mixed exponential and power function of temperature and stage.

The anchoveta, *Engraulis ringens* (Jenyns 1842), is subject to an intense (484,000 ton/year) and economically important fishery in the southeastern Pacific from Zorritos, Peru (4°30′ S) to Chiloe, Chile (42°30′ S). It usually occurs close to the coast (<30 nautical miles) in the upper 50 m

(Serra and Barria 1990[1]). Three main fishery stocks have been identified: (i) off northern Peru (largest), (ii) off southern Peru-Northern Chile, and (iii) off Central Chile (smallest) (Castro 2001). However, these fishery stocks should not be considered as separate biological populations since gene flow occurs between all of them (Ferrada et al. 2002).

Due to its wide latitudinal distribution (4° S–42° S), the anchoveta is a good subject for the study of temperature effects on development. Furthermore, this species inhabits coastal pelagic environments that also show seasonal variations in temperature (Castro et al. 2000; Castro and Hernandez 2000; Hernandez and Castro 2000; Castro 2001). In the southern range of distribution of the species, previous studies have shown that the incubation time for anchoveta eggs from Talcahuano (36° S) are strongly dependent on the experimental temperatures (Tarifeño et al. 1984)[2]. Gillooly et al. (2002) proposed a general model that, based on allometry and biochemical kinetics, predicts ontogenetic development time to be a function of body mass and temperature. This model would suggest a general definition of biological time that would be approximately constant and common to all organisms.

We measured the development time of *E. ringens* from Talcahuano (36°41′ S) and Antofagasta (23°39′ S) at different experimental temperatures, then analyzed and compared two spawning seasons (2000 and 2001). We determined whether differences occur in developmental time between populations of anchoveta along its latitudinal range. Additionally, by comparing the present results with previous data on egg incubation times (Tarifeño et al. 1984; Escribano et al. 1996; Sepúlveda et al. 2000)[3] we explored the possibility of finding differences among cohorts within the same population.

Materials and methods

Fertilized anchoveta eggs were collected from natural spawning areas 3–4 NM off Talcahuano (36°41′ S) off Antofagasta (23°39′ S) throughout the southern winter and spring seasons of 2001 (Fig. 1). We used oblique zooplankton samples from 5 min tows from the upper 16 m using a standard conical plankton net with a 60 cm diameter and 330 μm mesh. Each sample was individually transported in a 20 l plastic container to the lab, where eggs were sorted under a stereomicroscope, following descriptions by Escribano et al. (1996) and Moser and Ahlstrom (1985). Since the eggs were mainly spawned the night prior to collection, the embryo development was already in progress when samples were collected early the following morning. Therefore, stage III eggs (average egg volume: Antofagasta 0.243 ± 0.034 mm^3, Talcahuano 0.312 ± 0.030 mm^3, Llanos-Rivera and Castro 2004) were chosen as the initial stage for experimental incubations. Normally, samples were sorted within 2 h after sampling.

Developing embryos were held at the Marine Biological Station of the University of Concepcion at Coliumo Bay (36°41′ S), and at the University of Antofagasta Marine Laboratory (23°39′ S), inside controlled incubator rooms (5°C, 12:12 photoperiod). The replicated incubation systems were 1 l glass-jars placed inside 50 l temperature baths (5, 8, 10, 11, 12, 15, 18, 20 and 22°C). We held sorted fertilized eggs (10–15 per jar) in 0.5 μm filtered and UV sterilized seawater (salinity 34‰), with replicates (1–7) at each temperature and experimental (Table 1), similar to experiments carried out previously by Tarifeño et al. (1984), Sepúlveda et al. (2000) in Talcahuano, and by Escribano et al. (1996) in Antofagasta. All experimental protocols started with

[1] Serra, R. and P. Barría. 1990. Estado de las pesquerías pelágicas nacionales. Inf. Tec, IFOP-SUBPESCA, Santiago, 39 pp.

[2] Tarifeño, E., A. Arrizaga and G. Herrera. 1984. Influencia de la temperatura en el desarrollo de huevos larvas del jurel (*Trachurus murphyi*) en condiciones de laboratorios. Final Project Report. Proyecto DIUC 166/83. Pontificia Universidad Católica de Chile. Santiago, 24 pp.

[3] Sepúlveda, A., L. Cubillos, S. Nuñez, T. Canales, D. Bucarey and A. Rojas. 2000. Antecedentes biológicos del stock desovante de anchoveta y sardina común de la V y IX regiones. Informe Final Project Report FIP 97-04 200p +xi

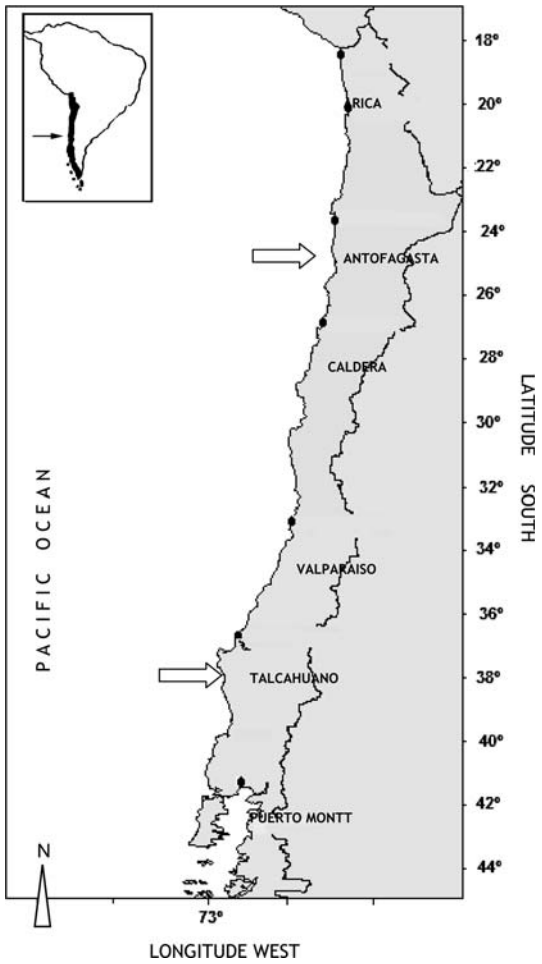

Fig. 1 *Engraulis ringens*. Map showing Chilean coastal areas where anchoveta embryos were collected (arrows) and recording sites for sea temperature showed in Fig. 5

embryo in stage III (Moser and Ahlstrom 1985). Soto et al. (2004) started their experiments with phase I eggs recently fertilized by captive adults, so we did not use their data in our comparative analysis. Development time (e.g., hours to hatch) was considered as the time required for 50% of the eggs to hatch. Percentage hatching was calculated from the number of incubated eggs within a given treatment and locality.

To assess differences among cohorts from the same population and between different localities, results from experiments reported here were compared with similar data reported before by Tarifeño et al. (1984), Sepúlveda et al. (2000) and Escribano et al. (1996), (Table 2). Statistical analyses were done by fitting linear regressions for each data set and by *T*-tests between slopes (Zar 1984). To compare temperature ranges where changes in development times could be more affected by temperature, the Q_{10} physiological coefficient (Hoar 1978; Kamler 1992; Davenport and Sayer 1993) was calculated and compared against a the null hypothesis proposed by Brett and Groves (1978) that $Q_{10} = 2.3$ for fish following the ''Krogh normal curve'' (Winberg 1956) instead of value 2 predicted from Van't Hoff's simple chemical findings (Davenport and Sayer 1993).

Results

Embryo development and larval hatching did not occur at 5°C and remained in the same initial incubation stage (III) even after 1 week without further development. After 24 h all incubated embryos become whitish and lost their initial translucent appearance, and then died. At 8°C, some embryos started their development, but

Table 1 *Engraulis ringens.* Experimental incubations with embryos of anchoveta collected from Talcahuano (36°41′ S) in 2000 and Antofagasta (23°39′ S) in 2001

Trial	Date	Temperatures	Number of replicates	Eggs/replicates
Talcahuano				
1	Jul 2000	5, 10, 15, 20	7	10
2	Jul 2000	5, 9, 12, 15, 18	1	50
3	Aug 2000	5, 10, 12, 15, 18, 22	3	30
4	Aug 2000	8, 10, 12, 15, 18, 20, 22	3	50
5	Aug 2000	8, 10, 12, 15, 18, 20, 22	3	50
6	Oct 2000	8, 10, 12, 15, 18, 20, 22	4	30
Antofagasta				
1	Jul 2001	10, 12, 15, 18, 20	3	100
2	Jul 2001	12, 15, 18, 20	3	100
3	Jul 2001	12, 15, 18, 20	3	100

Table 2 *Engraulis ringens.* Developing time (hours to hatch) of embryos of anchoveta from Antofagasta (23°39′ S) and Talcahuano (36°41′ S) under different incubation temperature

Sampling sites	Incubation temperature (°C)	Mean hours to hatch	Data source
Talcahuano 1983	23	20	Tarifeño et al. 1984
	18	30	
	13	67	
	11	96	
	8	160	
Talcahuano 1997	18	58	Sepúlveda et al. 2000
	16	63	
	15	69	
	11.5	93	
Talcahuano 2000	22	26	Current study
	20	30	
	18	39	
	15	46	
	12	73	
	10	97	
Antofagasta 1995	21	26	Escribano et al. 1996
	16	40	
	11	66	
Antofagasta 2001	20	24	Current study
	18	37	
	15	45	
	12	69	
	10	92	

only reached stages VIII–X without successful hatching. Furthermore, the embryos showed severe malformations (e.g., twisted notochord, disaggregated yolk) indicating an abnormal and unsuccessful development (Fig. 2). At experimental temperatures higher than 8°C, hatching did occur, reaching 92% at 15°C. At the extremes of the temperature range where hatching occurred (10 and 22°C), the average successful hatching percentages were only 68% and 65%, respectively, with the lowest hatching success (56%) occurring at 20°C. Hatching percentage showed the largest and lowest coefficients of variation at 20°C and 15°C, respectively (Fig. 3). Experiments with embryos from Antofagasta in 2001 did not show development below 10°C. In this case, embryos showed the same general pattern of malformation observed at Talcahuano samples, but at a higher temperature range (between 10°C y 12°C). Hatching success was over 95% at temperatures above 15°C.

The expected relationship between temperature and embryo development rates was achieved in embryos from both localities (i.e. shorter incubation times at higher temperatures; Table 2). Intercept, slopes and coefficient of

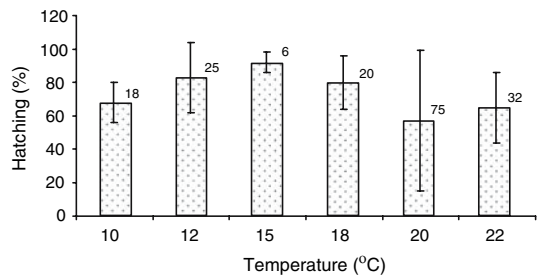

Fig. 3 *Engraulis ringens.* Mean hatching percentage of anchoveta embryos from Talcahuano (36°41′ S) under different temperature incubation. Lines: sd, and number cv

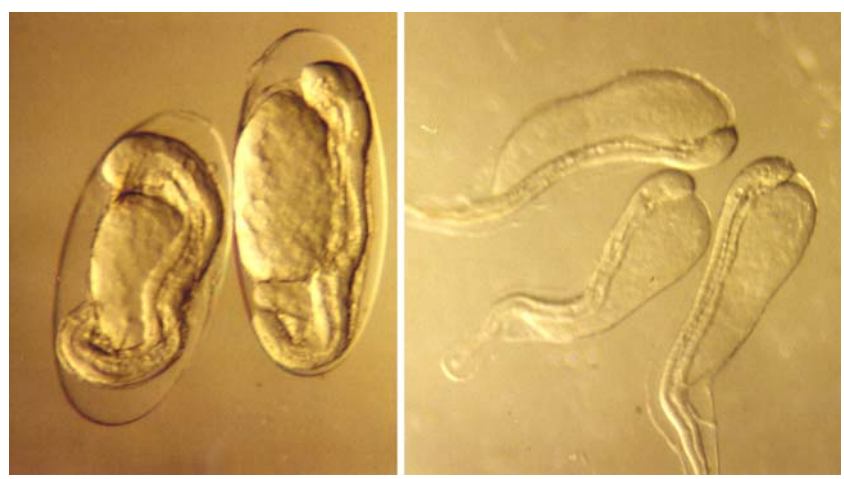

Fig. 2 *Engraulis ringens.* Malformation of anchoveta embryos (twisted notochord, disaggregated yolk) at 8°C from eggs sampled off Talcahuano in 2000

determination (R^2) values for Ln-transformed data of hours-to-hatch at different incubation temperatures were quite similar within embryos from the same area and between areas, suggesting that the relationship between these two factors does not change between the populations along the latitudinal range examined (Table 3).

To evaluate if temperature effects on embryo development time varied between cohorts spawned within the same area in different dates, data from our experiments in 2000 off Talcahuano were compared with results obtained in 1983 (Tarifeño et al. 1984) and in 1997 (Sepulveda et al. 2000). Similarly, the results obtained in Antofagasta in 2001 were compared to embryo data obtained in 1995 (Escribano et al. 1996). Slope comparisons within each locality clearly showed no statistical differences in Talcahuano data sets, and a marginally significant value ($P = 0.049$ instead 0.05) for Antofagasta data sets (Table 4). Since the comparison of slopes between the pooled data from both areas did not show significant differences ($P < 0.7657$), a general regression model was fit to the pooled data: $y = 5.57–0.109*x$ (Table 3, Fig. 4).

The Q_{10} physiological coefficient showed values that ranged from 1.7 to 4.7 with the lowest values between 15 and 18°C and the highest between 15 and 12°C for the embryos from Talcahuano during the 2000 spawning season. Meanwhile, Q_{10} values for Antofagasta's embryos from the 2001 spawning season were 1.9 at 15–18°C and of 8.7 between 18 and 20°C (Table 5).

Discussion

The objectives of this study were: (i) to determine and compare the incubation times of anchoveta, *E. ringens*, embryos from Talcahuano (36°41′ S) and Antofagasta (23°39′ S) during the 2000 and 2001 spawning seasons, (ii) to determine whether differences existed among cohorts of the same populations by comparing present results with previously published data, and (iii) to examine the temperature tolerance ranges for each population.

The expected pattern of hatching time decreased with increasing temperatures (Brett and Grove 1978, Kamler 1992) in both sites (Antofagasta and Talcahuano) and seasons (2000 and 2001 spawning seasons) as previously observed for anchoveta embryos (Tarifeño et al. 1984; Escribano et al. 1996; Sepúlveda et al. 2000). The effect of temperature on the incubation time

Table 3 *Engraulis ringens.* Regression parameters for the relationship between temperature (°C)—development time (Ln h) in embryos of anchoveta sampled off Talcahuano (36°41′ S) and Antofagasta (23°39′ S)

Locality	Equation	*n*	R^2	SSR	*P*-value	Source
Talcahuano 1983	$y = 5.94–0.132*x$	4	0.960	0.040	<0.001	Tarifeño et al.
Talcahuano 1997	$y = 5.40–0.076*x$	4	0.968	0.002	<0.001	Sepúlveda et al.
Talcahuano 2000	$y = 5.57–0.107*x$	52	0.959	0.557	<0.001	Current study
Antofagasta 1995	$y = 5.16–0.091*x$	10	0.852	0.188	<0.01	Escribano et al.
Antofagasta 2001	$y = 5.76–0.126*x$	9	0.956	0.068	<0.001	Current study
Talcahuano pooled	$y = 5.61–0.109*x$	60	0.937	1.008	<0.001	Current study
Antofagasta pooled	$y = 5.42–0.106*x$	19	0.888	0.344	<0.001	Current study
All pooled data	$y = 5.57–0.109*x$	79	0.915	1.669	<0.001	Current study

Table 4 *Engraulis ringens*. Slope analysis (*t*-test Zar 1984) for temperature versus development time regressions

Comparison	*t*-value	d.f.	*P*-value
Antofagasta 1995 versus Antofagasta 2001	2.142	15	0.0490*
Talcahuano 1983 versus Talcahuano 1997	2.240	2	0.1544
Talcahuano 1983 versus Talcahuano 2000	1.085	52	0.2829
Talcahuano 1997 versus Talcahuano 2000	1.069	52	0.2900
Talcahuano pooled versus Antofagasta pooled	0.299	75	0.7657

* $P < 0.05$

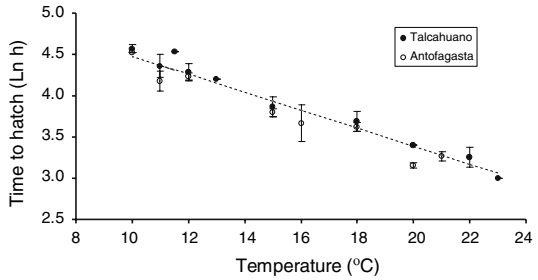

Fig. 4 *Engraulis ringens.* Mean Ln hours to hatch (±S.D.) plotted against experimental incubation temperatures for anchoveta embryos sampled off Talcahuano (36°41′ S) and Antofagasta (23°39′ S). Pooled data from 1983, 1997 and 2000 (Talcahuano) and 1995, 2001 (Antofagasta) spawning season. Line represent pooled model

of anchoveta embryos was similar in both localities despite the different thermal regimes occurring in each locality (i.e., warmer Antofagasta, colder Talcahuano). This result suggests that the biological processes driving the incubation time operate similarly with either increasing or decreasing temperature in both populations of anchoveta. Accordingly, the equation for the pooled data (Table 3, Fig. 4) could represent a general model for the relationship between temperature and incubation time for embryos of anchoveta from Antofagasta (23°39′ S) and Talcahuano (36°41′ S), and along its entire latitudinal range in the southeastern Pacific.

Table 5 *Engraulis ringens*. Values of Q_{10} calculated for development time of anchoveta embryos (hours to hatch) in different temperature ranges. Eggs sampled off Talcahuano (36°41′ S) and Antofagasta (23°39′ S). ($Q_{10} = [\mathrm{Rate}_1/\mathrm{Rate}_2]^{10/[\mathrm{Temperature}_1 - \mathrm{Temperature}_2]}$)

Locality	Temperature range (°C)	Q_{10}	Source
Talcahuano 2000	22–20	2.05	Current study
	20–18	3.71	
	18–15	*1.73*	
	15–12	4.65	
	12–10	4.14	
Talcahuano 1983	23–18	2.25	Tarifeño et al. 1984
	18–13	4.99	
	13–11	6.04	
	11–8	5.48	
Talcahuano 1997	*18–15*	*1.78*	Sepúlveda et al. 2000
	15–11.5	2.34	
Antofagasta 1995	21–16	2.37	Escribano et al. 1996
	16–11	2.72	
Antofagasta 2001	20–18	8.71	Current study
	18–15	*1.92*	
	15–12	4.15	
	12–10	4.88	

Although the regression of incubation time on temperature (Fig. 4) suggested that the effect of temperature on the development rate was similar under the temperature regimes at Antofagasta and Talcahuano, the Q_{10} values show a different view. In agreement with the conclusion of Kamler (1992) that the acceleration of the standard metabolic rate declines from low to high temperature, the temperature changes in the environment could have a stronger effect at colder temperatures since the Q_{10} values calculated for the present embryo incubation time data and those from Tarifeño et al. (1984) and Escribano et al. (1996) (Table 5) increase at lower temperatures. This suggests that the increasing temperature in the upper range rapidly accelerates embryo development, which in turn may induce a significant ecological effect when warming events occur in the environment. This pattern of Q_{10} changes suggests ranges of temperature optima of 12–15 and 15–18°C for Talcahuano and Antofagasta populations of anchoveta, respectively (Fig. 6).

The previous for anchoveta incubation time data are not consistent with latitudinal differences or ''physiological clines'' among geographically separated populations (23° and 36° S), as would be expected due to the different temperature regimes occurring in those coastal areas. Ferrada et al. (2002) proposed that the open genetic flow between anchoveta populations along its latitudinal distribution allows the same genotype frequencies between embryos from Talcahuano (36° S) and Iquique (20° S) and they pointed out that anchoveta populations have to be considered as one in a panmictic stage. However, Q_{10} data given by the present work clearly show different temperature optima for Talcahuano and Antofagasta populations and support the hypothesis that latitudinal differences do occur. Also, development did not occur at temperatures below 10°C in Antofagasta and abnormal development was observed in embryos reared at 10°C in this northern location. Whether these observations are signs of early population differentiation among stocks along the large range of distribution

or just the result of differences in oogenesis in females from different habitats remains to be determined.

A strong latitudinal pattern in sensitivity to temperature fluctuations was observed by Houde (1990) for early fish stages, but Pepin (1991) pointed out that variations in temperature do not appear to have any significant net effect on the early life history or survival of fish, because temperature has a significant influence on cumulative stage-specific mortality of fish embryos and yolk-sac larvae, where its effect on one stage is equal and opposite to its effect in the other. This conclusion does not agree with previous results (e.g. Houde 1989, 1990) that early fish life history survival should be more variable for fish that spawn in colder environments.

Another factor that could also affect the development time of fish embryos is egg size. Pauly and Pullin (1988) and Duarte and Alcaraz (1989) suggested that increasing initial egg size reduces development rates during the embryo stage, resulting in larger embryos that developed faster than smaller ones. In the case of the anchoveta, embryos from southern locations are larger than those spawned in lower latitudes (Llanos-Rivera and Castro 2004) hence developmental rates should occur faster. When compared at the same temperatures, however, our results show that development rates are the same in embryo from Talcahuano (south) and Antofagasta (north). However, under normal environmental conditions, these observations have to be complemented with the latitudinal variation in temperature since the larger embryos of the southern populations (Talcahuano) developed normally in colder waters while the smaller ones from the north did not (Llanos-Rivera and Castro 2006).

In an ecological context, anchoveta spawns throughout its latitudinal range during the winter when temperatures are lower and coincide with the local optima determined in this study, i.e. 15–18°C in northern Chile and 12–15°C in southern Chile (Castro 2001). At an even smaller spatial scale, Escribano et al. (1996) pointed out that in 1995 off Antofagasta higher concentrations of anchoveta embryos are associated with areas of greater upwelling. This would suggest that spawning events might be promoted by lower temperatures associated with upwelling waters that are rich in food for larval anchoveta. Similarly, Oliva et al. (2002)[4] pointed out that during the august 2001 spawning the distribution of anchoveta was restricted mainly to 14–16°C, with a greater abundance between 15 and 16°C. This temperature range fits the cooler part of the thermal regime in Antofagasta, yet encompasses the optimum registered in this study. Our results may also be connected to larger scale variations in changes in the dominance of pelagic small fish in the eastern Pacific. Chavez et al. (2003) pointed out that the Pacific Ocean undergoes physical and biological shifts about every 25 years. The half of this cycle, when waters are warmer than average is well fitted for the sardine ''regime'' (*Sardinops sagax*) meanwhile during the cooler waters, anchovies (*E. ringens*) become the dominant pelagic small fish (anchovies ''regimes''). Further studies directed towards determining optimal physiological ranges, although less common nowadays, might shed some light on the ecological aspects on inter-population differences associated with latitude or intraspecific fluctuations in abundance under variable conditions, such as those addressed in this study.

In the extensive latitudinal distribution of *E. ringens* along the Chilean coast, from Arica (18°09′ S) to Puerto Montt (41°29′ S) (Serra et al. 1979; Castro 2001), the coastal sea-surface temperatures measured throughout a 30-year period (1970–2000) indicate monthly average temperatures that ranged from 24.8°C to 8.1°C (Fig. 5), with extreme daily values between 25.7 and 6.0°C. The temperature range off Arica (18°09′ S), Antofagasta (23°39′ S), Caldera (27°04′ S) and Valparaiso (33°02′ S) ranged between 10 and 25°C, whereas at the southern areas, Talcahuano (36°41′ S) and Puerto Montt (41°29′), they showed lower temperatures ranging between 5 and 20°C. In other words, the southern and

[4] Oliva, J., C. Montenegro, O. Rojas, H. Reyes, V. Catasti, E. Díaz, P. Barría, R. Serra, V. Baros, A. Vargas, G. Claramunt, G. Herrera, P. Pizarro, J. Pizarro, Y. Muñoz, R. Escribano and M. Oliva. 2002. Evaluación del stock desovante de anchoveta por el método de producción de huevos en la I y II regiones. Final Project Report FIP (Chile) 2001–10. 200 pp.

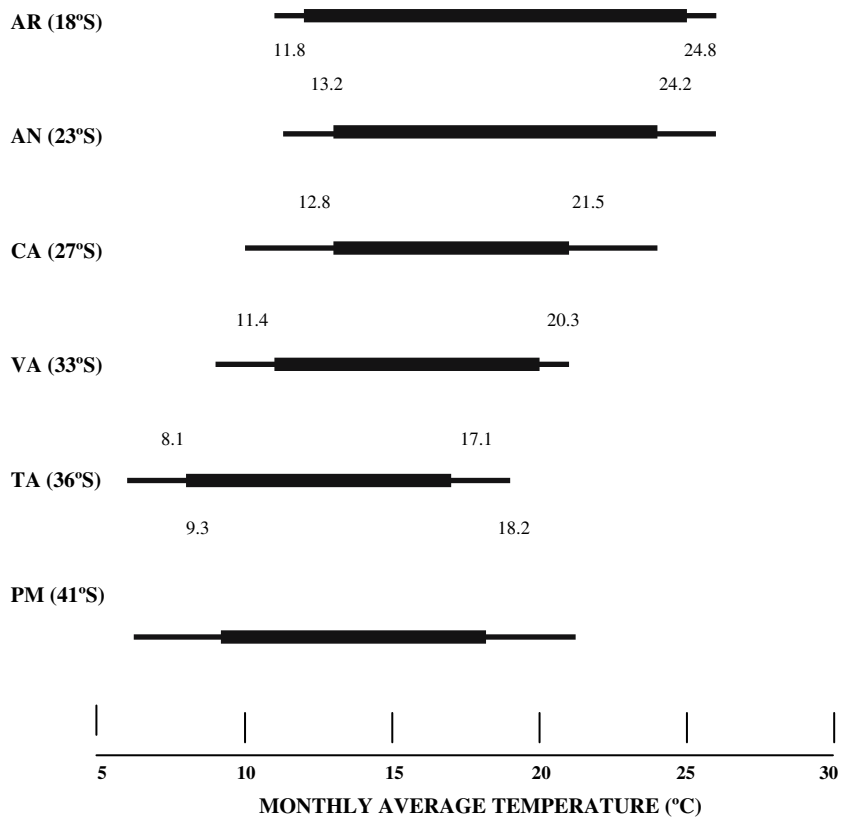

Fig. 5 *Engraulis ringens.* Ranges of monthly average temperature (thick line) and extreme values (thin line) for sea-surface temperature at Arica (AR), Antofagasta (AN), Caldera (CA), Valparaíso (VA), Talcahuano (TA) and Puerto Montt (PM) along the Chilean coastal sea waters during the 1970–2000 period. Numbers represent monthly average maximum and minimum temperature

northern populations may be exposed to a similar temperature difference (15°C) although the actual values are lower temperatures in the southern areas. Temperature variations below or above these ranges could impact on the population dynamics of *E. ringens* by reducing or increasing the development time of embryos, which, in turn, may impact hatching success, larval survival, and recruitment.

Due to the wide latitudinal distribution of anchoveta (4–42° S) and their periodical exposure to El Niño events, this species was used to assess the effects of sea temperature variations on early fish stages and to assess whether this environmental factor might be a valid constraint on fish distributions. The latter might become an important issue considering that some records show anchoveta occurring even further south than 41°S (Serra et al. 1979; Cubillos et al. 1999; Castro 2001). However, there is no information indicating whether these individuals are able to reproduce and contribute to the recruitment to the southern stock. In our experiments, hatching did not occur at temperatures <5°C at Talcahuano and <8°C at Antofagasta. The present results, plus those reported by Tarifeño et al. (1984) and Escribano et al. (1996), give a physiological basis for understanding the potential limits of *E. ringens* to the latitudinal expansion of this typically warm-temperate coastal pelagic species,

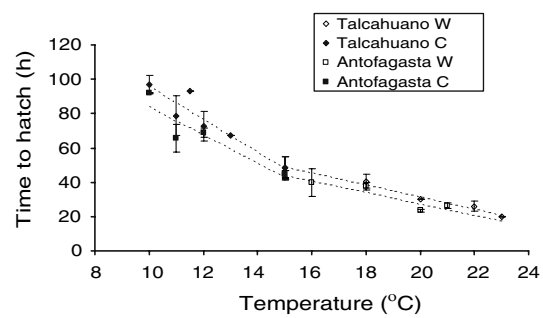

Fig. 6 *Engraulis ringens* Mean time (h) to hatch (±S.D.) plotted against experimental incubation temperatures for anchoveta embryos sampled off Talcahuano (36°41′ S) and Antofagasta (23°39′ S). Line represent model adjust for warm and cold range temperature in each area

which seems to be undergoing a geographical expansion toward cooler and higher latitude waters in the southeastern Pacific.

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