**Abstract**—Larval growth rates of the anchoveta *Engraulis ringens* were determined for two periods during the winter spawning season off Talcahuano, central Chile. Because winter is the season of minimum plankton production during the year, we hypothesized that larval growth rates during winter should be constantly low because of decreased larval fish food availability. Our results, however, indicate that 1) mean larval growth rates determined from three growth models in winter (mid-July through mid-September) were as high as in other periods of the year (linear, Gompertz, and von Bertalanffy; 0.47 mm/d, 0.50 mm/d, and 0.48 mm/d, repectively); 2) differences in larval growth rates occurred in two groups of cohorts spawned in the two periods during the spawning season (0.40 mm/d vs. 0.57 mm/d); and, 3) larval food (dinoflagellates, copepod eggs, and copepod nauplii) concentrations in the field were relatively high and not very variable during the study. Hydrography of the water column, however, varied throughout the season. During the last weeks of the study seawater temperature was higher, indicating intrusion of offshore warmer waters into the coastal zone. The presence of these warmer waters suggests that differences in growth rates between groups of cohorts may have resulted from larval development in water with different characteristics. Consequently, for a coastal upwelling species such as the anchoveta, increased growth rates in some cohorts may be advantageous considering that its main spawning season occurs in winter when the environmental conditions fluctuate markedly in short time scales.

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# Larval growth of the anchoveta *Engraulis ringens* during the winter spawning season off central Chile

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The anchoveta *Engraulis ringens* (also known as "Peruvian anchoveta," FAO, 1988) has traditionally been one of the most important pelagic resources in the world in terms of landings (Pauly and Palomares, 1989). After strong fluctuations in abundance during the last three decades, especially marked during the anchoveta collapse in the early seventies, the stocks have rebounded. Catches in recent years have reached over 12 million tons and constitute one of the largest fisheries of the world.

Within its long latitudinal distribution range from 4°S to 40°S, several major spawning areas have been reported. The most important spawning areas have been traditionally located off Northern Peru, from off Southern Peru to off Northern Chile, and off Central Chile (Bernal et al., 1983). Despite its wide latitudinal range and paramount economic importance for the world fish markets, other than distribution and abundance, little information exists on basic biological parameters during the larval phase. For the larval stage, reseachers have documented information on the age of onset of feeding, feeding habits, and validation of daily deposition of ring increments in the otoliths (Rojas de Mendiola and Gómez, 1980, 1981; Ware et al., 1981; Muck et al., 1989; Morales-Nin, 1989; Villavicencio, 1989; Llanos, 1990). Information on larval growth rates in the wild, however, have been reported only for the southern stock and, unfortunately, only for seasons other than the major winter spawning seasons (Herrera et al., 1985).

There is a marked seasonality in the southern spawning area of the anchoveta. During spring, summer, and early fall, southerly winds predominate and lead to very intense upwelling events. During winter, intense northerly winds dominate, and upwelling events develop only occasionally. This marked seasonality in the oceanography also leads to changes in environmental conditions that may affect larval growth. During winter, due to the low frequency of upwelling events, the general production of the area is lower than in summer. Similarly, the very intense north winds may produce high levels of turbulence in the water column, thus dispersing the potential larval food patches (Lasker 1975, 1978). On the basis of these harsh environmental conditions, it has been proposed that food for larval anchoveta off Talcahuano might be limited during winter (Herrera et al., 1985; Bernal et al., 1990). However, because the anchoveta has been historically an important fishery of central Chile (1996 landings in the area reached ca. 300,000 metric tons, SERNAPESCA, 1996), there must be some mechanisms by which relatively high levels of larval survival can be achieved: either feeding conditions are not permanently harsh or factors other than food enhance larval survival, at least for some periods within the winter spawning season.

The objectives of our study were 1) to determine whether intraseasonal differences in growth rates occur between groups of cohorts of larval anchoveta spawned throughout the winter spawning season, and 2) to assess the role of two environmental factors (larval food and temperature) as potential factors affecting larval growth rates. Because some basic information for the deter-

mination of growth rates was still missing, we first determined the age of deposition of the first ring increment on larval otoliths and then described the growth functions of larvae caught in the wild, using three common growth models (the linear, Gompertz, and von Bertalanffy). Finally, we determined the mean growth rates for larval anchoveta spawned over the entire sampling winter season, and for two groups of cohorts spawned during that season but which faced different environmental conditions.

## Methods

### Larval growth in the wild

Larval anchoveta were collected in eight cruises from a grid of nine stations in the coastal zone off Talcahuano, central Chile (Fig. 1), during the winter of 1995 (12, 18 July; 1, 8, 17, 30 August; 4, 11 September). In each cruise, ichthyoplankton samples were collected with a bongo net (mesh size: 500 µm, diameter of mouth of net: 60-cm) equipped with a flow meter to quantify the volume of water sampled from the surface to a depth of 40 m. Once on board, half of the samples were preserved in 4% formalin and the other half in 96% ethanol for otolith analysis. At all stations, sea water samples were collected from nine depths (0, 5, 10, 15, 20, 30, 40, 60, 80 m) in 4-liter Niskin bottles for determination of temperature and salinity, and for identification and quantification of microplankton (dinoflagellates, copepod eggs, and copepod larvae) as potential larval food.

In the laboratory, anchovy larvae from both subsamples were identified, sorted, and counted. From the subsamples preserved in ethanol, 112 larvae within a size range between 5.68 and 20.74 mm (corrected for shrinkage, see below) were measured and their otolits were extracted and mounted in immersion oil. Otolith ring counts and otolith diameters were determined with the aid of a light microscope attached to a video camera and monitor to facilitate the reading of daily rings. Each otolith was counted twice and those counts where the readings differed in three or more rings were discarded. Larval lengths were corrected for shrinkage by using the algorithms proposed by Theilacker (1980) for larval northern anchovy (*Engraulis mordax*). Three models were used to describe the growth and growth rates of larval anchovy: the linear, Gompertz, and von Bertalanffy models. These models were used to describe growth for 1) all larvae spawned during winter (1 July–11 September) of 1995, and 2) for two groups of cohorts spawned during a) 1 July through 17 August, and b) from 18 August through 11 September. To classify the larvae as belonging to the first or second period, spawning dates were backcalculated as "the number of rings + 2" (see day of first ring deposition in the "Results" section). All statistical tests (regressions, analyses of variance, covariance, and models) were carried out with the commercial statistical software package STATISTICA, 1993.

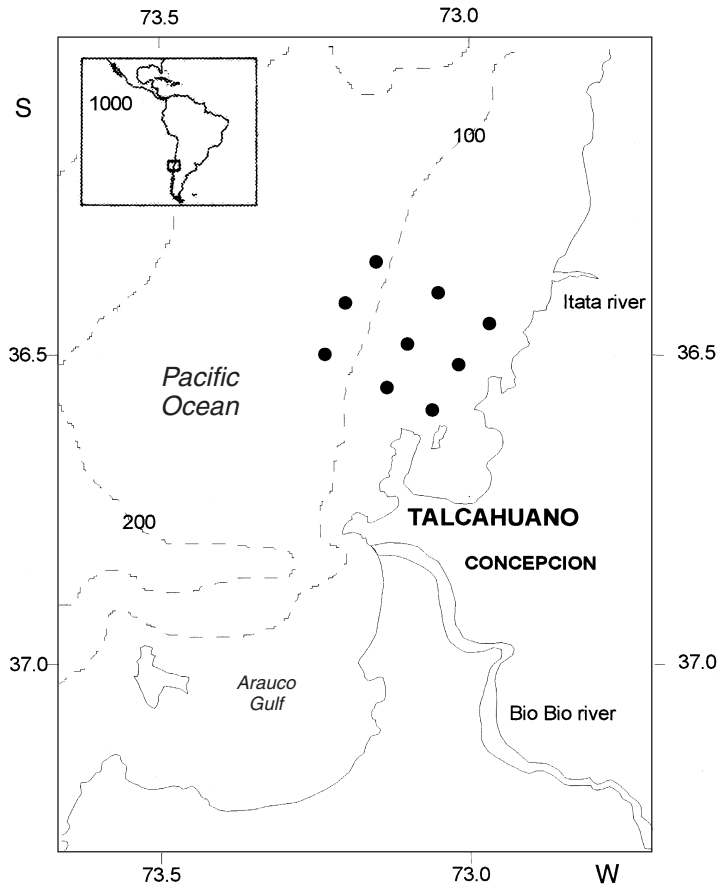


**Figure 1**

Survey area of ichthyoplankton during the 1995 anchoveta winter spawning season off Central Chile. Dots represent sampling stations.

### First increment deposition

Anchovy eggs were collected from a coastal station off Talcahuano during the winter spawning season on 1997. At that station, gentle vertical tows were carried out with a bongo net from 0 to 40 m for collections of ichthyoplankton. The samples were placed in a 20-gal cooler at 12–13°C and transported to the Universidad de Concepcion Marine Station at Dichato. The transit time to the station took about 45 min. At the laboratory, between 20 and 60 anchovy eggs were sorted and placed in ten, 700-mL transparent plastic jars and incubated at 10°C and 14°C in light and dark cycles of 14:10 h and 12:12 h, respectively. One third of the water contained in the jars was replaced daily throughout the duration of the study. All larvae hatched in a given day were transplanted to new jars containing water at the same temperature as that used for hatching and in which *Isocrysis* sp. and powdered larval food were added daily. Every day a variable number of larvae were extracted from the jars for determination of fresh larval length, preserved in ethanol, remeasured, and dissected for otolith analysis (ring counts and diameter).

## Results

### First increment deposition

Only thirteen larvae from the rearing experiments in the laboratory were analyzed for determination of age at the first increment deposition, and because of the low number of larvae, the data from the treatments were analyzed together. These preliminary experiments showed that no larvae formed the first ring on the otoliths at hatching (two larvae were analyzed at hatching). Although the first ring on the otoliths was first observed in a larva at end of the first larval day after hatching (two larvae were analyzed), most larvae formed their first ring during the third day after hatching (four out of six larvae, 3-days-old or older). The larva analyzed at the end of the fourth day had two rings deposited; therefore it formed its first ring during the third day. At the end of the third day after hatching, all larvae had deposited their first ring. The mean diameter of the otolith focus for those larvae hatched in our experiments was 10.23 (SD=1.25) µm and the mean diameter of the otolith with their first increment formed was 12.83 (SD=1.56) µm.

The relation between the number of rings and otolith diameters from anchoveta larvae collected in the wild was well described by a linear regression ($r^2$=0.90; $n$=112; $P$<0.001)(Fig. 2). From this relationship, a larval anchoveta with one ring should have an estimated otolith diameter of 12.6 micrometers, which is close to the mean otolith diameter measured from larvae reared in our laboratory (mean=12.83 µm, SD=1.56). A power model was used to describe the relation between otolith diameter and larval length (corrected for shrinkage after Theilacker 1980) of wild larvae ($r^2$=0.79; $n$=112; $P$<0.001) (Fig. 3). According to these two relationships, a larva with one increment (12.6-µm otolith diameter) should have a larval length of 5.6 mm.

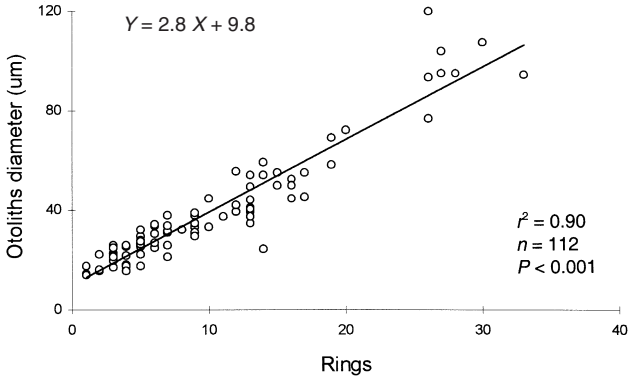


**Figure 2**

Linear regression showing the relation between the number of otolith rings formed and the otolith diameters of anchoveta larvae caught in the wild.

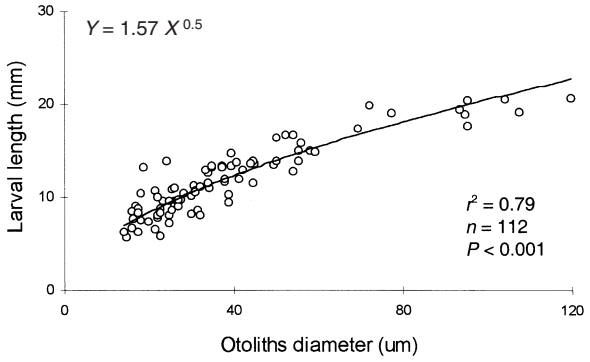


**Figure 3**

Relation between otolith diameter and length in larval anchoveta during the winter spawning season of 1995.

### Larval growth of larvae caught in the wild

Because deposition of the first ring in most larvae occurred during the third day after hatching, age of larvae caught in the wild was estimated by adding two days to the number of rings in their otoliths. The standard lengths of larvae used in the growth models varied between 5.68 mm and 20.74 mm, and their age ranged from 3 to 35 days.

The three growth models used to describe anchovy larval growth during the winter of 1995 were highly significant ($P$<0.001) (Fig. 4, Table 1). The linear model yielded a daily growth rate of 0.47 mm/d ($n$=112 larvae; $r^2$=0.82); the Gompertz model yielded a mean daily growth rate of 0.50 mm/d ($n$=112 larvae; $r^2$=0.84); and the von Bertalanffy model yielded a mean daily growth rate of 0.48 mm/d ($n$=112 larvae; $r^2$=0.84). Estimated larval length at the end of the third day after hatching (day of the first ring deposition) varied from 7.81 mm with the linear model to 7.17 mm with the Gompertz model and 6.13 mm with the von Bertalanffy model.

The results of the analyses of growth rates between groups of cohorts spawned early versus late in the winter season varied according to the models used to describe growth. The larval growth rates determined from the linear model revealed that the group of daily cohorts spawned earlier in the season grew slower (1 Jul–17 Aug: 0.40 mm/d; $n$=63) than the group of larvae spawned later in the season (18 Aug–11 Sep: 0.57 mm/d; $n$=49) (ANCOVA, $F$=26.2, $n$=112, $P$<0.001; Zar, 1984). For both groups of cohorts, the linear regressions used to describe larval growth were significant ($P$<0.001) and explained over 78% and 74% of the variance in the respective data sets. A comparison of larval growth rates between periods using the Gompertz and von Bertalanffy models, however, showed no differences between larvae spawned early versus larvae spawned later in winter (Gompertz: $F$=1.08, $n$=112, $P$>0.05; von Bertalanffy: $F$=0.82, $n$=112, $P$>0.05; analysis of residual sum of squares, ARSS; Chen et al., 1992).

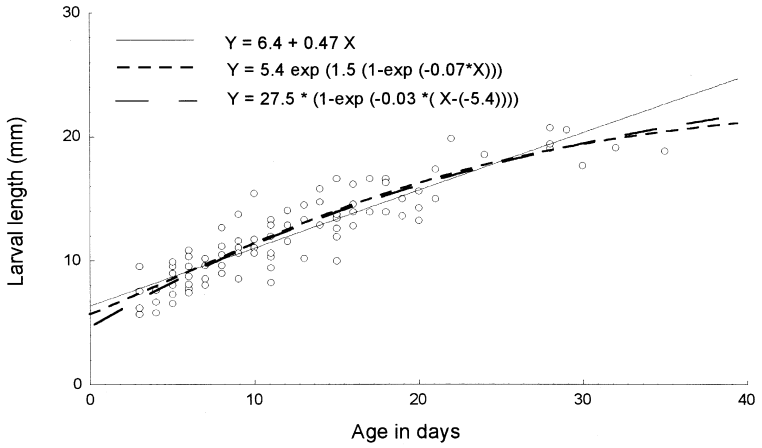


**Figure 4**

Models usedd to describe larval growth of the anchoveta *Engraulis ringens* during the 1995 winter spawning season off central Chile: linear model (——); Gompertz model (– – –); and von Bertalanffy model (— — —). Basic statistics for each model are shown in Table 1.

**Table 1**

Growth models used to determine growth rates for larval anchoveta off central Chile during the 1995 winter spawning season (mid July through mid September). RSS = residual sum of squares; $r^2$ = coefficient of determination.

| Model | | Parameters | RSS | $r^2$ | $P$ |
|---|---|---|---|---|---|
| Linear | $Y = a + bX$ | $a = 6.4$<br>$b = 0.47$ | 254.1 | 0.82 | <0.001 |
| Gompertz | $L = L_0 \exp(G(1 - \exp(-gt)))$ | $L_0 = 5.4$<br>$G = 1.5$<br>$g = 0.07$ | 227.7 | 0.84 | <0.001 |
| von Bertalanffy | $L = L_\infty(1 - \exp(-K(t-t_0)))$ | $L_\infty = 27.5$<br>$K = 0.03$<br>$t_0 = -5.4$ | 227.1 | 0.84 | <0.001 |

Larval food (dinoflagellates, copepod eggs, and nauplii) occurred in relatively high concentrations throughout the season (Fig. 5). No differences in dinoflagellate densities (Mann-Whitney $U$=4.00; $P$=0.296), copepod egg densities (Mann-Whitney $U$=7.00; $P$=0.861), and copepod nauplii densities (Mann-Whitney $U$=5.00; $P$=0.456), were detected between the periods used to classify both groups of larval cohorts during the season. Sea surface temperature, another factor that may affect larval growth, was higher (Mann-Whitney $U$=19; $P$=0.025) during the second period of the spawning season (maximum. sea surface temperature: 13.5°C), probably as a result of the intrusion of offshore warmer waters to the coastal zone (Fig. 6) During the first period of the season, instead, when some of the upwelling events and the river plume were stronger and farther offshore (Castro et al., 2000), the sea surface temperature reached a minimum (11.1°C) in the coastal area.

## Discussion

The deposition of the first ring in the larval otoliths has been associated with events in the early life history of fishes, such as the onset of feeding or eye pigmentation. For northern anchovy, *Engraulis mordax*, for instance, the deposition of the first increment takes place at the initiation of exogenous larval feeding or after yolksac absorption which occurs five or six days after hatching (Brothers et al., 1976; Methot and Kramer, 1979). Bay anchovy, *Anchoa mitchilli*, completes its first otolith ring

at the end of the second day after hatching—a time which corresponds to the time of yolksac depletion (Leak and Houde, 1987). Mediterranean anchovy, *Engraulis encrasicolus*, deposits its first increment during the second day after hatching with completion of yolk absorption (Palomera et al., 1988). In our rearing experiments larval anchoveta finished forming their first otolith increment at the end of the third day after hatching, which coincides with the end of the eye pigmentation.

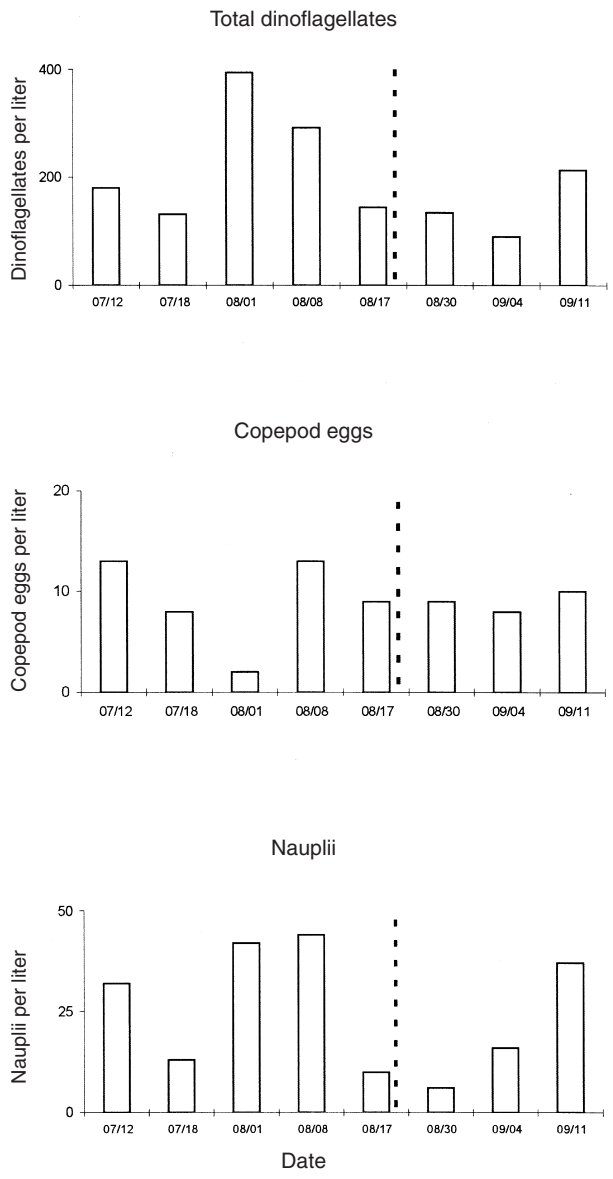


**Figure 5**

Mean density of potential larval food items in field during the winter spawning season of the anchoveta *Engraulis ringens* off Talcahuano, central Chile, in 1995: dinoflagellates, copepod eggs, and copepod nauplii. The vertical dashed line indicates the separation of periods considered in the groups of larval cohorts.

Larval anchoveta finished forming their first otolith increment at a larval length of 5.6 mm (estimated from the rings and otolith diameter and from the otolith diameter and larval length relationships). Observations of laboratory-reared anchoveta (*E. ringens)* larvae off Peru indicated that the mouth and eyes become functional at 64 h after hatching at a larval length of 4.03 mm (Ware et al., 1981). Initiation of larval feeding, however, varied from 3.5 to 6.8 days after hatching (mean 4.4 d), which corresponded to estimated larval lengths between 4.10 and 4.16 mm. If the deposition of the first ring in larval anchoveta coincided with the onset of feeding, then our estimations of 5.6 mm at the end of the third day after hatching were slightly higher than those estimated by Ware et al., (1981).

The three models used to fit the age and larval length data of anchoveta larvae collected during the winter spawning season in 1995 fitted the age and larval anchovy length data appropriately for the winter spawning season of 1995. A visual inspection, however, revealed a slight decrease in growth rate as the larvae increased in age, which suggests that the nonlinear models (von Bertalanffy and Gompertz) would describe larval growth better beyond the ages determined in our study.

Growth rates calculated with the three growth models (linear=0.47 mm/d; Gompertz=0.50 mm/d; and von Bertalanffy=0.48 mm/d) were very similar to estimations for anchoveta in other seasons (larval size range 5.0–20mm=0.45 mm/d, 12.5°C, Herrera et al., 1985) and within ranges reported for other engraulids. Methot and Kramer (1979) estimated northern anchovy larval growth rates between 0.34 and 0.55 mm/d between 13.0° and 16.2°C; for bay anchovy, *Anchoa mitchilli*, larval growth rates between 22° and 30°C ranged from 0.25 to 0.58 mm/d (Fives et al., 1986; Leak and Houde, 1987; Castro and Cowen, 1991); and for Mediterranean anchovy, *Engraulis encrasicolus,* growth rates ranged between 0.9 and 0.96 mm/d for 8-mm larvae at 20°C (Palomera et al., 1988). If only the larval anchovies from the upwelling areas of California and central Chile are compared, then the growth rates determined for the anchoveta in our study (0.40–0.57 mm/d at sea temperatures between 11.1° and 13.5°C), are slightly higher than those estimated for the northern anchovy at similar temperatures (0.39–0.47 mm/d at 13.0–13.2°C; Methot and Kramer 1979).

Some intraseasonal variability in growth rates of the anchoveta was observed between groups of cohorts during the winter spawning season, when rates from linear growth models were compared. Larval growth rates determined with the linear model (0.40 vs. 0. 57 mm/d) were within the same range reported for cohorts of other clupeiforms spawning at different times during the year or under different environmental conditions within the same spawning season (Methot and Kramer, 1979, Leak and Houde, 1987). Larval food, as a potential factor affecting larval growth rates, did not seem to be limited throughout the

entire sampling season. In fact, observed larval food concentrations may be considered high compared with concentrations reported for the same species in lower latitudes (Walsh et al., 1980). Differences in seawater temperature experienced by both groups of cohorts spawned during winter, however, may have accounted for the apparent differences in larval growth rates. An increase in water temperature occurred during the last weeks of sampling owing to an intrusion of offshore warmer waters into the coastal zone (Castro et al., 2000). Response to changes in seawater temperature as the spawning seasons progress is known for other anchovy species (*A. mitchilli*, Leak and Hode, 1987; Rilling and Houde, 1999). However, earlier evidence may have not been so conclusive for larval anchovy at upwelling areas (i.e. *E. mordax*, Methot and Kramer, 1979; Butler, 1989), probably because of the difficulties of determining the temperature of the water where the larvae actually developed, especially given the frequent changes in hydrographic conditions common in coastal upwelling areas.

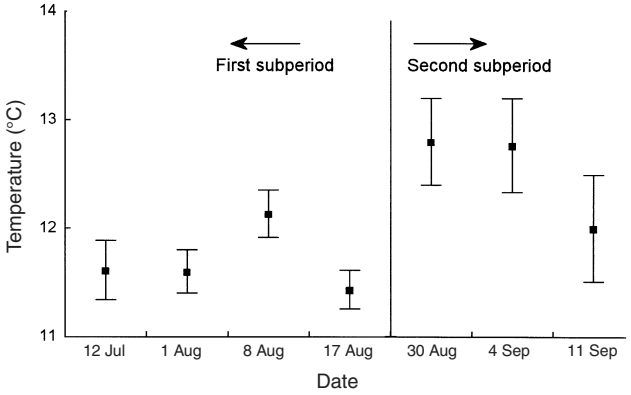


**Figure 6**

Mean sea surface temperature during the winter spawning season of the anchoveta *Engraulis ringens* off Talcahuano, central Chile, in 1995.

Because growth may be dependent on environmental factors (Pepin, 1991), seasonal variations in growth rates were expected among the cohorts spawned during the year. In our study, we documented potential differences in growth rates of groups of cohorts spawned a few weeks apart during the main spawning season. For coastal species living in upwelling areas, changes in growth rates among cohorts may be beneficial because environmental conditions may change markedly in short time scales (from days to a few weeks). With this scenario, increases in growth rates in some cohorts (given the right conditions during a few weeks) may be advantageous because the main spawning season for *E. ringens* occurs in winter. At the end of the season we expected a large pool of late larvae and early juveniles within a similar size range that had grown at different rates because they were exposed to different conditions. Given the relationship between environmental conditions and larval development, and the wide distribution range of the anchoveta (from 4°S to 40°S), differences in growth rates are to be expected in larval anchovies growing in different latitudes. Future studies should evaluate whether the models and growth rate changes determined off Talcahuano (37°S), close to the southern limit of distribution for the anchoveta, also apply for larvae growing in lower latitudes, such as spawning areas off northern Chile (18–24°S) and Peru (4–14°S) .

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