

Seasonal growth of small pelagic fish off Talcahuano, Chile (37°S, 73°W): a consequence of their reproductive strategy to seasonal upwelling?

Luis A. Cubillos^{ab*}, Dagoberto F. Arcos^a, Doris A. Bucarey^a, Mariella T. Canales^a

^a Instituto de Investigación Pesquera, Casilla 350, Talcahuano, Chile

^b Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile

Received 18 October 1999; accepted 14 February 2001

Abstract – Is the seasonal growth of *Strangomera bentincki* (Clupeidae) and *Engraulis ringens* (Engraulidae) a consequence of their reproductive strategy to adapt to the seasonal upwelling ecosystem they inhabit? This question is addressed by analysing monthly length-frequency data, gonadosomatic index and condition factor of the species in relation with the seasonal patterns of environmental variables. Modal progression analysis of mean length-at-age of cohorts along the time axis was used to study the growth in the period 1990–1997. A seasonally oscillating growth curve was estimated for both species, with the slowest growth rate occurring between April and May, a few months before the higher reproductive activity occurring in August–September. The reproductive strategy is to spawn when environmental conditions are related with onshore transport in winter (August), favouring the concentration and retention of eggs and larvae. One month later, a moderate upwelling determines an enrichment in food particles and the spawning area is transformed in a nursery area for juveniles. The reproductive strategy is combined with an ‘energy storage strategy’ during the period of upwelling. The energy stored is used for reproduction several months later, affecting the growth process of the species. It is concluded that the regularity in the seasonal growth in both species is a response, from an evolutionary point of view, of a long-term reproductive adaptation to the seasonal upwelling ecosystem of the central southern area off Chile. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

length-frequency data / seasonal growth / reproductive strategy / upwelling ecosystem / Clupeidae / Engraulidae / Talcahuano (Chile)

Résumé – Crecimiento estacional de peces pelágicos en Talcahuano, Chile (37°S, 73°W): ¿consecuencia de su estrategia reproductiva a un sistema de surgencia estacional? Se analiza la estrategia reproductiva de *Strangomera bentincki* (Clupeidae) y *Engraulis ringens* (Engraulidae) utilizando el índice gonadosomático y factor de condición de las hembras respecto del ciclo estacional de variable ambientales, mientras que el crecimiento fue determinado utilizando datos de frecuencia de tallas. Se usó el método de análisis de progresión modal de longitudes medias por cohortes para estudiar el crecimiento, y se encontró curvas con cambios estacionales en la tasa de crecimiento para ambas especies. La tasa de crecimiento más baja ocurrió entre Abril y Mayo, antes del período de mayor actividad reproductiva entre agosto y septiembre. La estrategia reproductiva es desovar bajo condiciones ambientales relacionadas con un transporte hacia la costa en invierno, favoreciendo la concentración y retención de huevos y larvas. Un mes después, ocurre enriquecimiento de alimento planctónico debido a una surgencia moderada transformándose el área de desove en un área de crianza de juveniles. Esta estrategia reproductiva es combinada con una ‘estrategia de almacenamiento de energía’ durante el período de surgencia. La energía almacenada es utilizada en la reproducción varios meses después, afectando el proceso de crecimiento de las especies. Se concluye que la regularidad en el crecimiento estacional de ambas especies es una respuesta poblacional, desde un punto de vista evolutivo, a la adaptación reproductiva poblacional al ecosistema de surgencia estacional del área centro-sur de Chile. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

frecuencia de tallas / crecimiento estacional / estrategia reproductiva / ecosistema de surgencia / Clupeidae / Engraulidae / Talcahuano (Chile)

1. INTRODUCTION

Several hypotheses have been postulated to explain both recruitment variability in fish populations and the

reproductive strategies adopted by them to enhance offspring survival (see Cole and McGlade, 1998 for a review). In terms of reproductive ecology of coastal pelagic species, Parrish et al. (1983) and Bakun and

*Correspondence and reprints.

E-mail address: inpesca@inpesca.cl (L.A. Cubillos).

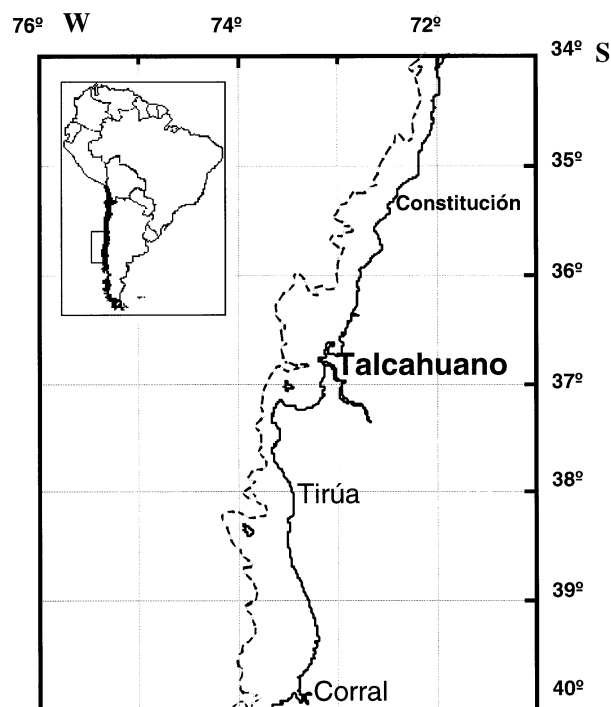


Figure 1. Study area showing the 200 m isobath.

Parrish (1982, 1990) concluded that reproduction takes place at times and in areas where turbulence and offshore transport are low. However, these studies contrast with the study of Fréon et al. (1997) on reproductive ecology of *Sardinella aurita* off the coast of Venezuela. According to Fréon et al. (1997), major reproduction of *S. aurita* did not occur in an area and at a time when offshore transport and turbulence were low. The reproductive strategy of this population apparently gives priority to optimising food availability for the offsprings and not to preventing eggs and larvae being transported offshore.

In Chile, the small pelagic fish *Strangomera bentincki* (Norman, 1936) and *Engraulis ringens* (Jenyns, 1842), locally known as ‘sardina común’ and ‘anchoveta’, are important resources for a fleet of seiners operating off central southern Chile (34°S, 40°S, figure 1), with Talcahuano (37°S, 73°W) as their main port of landings (Cubillos et al., 1998). Off central southern Chile, these species inhabit an environment of high biological productivity due to the seasonal occurrence of upwelling events (Arcos and Navarro, 1986; Arcos, 1987), mainly from middle September to late March (austral spring–summer).

Cubillos et al. (1999) studied the reproductive period of *S. bentincki* and *E. ringens*, and postulated that the higher reproductive activity occurring in winter (peak in August), just before the upwelling season, can be suggestive of adaptive responses to the environment.

In this paper, we studied the reproductive strategy of *S. bentincki* and *E. ringens* in the seasonal upwelling ecosystem off central southern Chile, and the consequences for the growth of the species. In fact, according to Cubillos and Arancibia (1993) the most reduced growth rate of the species tends to occur in winter. In this way, it has been postulated that in spawning fish invest more energy to produce gametes rather than growth. Therefore, the fastest growth rate (six months later) would be related to increased productivity of the coastal waters at the time of coastal upwelling. The goal of this paper is to corroborate the ideas of Cubillos and Arancibia (1993) and Cubillos et al. (1999), and to postulate that the seasonally oscillating growth rate of *S. bentincki* and *E. ringens* is a consequence of the reproductive strategy of these small pelagic fish to the seasonal upwelling ecosystem of central southern Chile.

2. MATERIALS AND METHODS

2.1. Environmental data

Environmental variables were taken from the following time series: sea surface temperature (*SST*) and mean sea level (*MSL*) from the tidal station at Talcahuano (36°41’S, 73°06’W), and wind data from Carriel Sur (36°46’S, 73°03’W) meteorological station (figure 1). Hourly wind intensity and direction data were used to compute an upwelling index for Talcahuano, according to the methodology of Bakun (1973) and Arcos and Navarro (1986). Monthly averages of the environmental variables were used to compute the seasonal signal for the period 1990–1997.

2.2. Biological data

During 1990–1997, length frequency data have been sampled from the fisheries of *S. bentincki* and *E. ringens* in Talcahuano (37°S, 73°W). Each length-frequency data set corresponds to monthly summaries of random daily samples obtained from the catch of vessels participating in the fisheries (table I). Before 1995, sample sizes were smaller than those for the period 1995–1997. However, a minimum of 32 sampling units per month, distributed by weeks and size of vessels were obtained since 1995. The sampling unit is a 5 L container, but a 2 L sub-sample was used to acquire the data. Body size was measured as total length (*TL*) to the nearest 0.5 cm. Suitable monthly sample sizes were available for almost all the period under analysis.

In addition, we used specific biological data from individual fish, total length (to the nearest 0.5 cm), total weight (0.01 g), and female gonadal weight (0.01 g) covering the period 1993–1997. The data were obtained from weekly random samples from the fishery (see Cubillos et al., 1999 for details).

Table I. Number of individuals in the length frequency data sampled from *Strangomera bentincki* and *Engraulis ringens* fisheries.

| Year | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Total |
|---------|------|------|------|------|------|------|------|------|------|------|------|------|--------|
| 1990 | | | | | | | | | | | | | |
| Sb | – | – | – | – | – | – | 1052 | 415 | 171 | 382 | 270 | 913 | 3203 |
| Er | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Samples | – | – | – | – | – | – | (10) | (4) | (2) | (4) | (2) | (4) | – |
| 1991 | | | | | | | | | | | | | |
| Sb | 2599 | 2043 | 2129 | 1863 | 783 | 1785 | 2520 | 2595 | 1803 | 3110 | 1994 | 2225 | 25 449 |
| Er | 423 | 463 | 718 | 777 | 623 | 217 | – | 1226 | 973 | 1441 | 935 | 674 | 8470 |
| Samples | (17) | (14) | (14) | (13) | (4) | (8) | (10) | (13) | (10) | (18) | (16) | (16) | – |
| 1992 | | | | | | | | | | | | | |
| Sb | 2182 | 1922 | 1049 | 615 | 640 | 278 | 389 | 116 | 427 | 370 | 1086 | 808 | 9882 |
| Er | 667 | 1483 | 1784 | 1144 | 1098 | 579 | 1987 | 457 | 377 | 600 | 797 | 161 | 11 134 |
| Samples | (19) | (19) | (18) | (19) | (10) | (3) | (12) | (12) | (4) | (5) | (10) | (5) | – |
| 1993 | | | | | | | | | | | | | |
| Sb | 973 | 450 | 340 | 183 | 472 | 169 | 1048 | 966 | 642 | 839 | 2183 | 1129 | 9394 |
| Er | 435 | 605 | 1110 | 1269 | 850 | 401 | 832 | 873 | 997 | 730 | 176 | 426 | 8704 |
| Samples | (8) | (7) | (10) | (9) | (8) | (2) | (6) | (6) | (8) | (8) | (12) | (9) | – |
| 1994 | | | | | | | | | | | | | |
| Sb | 1479 | 677 | 71 | 246 | 338 | 851 | 852 | 842 | 455 | 1487 | 1795 | 1791 | 10 884 |
| Er | 1123 | 681 | 894 | 866 | 1070 | 560 | 1111 | 1364 | 1185 | 1106 | 676 | 1607 | 12 243 |
| Samples | (15) | (9) | (6) | (5) | (7) | (6) | (10) | (11) | (8) | (15) | (11) | (15) | – |
| 1995 | | | | | | | | | | | | | |
| Sb | 1101 | 963 | 2757 | 1024 | 1994 | 617 | 1267 | 1873 | 1462 | 3258 | 2006 | 5447 | 23 769 |
| Er | 1177 | 839 | 3591 | 3170 | 4427 | 1355 | 3037 | 629 | 4374 | 2645 | 1240 | 378 | 26 862 |
| Samples | (11) | (11) | (34) | (26) | (43) | (12) | (29) | (18) | (39) | (43) | (23) | (54) | – |
| 1996 | | | | | | | | | | | | | |
| Sb | 5003 | 4767 | 4523 | 3487 | 2409 | 2579 | 2961 | 2408 | 2462 | 2624 | 1006 | 2971 | 37 200 |
| Er | 127 | 431 | 860 | 791 | 728 | 637 | 776 | 1193 | 1990 | 1932 | 69 | 37 | 9571 |
| Samples | (53) | (44) | (44) | (33) | (24) | (27) | (30) | (26) | (30) | (32) | (9) | (26) | – |
| 1997 | | | | | | | | | | | | | |
| Sb | 4610 | 3831 | 2427 | 2036 | 1970 | 1633 | 2325 | – | – | – | – | – | 18 832 |
| Er | 421 | 1146 | 1052 | 1868 | 1299 | 567 | 699 | – | – | – | – | – | 7052 |
| Samples | (40) | (34) | (25) | (26) | (23) | (16) | (23) | – | – | – | – | – | – |

Sb: *Strangomera bentincki*; Er: *Engraulis ringens*; the number of monthly samples is shown in parentheses.

2.3. Reproductive strategy

The gonadosomatic index (*GSI*) and the condition factor (*CF*) of Fulton ($CF = 100 \times W \times L^{-3}$; from Wootton, 1992) for only females of both species were computed. This is not exact when dealing with allometric growth, but this simple equation has been used instead of $CF = 100 \times W / a L^b$ because we do not deal here with *CF* per length (P. Fréon, personal communication). Then, monthly averages were obtained to conform a time series. Higher values of *GSI* and *CF* are indicating a major reproductive season and good conditions for fish within an annual cycle, respectively. The seasonal signal was computed for the period 1993–1997, and compared with the seasonal signal of the environmental variables.

2.4. Growth analysis

The computer software MIX (McDonald and Green, 1988) was used to analyse the length frequency data. MIX considers a length frequency data as a mixture of probability density functions (PDF), and was used to analyse a single histogram or mixture of PDFs. We

assumed age to have a normal PDF in the mixture. Thus, the number of parameters to be estimated is the total number of ages present in the mixture, multiplied by the 3 parameters of each normal PDF, i.e. the proportion in the distribution mixture (*p*), the mean (*μ*) and the standard deviation (*σ*) of length-at-age. We determined the number of ages of the histogram by visual analysis, while the parameters were estimated without constraints by using maximum likelihoods according to McDonald and Pitcher (1979).

Once the mean, standard deviation, and proportion of ages were estimated from each of the monthly length frequency data set, cohorts were identified by modal progression analysis (MPA). The MPA consists in plotting the means to form a time series, in which the progression through time of the mean length of a cohort can be followed. The mean lengths that are believed to belong to the same cohort are linked. Then, relative ages (in months) were assigned to the mean lengths belonging to each of the cohorts, by considering July 1 as a fixed birth date because the major spawning season begins in July and extends until September (Cubillos et al., 1999). The age in months

was transformed to years by dividing age in months by 12. The mean length-at-age of all cohorts were used to estimate the parameters of the von Bertalanffy growth function modified by Somers (1988) to take into account seasonal growth

$$L_i = L_\infty \left[1 - \exp \left\{ -K(i - t_0) - \frac{CK}{2\pi} \left[\sin(2\pi(i - t_s)) - \sin(2\pi(t_0 - t_s)) \right] \right\} \right] \quad (1)$$

where L_i is the mean length-at-age i , L_∞ is the asymptotic length (in centimetres), K is a growth coefficient (in year⁻¹), t_0 is 'age of the fish at zero length', C is a dimensionless constant expressing the amplitude of the growth oscillations, and t_s is the phase of a growth oscillation within a year (with reference to $i = 0$). Both parameters, C and t_s should be in the range [0,1]. When $C = 0$, the growth is continuous, without seasonal oscillation. $C = 1$ implies that the growth rate (dL/dt) is exactly equal to zero per year at some moment within the year. For practical purposes, t_s was replaced by $WP (= t_s + 0.5)$, representing a winter point that indicates the moment in which the growth rate is the slowest within the annual cycle. The parameters of equation 1 were estimated by non-linear regression using the Marquardt algorithm.

2.5. Variance of length-at-age

According to Roa (1993) and Roa and Ernst (1996), there are two components of variability in a length-at-age data of cohorts: intra-cohort and inter-cohort variance of length-at-age. The intra-cohort variance is the weighted mean of all variances (e.g. estimated by MIX) of lengths of a given cohort. This mean variance is an inherent property of the cohort due to the length distribution of individuals hatched during the same reproductive season. The inter-cohort variance is the variance of the mean lengths around the weighted mean of all cohorts of a given age. This weighted variance of the mean results from different lengths-at-age in which cohorts advance through ages in post-recruitment life. We used the following expressions for intra-cohort (σ_{intra}^2) and inter-cohort (σ_{inter}^2) variances of year classes:

– intra-cohort:

$$\sigma_{intra,i}^2 = \frac{\sum_{k=1}^{Kmax} \sigma_{i,k}^2 n_{i,k}}{\sum_{k=1}^{Kmax} n_{i,k}} \quad (2)$$

– inter-cohort:

$$\sigma_{inter,i}^2 = \frac{\sum_{k=1}^{Kmax} n_{i,k} \left(\mu_{i,k} - \left(\frac{\sum_{k=1}^{Kmax} \mu_{i,k} n_{i,k}}{\sum_{k=1}^{Kmax} n_{i,k}} \right) \right)^2}{\sum_{k=1}^{Kmax} n_{i,k}} \quad (3)$$

where i indexes ages ($i = 1, 2, \dots, I_{max}$); k indexes cohorts ($k = 1, 2, \dots, K_{max}$), $\sigma_{i,k}^2$ is a variance estimated by MIX; $n_{i,k}$ is the number of individuals belonging to ages i of cohort k , which was estimated by multiplying the monthly sample size (n) by the proportion estimated by MIX ($p_{i,k}$); and $\mu_{i,k}$ is the mean length of age i in cohort k estimated by MIX. In equations 2 and 3, the influence of cohorts is being reduced and only changes in the intra-cohort and inter-cohort variance of length-at-age through ages were analysed. We computed the coefficient of variation ($CV = 100 \times SD / mean$) to compare the intra and inter-cohorts variation of length-at-age.

3. RESULTS

3.1. Seasonal cycle in environmental variables

Monthly variations of the sea surface temperature (*SST*), the mean sea level (*MSL*), and the upwelling index (*UI*) are shown in figure 2. Seasonal fluctuations can be observed in the environmental variables. This seasonal cycle can be better observed if the monthly patterns are averaged by year (figure 3). The *SST* is about 14°C between December and February (summer in southern hemisphere) and 11°C in July (winter). The *MSL* are at maxima in winter (June–July) and minima in spring (September–November). The *UI* is negative during May–August, indicating that downwellings tend to occur there (convergence in the coast). Upwellings occur in October–March. September and April are transitional months for downwelling and upwelling events in the study area. Note that *MSL* is higher when the *UI* is negative in winter, which is indicative of the convergence in the coast.

3.2. Reproductive and condition indexes

During 1993–1997, the *GSI* and the *CF* demonstrated a similar seasonal pattern for both species (figure 4). The *GSI* for *S. bentincki* is increasing from February to August (peak in August). This trend suggests a progressive increase in reproduction and spawning in August because *GSI* declines from October to January. This seasonal pattern contrast with the seasonal oscillation in the *CF*. It declines from April to September and increases from October to January (figure 5). Similar seasonal pattern can be observed in the *CF* of *E. ringens*. However, the *GSI* of this species increases from April to September, while the *CF* is declining from April to July–August (figure 5).

3.3. Growth

Mean lengths-at-age are easily discriminated from length frequency data of *S. bentincki* and *E. ringens* because of the dominance and progression of modes in time (figure 6). The mean length and standard deviation obtained by MIX analysis are summarized in figure 7. A careful analysis of this figure suggests a

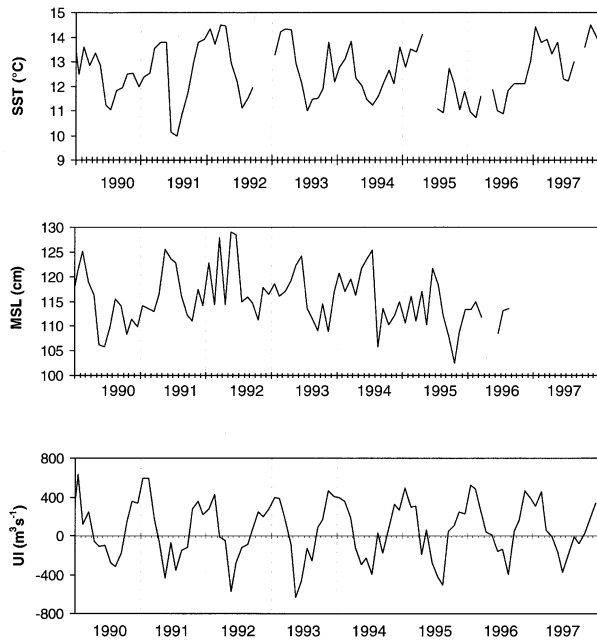


Figure 2. Monthly average values of sea surface temperature ($SST, ^\circ\text{C}$), mean sea level (MSL, cm), and upwelling index ($UI, \text{m}^3\cdot\text{s}^{-1}$) time series at Talcahuano, Chile (37°S , 73°W).

seasonality in the growth and recruitment of both species. It is observed that *S. bentincki* of smaller mean length usually enter into the fishery in November each year, and during January or May–August for *E. ringens*. After recruitment, a progression in the mean length of cohorts of both species can be followed, and the growth in length can be inferred (figure 8). In the case of *S. bentincki*, recruits between 5 to 6 cm TL had a relative age of 4 months (0.333 years in November), while recruits of *E. ringens*, of about 7 to 8 cm TL, were 6 months old (0.5 years in January).

The growth curves are from pooled data of *S. bentincki* and *E. ringens* (figure 9). There was regularity in growth for all cohorts in both species (figures 8 and 9). The growth parameters describing the seasonally oscillating growth curve of each species are shown in table II. The K value for *E. ringens* was less than K of *S. bentincki*, and *E. ringens* attains a larger asymptotic size than *S. bentincki*.

The amplitude of the seasonal growth parameter is about 1, suggesting a remarkable reduction in the length growth rate within the annual cycle. The winter point (WP) at the slowest length growth rate was similar for both species ($WP = 0.312$ for *E. ringens*, and $WP = 0.363$ for *S. bentincki*). The slowest growth rate occurred prior to winter (April–May, southern hemisphere), while the fastest length growth rate occurred six months later (October–November, figure 8).

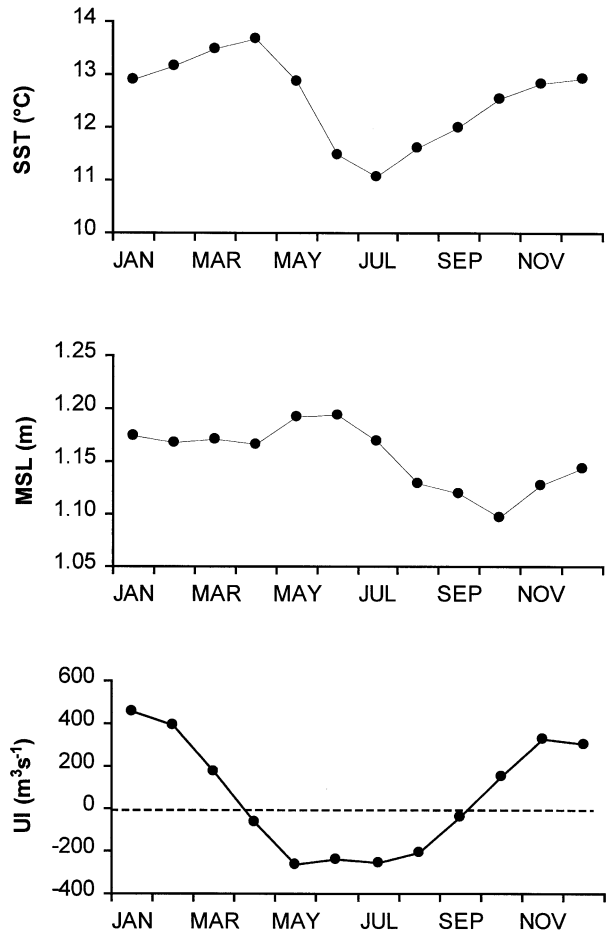


Figure 3. Seasonal signal of sea surface temperature ($SST, ^\circ\text{C}$), mean sea level (MSL, m), and upwelling index ($UI, \text{m}^3\cdot\text{s}^{-1}$) time series at Talcahuano, Chile (37°S , 73°W) (1990–1997).

3.4. Variance of length-at-age

For both species the CV of the intra-cohort variance of length-at-age decreased with age (figure 10). A regression of CV on age ($CV = a + b\cdot\text{age}$) was significant with parameters $a = 14.82$ ($IC \pm 1.23$ at 95%) and $b = -4.27$ ($IC \pm 0.67$ at 95%) ($r^2 = 0.84$, $n = 34$, $P < 0.05$) for *S. bentincki*, and $a = 15.24$ ($IC \pm 1.50$ at 95%) and $b = -2.85$ ($IC \pm 0.572$ at 95%) ($r^2 = 0.701$, $n = 45$, $P < 0.05$) for *E. ringens*.

Instead, the CV related to the inter-cohort variance of length-at-age remained constant through ages in the case of *S. bentincki*, while that quantity tended to diminish with age in *E. ringens* (figure 10). The relationship between inter-cohort- CV and age was not significant for *S. bentincki* ($P > 0.05$), but that relationship was significant in the case of *E. ringens*, with parameters $a = 6.183$ ($IC \pm 1.569$ at 95%) and $b = -1.39$ ($IC \pm 0.689$ at 95%) ($r^2 = 0.345$, $n = 34$, $P < 0.05$).

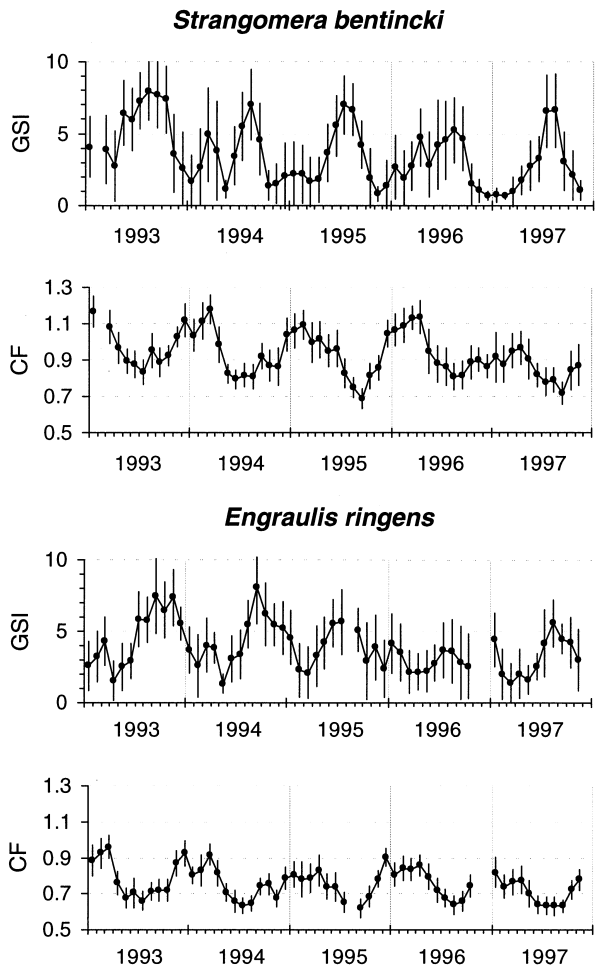


Figure 4. Monthly average of females gonadosomatic index (*GSI*) and condition factor (*CF*) for *S. bentincki* and *E. ringens* in the central southern area of Chile (1993–1997). Bars represent the standard deviation of the individual data (from Cubillos et al., 1999).

4. DISCUSSION

4.1. Reproductive strategy

In the area off central southern Chile, there are notable seasonal changes in environmental variables related to seasonal oceanographic regimes. Two seasons of different oceanographic conditions can be identified. A first period (upwelling season), from spring through the end of summer, is characterized by strong southwest winds that induce offshore movement of subantarctic surface waters (SAS) and upwelling of equatorial subsurface waters (ESS) along the coast. A second period (downwelling season), from fall to the end of winter, is characterized in turn by the constraint of SAS waters toward the coast and the deepening of the ESS toward the slope of the shelf (Bernal et al., 1982; Arcos and Navarro, 1986; Arcos, 1987; Ahumada, 1989; Strub et al., 1998).

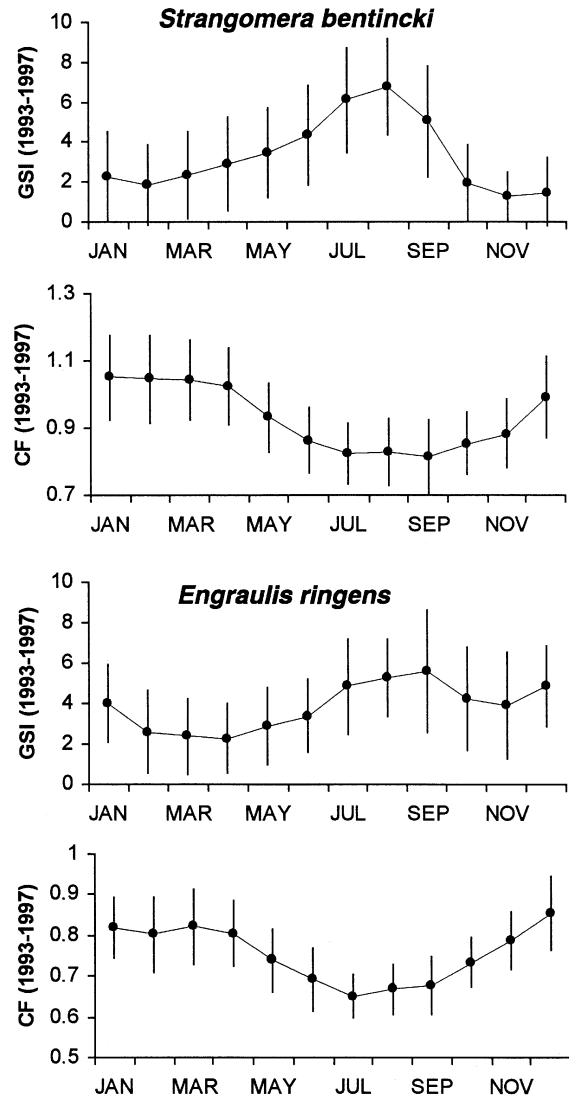


Figure 5. Seasonal signals of female gonadosomatic index (*GSI*) and condition factor (*CF*) for *Strangomera bentincki* and *Engraulis ringens* in the central southern area of Chile (1993–1997).

Peak reproduction of *S. bentincki* and *E. ringens* occurs between August and September (austral winter, Brandhorst and Rojas, 1965; Serra et al., 1979; Arizaga, 1981; Cubillos et al., 1999). Winter environmental conditions are characterized by: a) the presence of downwelling due to northerly winds, and therefore onshore transport, b) colder waters, with sea surface temperature about 11 to 12°C along the coast, and c) higher mean sea level due to onshore transport and a general surface coastal circulation to the south (Arcos, 1987; Ahumada, 1989). In this way, the benefit of the reproductive strategy of both clupeoids off central southern Chile, would be the retention of eggs and larvae near shore (onshore transport).

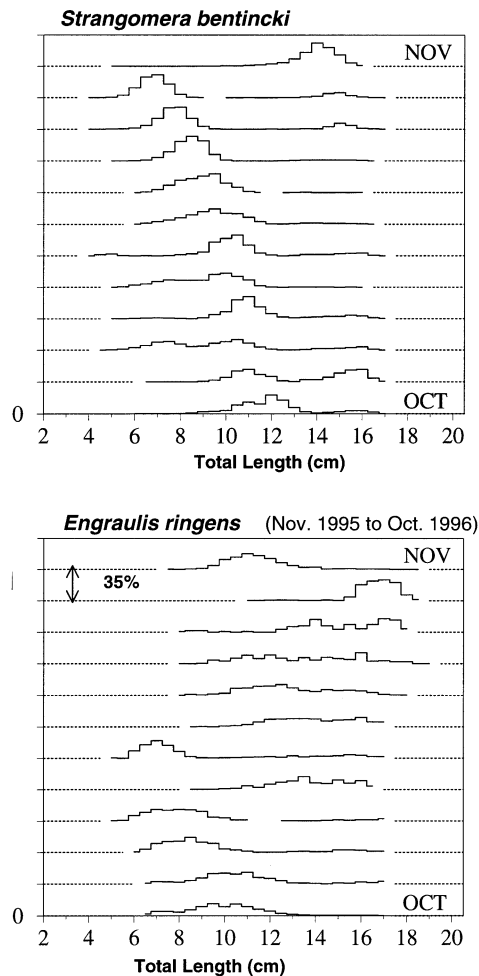


Figure 6. Examples of length frequency data for *Strangomera bentincki* and *Engraulis ringens*.

The wind pattern of the area changes from quasi-permanent north winds to intermittent south winds that produce moderate upwelling (Arcos and Navarro, 1986; Arcos et al., 1996). A moderate upwelling from September to October would be favourable for an enrichment and concentration of food particles, resulting in increased growth and survival of larvae and juveniles. The spawning area, therefore, would be transformed into a nursery area for old larvae and juveniles inhabiting a moderate upwelling regime. According to the length frequency data, recruitment of both species tends to occur during November–January. From January to February, the upwelling associated with southerly winds is intense, resulting in offshore transport and recirculation of water because of the presence of bays and gulfs (Cáceres and Arcos, 1991; Cáceres, 1992). Therefore, juveniles would be avoiding offshore advection between January and February, resulting in the expenditure fraction of the accumulated energy.

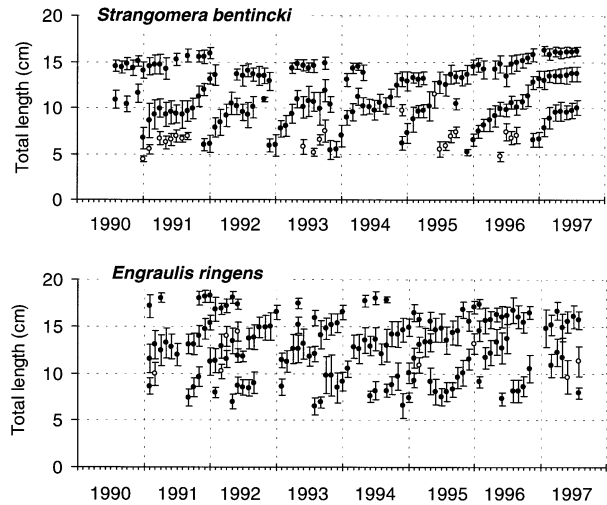


Figure 7. Mean length (\pm standard deviation) of age classes identified from the length frequency data analysis for *S. bentincki* and *E. ringens* in the 1990–1997 period.

The populational strategy of *S. bentincki* and *E. ringens* to the seasonal upwelling ecosystem consists of taking advantage of higher productivity associated with the enrichment of the coastal waters, to invest in growth and to accumulate energy reserves. At the end of winter both species are taking advantage of downwelling (convergence) to spawn and to retain eggs and larvae near the coast. This agrees with Bakun (1996), who defined three broad categories of oceanographic processes thought to be important in influencing re-

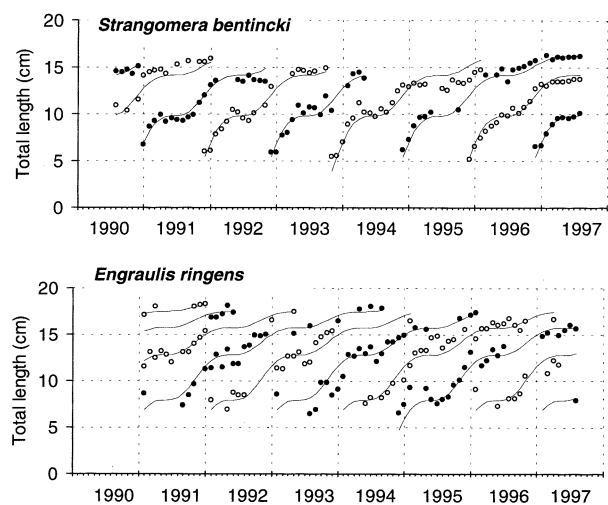


Figure 8. Cohorts of *S. bentincki* and *E. ringens*. In both cases, the growth curve from pooled data of cohorts have been superimposed. Cohorts have been alternated with empty and solid dots to facilitate the growth interpretation of each cohort. Note the growth curve has its origin in winter (southern hemisphere).

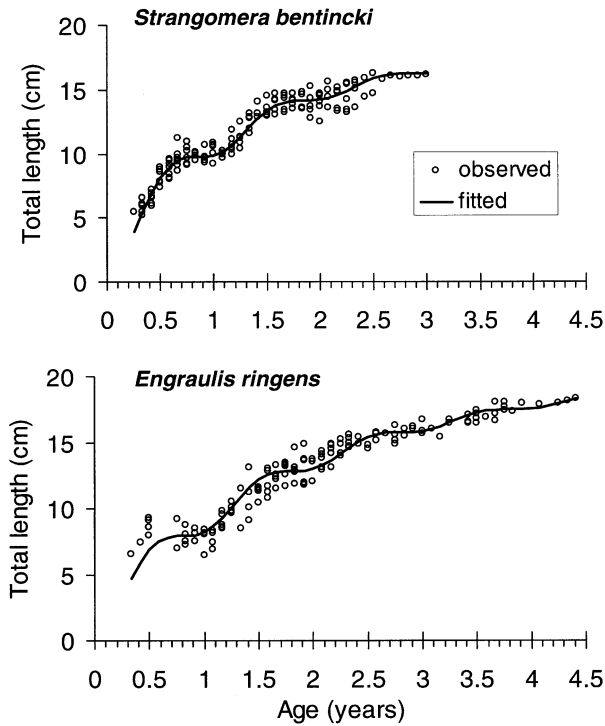


Figure 9. Seasonal oscillating growth curves for pooled data of cohorts of *S. bentincki* and *E. ringens* between 1990 and 1997 in the central southern area off Chile.

cruitment success; namely enrichment of the food chain (upwelling, mixing, etc.), retention of the eggs and larvae within suitable nursery areas (reduction in offshore transport and advection), and concentration of food particles (water column stability, convergence, presence of fronts, etc.) for the first-feeding larvae and subsequent stages.

The peak of reproduction did not coincide with the maximal *CF* that occurred between December and April, but instead with its minima. Arrizaga (1981)

Table II. Growth parameters of *Strangomera bentincki* and *Engraulis ringens* describing the von Bertalanffy growth function modified to take into account seasonal growth oscillation.

| Parameters | <i>S. bentincki</i> | <i>E. ringens</i> |
|----------------------------|---------------------|-------------------|
| L_{∞} (cm TL) | 18.1 (0.6) | 20.1 (0.6) |
| K (year^{-1}) | 0.745 (0.07) | 0.514 (0.05) |
| t_0 (year) | -0.330 (0.09) | -0.042 (0.19) |
| C | 0.998 (0.10) | 0.997 (0.16) |
| WP | 0.363 (0.02) | 0.312 (0.03) |
| r^2 | 0.948 | 0.929 |
| SSQ | 65.73 | 105.33 |
| n | 150 | 144 |

The standard deviation of parameter is shown in parentheses; C : amplitude of seasonal growth; WP: winter point or phase of seasonal growth; SSQ: sum of square, n : number of data.

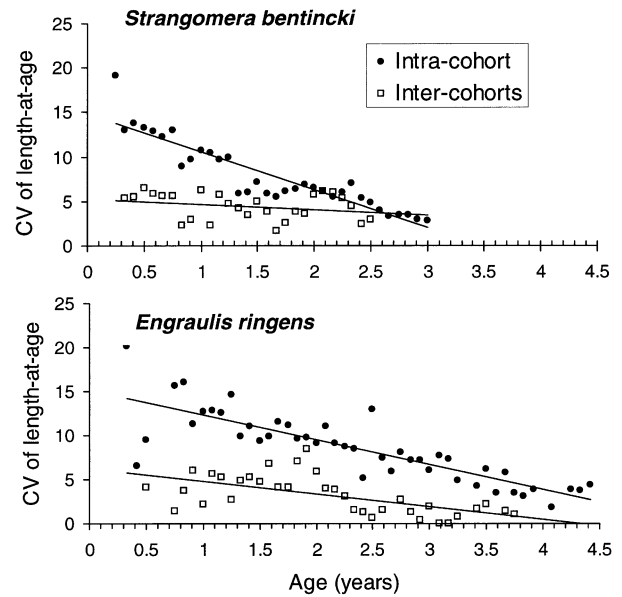


Figure 10. Intra-cohort and inter-cohorts variation of length-at-age for *S. bentincki* and *E. ringens*.

studied the seasonal cycle of fat content in *S. bentincki* between 1966 and 1967, observing higher values between December and April, and lower from September to October. Therefore, it is probable that the steady increase in *CF* from November to January is related to the accumulation of energetic reserves associated with high productivity linked with the upwelling season. Thus, the energy available during the period of major productivity is not immediately used for reproduction, but stored as fat and metabolised for reproduction several months later. This storage strategy is similar to that found by Fréon et al. (1997) for *Sardinella aurita* off the coast of Venezuela. However, the reproductive strategy of this population apparently gives priority to optimising food availability for the offsprings and not to preventing eggs and larvae being transported offshore. According to Fréon et al. (1997), this is an unexpected reproductive strategy for small pelagic fish. In the case of the populations of clupeoids off central southern Chile, the reproductive strategy is to concentrate eggs and larvae onshore, according to the 'triad' hypothesis of Bakun (1996). However, because the storage strategy can be energetically costly (Wootton, 1979), the growth of both species is being affected by the strategy of energy re-allocation.

Recently, Castro and Hernández (2000) have suggested that the seasonal patterns of energy allocation, and aspects of offspring biology and oceanography may explain the winter reproductive strategy of *E. ringens*. Thus, maximal spawning during winter would benefit from higher adult energy reserves stored earlier in the season and from the general oceanographic processes conducive to eggs and larvae retention

nearshore in average winters (north winds), which changes as the upwelling season resumes in mid-spring.

4.2. On the seasonal growth

The growth of *S. bentincki* has been studied by interpreting annual rings in *sagittae* otoliths (Aguayo and Soto, 1978) and by analysing length frequency data (Arrizaga, 1981). In the area off Talcahuano, growth of *E. ringens* has been studied only by interpreting length frequency data (Cubillos and Arancibia, 1993). These studies have not considered seasonal growth, except in Cubillos and Arancibia (1993). According to the authors, the fastest growth rate was estimated to occur during November–December for both species, the slowest growth rate was estimated to be during the middle of May for *S. bentincki*, and the middle of June for *E. ringens*. In this study, the slowest growth rate for *S. bentincki* and *E. ringens* occurred between April–May, and the fastest growth rate during October–November. This seasonal growth rate was very regular and consistent during the period of study.

The intra-cohort variation of length-at-age diminished with the age. This result is effect of the spreading of birth-dates in the cohorts and, therefore, it is indicative of the spawning process. According to Fréon (1984), the effect of different birth-date on the variance of length within a cohort tends to be more and more smoothed with age. This effect is unlikely to be compensated by the natural variability in growth. In the case of *S. bentincki* the inter-cohort CV of length-at-age was constant through all ages. In other words, the variability in mean length tends to increase with age, that is, mean size-at-age does not converge with mean growth. We assume this effect may be due to low occurrence of older cohorts of *S. bentincki*. Also, because the faster growth of *S. bentincki* it is difficult to separate the older cohorts in the length frequency data. Nevertheless, the average size-at-age of individuals born in different reproductive seasons had low interannual variability.

The low interannual variability in seasonal growth could be suggestive that growth in length of these small pelagic fish is a consequence of their adaptation to the seasonal coastal upwelling ecosystem of central southern Chile. This adaptation must be an advantageous reproductive strategy in terms of the use and exploitation of the environment they inhabit. The fastest growth rate during spring is related to the higher productivity in the coastal waters (increased food) as a consequence of the coastal upwelling events. In turn, the slowest winter growth rate between April to May may result from the energy storage strategy and the reproductive condition of the individual. Higher reproductive activity occurs from middle of June to September (Cubillos et al., 1999), suggesting that the individual may be spending more energy to produce gametes than growth (Cubillos and Arancibia, 1993).

5. CONCLUSION

We concluded that *S. bentincki* and *E. ringens*, both inhabitants of the seasonal coastal upwelling ecosystem of central southern Chile, have a similar growth process as a consequence of their adaptation, from an evolutionary point of view, to the seasonal oceanographic regularities of the habitat. The populational strategy is to spawn at the end of winter to enhance survival of eggs and larvae during moderate upwelling. Both *S. bentincki* and *E. ringens* take advantage of the time of higher productivity associated with the enrichment of coastal waters to grow and store energy that will be used in reproduction during winter. This reproductive strategy is not different from the reproductive ecology of coastal pelagic species, but the reproductive strategy is combined with an energy storage strategy due to the probably rigorous winter conditions in terms of food availability for adults in the area.

Acknowledgements. Most of this work was based on a thesis of the first author for the degree of Master of Science (major in oceanography) at the Department of Oceanography, University of Concepción, Chile. We are grateful to an anonymous referee, to Dr Pierre Fréon and Dr Larry Hutchings for the comments and suggestions in an early version of the manuscript. We also thank SHOA (*Servicio Hidrográfico y Oceanográfico de la Armada de Chile*) and DMC (*Dirección Meteorológica de Chile*) for providing the environmental time series used in this paper.

References

- Aguayo, H.M., Soto, S.B., 1978. Edad y crecimiento de la sardina común (*Clupea (Strangomera) bentincki*) en Coquimbo y Talcahuano. Invest. Pesq. (Chile) 27, 1–55.
- Ahumada, R., 1989. Producción y destino de la biomasa fitoplanctónica en un sistema de bahías en Chile central: una hipótesis. Biol. Pesq. (Chile) 18, 53–66.
- Arcos, D.F., Navarro, N., 1986. Análisis de un índice de surgencia para la zona de Talcahuano, Chile (Lat. 37°S). Invest. Pesq. (Chile) 33, 91–98.
- Arcos, D.F., 1987. Seasonal and short time scale variability in copepod abundance and species composition in an upwelling area off Concepción coast, Chile. PhD thesis. State University of New York, Stony Brook.
- Arcos, D.F., Núñez, S., Acuña, A., 1996. Variabilidad de pequeña escala en la zona nerítica del sistema de surgencia de Talcahuano (Chile central): identificación y dinámica de áreas de retención larval. Gayana Oceanol. 4, 21–58.
- Arrizaga, A., 1981. Nuevos antecedentes biológicos para la sardina común, *Clupea (Strangomera) bentincki* Norman 1936. Bol. Soc. Biol. Concepción 52, 5–66.
- Bakun, A., 1973. Coastal upwelling indices, west coast of North America, 1946–1971 NOAA Technical Report

- NMFS-SSRF 671. U.S. Department of Commerce, Washington, DC.
- Bakun, A., Parrish, R.H., 1982. Turbulence, transport, and pelagic fish in the California and Peru current systems. *CalCoFI Rep.* 23, 99–112.
- Bakun, A., Parrish, R.H., 1990. Comparative studies of coastal pelagic fish reproductive habitats: the Brazilian sardine (*Sardinella aurita*). *J. Cons. Int. Explor. Mer* 46, 269–283.
- Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. University of California Sea Grant, UCSD, San Diego, CA and Centro de Investigaciones Biológicas de Noroeste, La Paz, Baja California.
- Bernal, P., Robles, F., Rojas, O., 1982. Variabilidad física y biológica en la región meridional del sistema de corrientes Chile-Perú. *Monogr. Biol.* 2, 75–102.
- Brandhorst, W., Rojas, O., 1965. Sobre la biología de la sardina común (*Clupea bentincki bentincki* Norman) en aguas chilenas entre Coquimbo y Talcahuano. *Bol. Cient. Inst. Fom. Pesq. Chile* 1, 71–91.
- Cáceres, M., Arcos, D., 1991. Variabilidad en la estructura espacio-temporal de un área de surgencia frente a la costa de Concepción. Chile. *Invest. Pesq. (Chile)* 36, 27–38.
- Cáceres, M., 1992. Vórtices y filamentos observados en imágenes de satélite frente al área de surgencia de Talcahuano. Chile central. *Invest. Pesq. (Chile)* 37, 55–66.
- Castro, L.R., Hernández, E.H., 2000. Early life survival of the anchoveta *Engraulis ringens* off central Chile during the 1995 and 1996 winter spawning seasons. *Trans. Am. Fish. Soc.* 129, 1107–1117.
- Cole, J., McGlade, J., 1998. Clupeoid population variability, the environment and satellite imagery in coastal upwelling systems. *Rev. Fish Biol. Fish.* 8, 445–471.
- Cubillos, L., Arancibia, H., 1993. On the seasonal growth of common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*) off Talcahuano. Chile. *Rev. Biol. Mar. (Valparaíso)* 28, 43–49.
- Cubillos, L., Canales, M., Hernández, A., Bucarey, D., Vilugrón, L., Miranda, L., 1998. Poder de pesca, esfuerzo de pesca y cambios estacionales e interanuales en la abundancia relativa de *Strangomera bentincki* y *Engraulis ringens* en el área frente a Talcahuano, Chile (1990–97). *Invest. Mar. Valparaíso* 26, 3–14.
- Cubillos, L., Canales, M., Bucarey, D., Rojas, A., Alarcón, R., 1999. Época reproductiva y talla media de primera madurez sexual de *Strangomera bentincki* y *Engraulis ringens* en la zona centro-sur de Chile en el período 1993–1997. *Invest. Mar. Valparaíso* 27, 73–86.
- Fréon, P., 1984. La variabilité des tailles individuelles à l'intérieur des cohortes et des bancs de poissons I: observations et interprétation. *Oceanol. Acta* 7, 457–468.
- Fréon, P., El Khattabi, M., Mendoza, J., Guzmán, R., 1997. Unexpected reproductive strategy of *Sardinella aurita* off the coast of Venezuela. *Mar. Biol.* 128, 363–372.
- McDonald, P.D.M., Pitcher, T.J., 1979. Age groups from size-frequency data: a versatile and efficient method for analyzing distribution mixtures. *J. Fish. Res. Board Can.* 36, 987–1001.
- McDonald, P.D.M., Green, P.E.J., 1988. User's guide to program MIX: an interactive program for fitting mixtures of distributions. *Ichthus Data Systems*, Hamilton.
- Parrish, R.H., Bakun, A., Husby, D.M., Nelson, C.S., 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. In: Sharp, G.D., Csirke, J. (Eds.), *Expert consultation to examine changes in abundance and species composition of neritic fish resources*, San José, Costa Rica, FAO Fish. Rep., 291, pp. 731–777.
- Roa, R., 1993. Annual growth and maturity function of the squat lobster *Pleuroncodes monodon* in central Chile. *Mar. Ecol. Prog. Ser.* 97, 157–166.
- Roa, R., Ernst, B., 1996. Age structure, annual growth, and variance of size-at-age of the shrimp *Heterocarpus reedi*. *Mar. Ecol. Prog. Ser.* 137, 59–70.
- Serra, J.R., Rojas, O., Aguayo, M., Hinostroza, F., Cañón, J., 1979. Sardina común *Clupea (Strangomera) bentincki* Teleostomi Clupeiformes-Clupeidae. Estado actual de las principales pesquerías nacionales: Bases para un desarrollo pesquero. *Peces. CORFO AP Instituto de Fomento Pesquero*, Santiago.
- Somers, I.F., 1988. On a seasonally growth function. *Fish-byte* 6, 8–11.
- Strub, P.T., Mesías, J., Montecinos, V., Rutland, J., Salinas, S., 1998. Coastal ocean circulation of western South America. Coastal segment (6,E). In: Robinson, A., Brink, K. (Eds.), *The Sea*, vol. 11. John Wiley and Sons Inc, New York, pp. 273–313.
- Wootton, R.J., 1979. Energy cost of egg production and environmental determinants of fecundity in teleost fishes. *Symp. Zool. Soc. London* 44, 133–155.
- Wootton, R.J., 1992. *Ecology of teleost fishes*, 2nd edition. Chapman and Hall Ltd, London.