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

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Monthly abundance estimation for common sardine *Strangomera bentincki* and anchovy *Engraulis ringens* in the central-southern area off Chile (34–40°S)

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Abstract

Abundance, biomass, recruitment and fishing mortality of common sardine, *Strangomera bentincki*, and anchovy, *Engraulis ringens*, are estimated for stocks distributed in the central-southern area (34–40°S) off Chile. Monthly length–frequency data, from July 1990 to November 1999, were used to identify cohorts, to analyze growth, and to determine the monthly age composition of the catches. The abundance of cohorts was estimated using cohort analysis on a monthly time-scale that is sufficiently small for capturing the rapid seasonal changes that characterize both resources. An ADAPT approach was used to estimate the unknown parameters by using catch per unit effort (CPUE) data as auxiliary information. Growth was a regular process for different cohorts of both species, and a seasonal oscillating growth curve was fitted. The parameters of the seasonal von Bertalanffy growth function were: $L_\infty = 17.7$ cm, $K = 0.79$ yr^{-1}, $t_0 = -0.347$ yr, $C = 0.996$, and winter point (WP) = 0.373 ($r^2 = 0.930$, $n = 207$, $P < 0.05$) for common sardine; $L_\infty = 20.8$ cm, $K = 0.444$ yr^{-1}, $t_0 = -0.392$ yr, $C = 0.849$, and WP = 0.310 ($r^2 = 0.906$, $n = 203$, $P < 0.05$) for anchovy. The growth rates were slowest between April and May, before the spawning season. Recruitment of common sardine occurred in November, while recruitment of anchovy tended to occur in January. The yearly pulse of recruitment dominates the population dynamics of both species, and it was observed that the recruitment of the two species varies inversely. The 1997 cohort of common sardine was the lowest in the 1990s, but recruitment of anchovy was higher, probably as a consequence of the 1997–1998 El Niño event. The biomass of the common sardine stock declined from 1997 to 1999, while fishing effort was growing. On the contrary, the biomass of anchovy was higher in 1998 and 1999 due to the stronger cohorts of 1996 and 1997. Evidence for density-dependent catchability was found for sardine, but not for anchovy. At present, both species can be considered as overfished because a growing trend in fishing effort is not compensated by the productivity of the stocks. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Small pelagic fish; Abundance; Cohort analysis; Stock assessment; Talcahuano (Chile)

1. Introduction

The small pelagic fish common sardine, *Strangomera bentincki* (Norman, 1936), and anchovy, *Engraulis ringens* (Jenyns, 1842), are important resources off central-southern Chile (34–40°S), where Talcahuano is the main port for landings (Fig. 1, Cubillos et al.,

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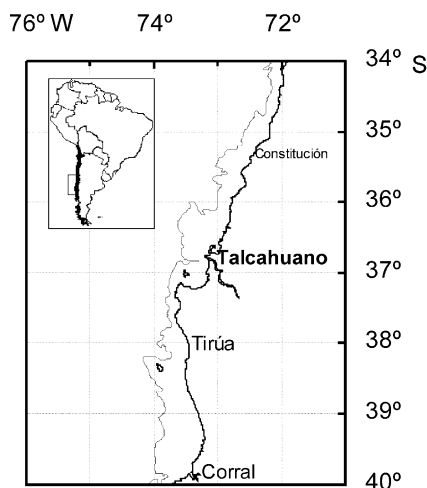*E-mail address*: inpesca@inpesca.cl (L.A. Cubillos).

Fig. 1. Study area showing the 200 m isobath.

1998a). Both species are caught in coastal waters by artisanal and industrial seiners, with catches ranging from about 400,000 to 1,500,000 t between 1990 and 1999 (Fig. 2).

There are several studies describing the biological and fishery aspects of the resources before 1977, when the species were the main pelagic fish resources exploited in the area of Talcahuano (Serra, 1978, 1983; Aguayo and Soto, 1978; Arrizaga, 1981; Guerrero and Yáñez, 1986; Fonseca et al., 1986; Yáñez et al., 1990, 1992). However, few studies document the most recent period of higher yield in the 1990s (Cubillos and Arancibia, 1993a,b; Galleguillos et al.,

1997; Arancibia et al., 1994; Cubillos et al., 1998a,b, 1999). Overall, the most important fishery and biological aspects of common sardine and anchovy are: (i) short life span; (ii) fast growth in length, with seasonally oscillating growth rate; (iii) high natural mortality; (iv) spawning time at the end of winter time; (v) catches heavily dependent on yearly pulses of recruitment; (vi) seasonal fishery, with higher catches and fishing effort during January–March every year.

In stock assessments for common sardine and anchovy prior to 1977 (Serra, 1978; Yáñez et al., 1992), equilibrium production models were applied. Although Yáñez et al. (1992) attempt to include environmental cues, the approach probably is wrong because the implicit assumption is that the stock is at equilibrium, a condition rarely occurring (Hilborn and Walters, 1992). Recently, Barría et al. (1998) use annual age composition data covering the period 1990–1996 to perform age-structured stock assessments of the species. However, an age-structured stock assessment on a yearly time-scale does not seem recommended for the species because the low number of age classes and the highly seasonal fishery could affect the estimates of abundance.

To avoid problems related to the small number of age classes, this paper aims to estimate the abundance, biomass, recruitment and fishing mortality of common sardine and anchovy by cohorts on a time-scale (1 month) that is sufficiently small for capturing the rapid changes that characterize both resources.

2. Materials and methods

2.1. Data source

During 1990–1999, length–frequency data have been collected from the fishery of common sardine and anchovy in Talcahuano (Fig. 1). Each length–frequency data set corresponds to monthly summaries of random daily samples obtained from the catches. 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 (Cubillos et al., 2001). The period of study is from July 1990 to November 1999 in the case of common sardine, and from January 1991 to November 1999 for anchovy.
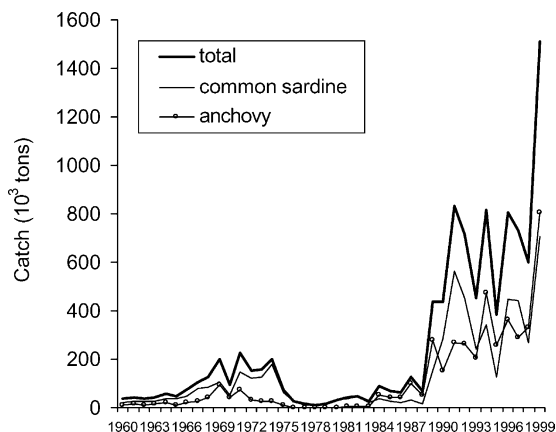

Fig. 2. Catch history of common sardine (*S. bentincki*) and anchovy (*E. ringens*) in the central-southern area off Chile.

Nominal catch rates have been standardized according to Cubillos et al. (1998a), and updated to November 1999. The unit of fishing effort was fishing trips with captures from boats of 50 m^3 hold capacity. Unfortunately, the number of total trips was not available for small boats (<80 m^3 hold capacity) during the period of study. This fraction of the fleet is important, contributing with more than 50% of total catches (Cubillos et al., 1998a). In addition, it should be noted that catch rates were standardized for both species together, because it is difficult to separate the fishing effort allocated for each species. Apparently, fishermen do not prefer a given species, because the price is similar and because both species are destined for fish-meal production. The standardized monthly catch per unit effort (CPUE) was computed for each species separately by using the proportion of each in the total yield.

2.2. Age composition and identification of cohorts

The software MIX (McDonald and Green, 1988) was used to analyze the length–frequency data. MIX uses the statistical–numerical algorithms described by McDonald and Pitcher (1979) and considers length–frequency data as a mixture of probability density functions (pdf). We assumed age of cohorts to have a normal pdf in the mixture, and we determined the number of ages (cohorts) in each length–frequency data visually. Thus, the number of parameters to be estimated is the total number of ages present in the mixture, times the three parameters of each normal pdf, i.e. the proportion in the mixture, the mean and the standard deviation of length at age. Cubillos et al. (2001) studied the growth in length by applying MIX to length–frequency data for the period between July 1990 and July 1997. In this way, the age composition and growth parameters must be considered an update of the results of Cubillos et al. (2001) for the period between August 1997 and November 1999.

Once the mean, standard deviation and proportion of ages were estimated from each 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 which are believed to belong to the same cohort are linked. Then, relative ages (in months) were assigned to the mean lengths belonging to each cohort by considering 1 July as a fixed birth date, because the major spawning season begins in July and extends until September (Arancibia et al., 1994; Cubillos et al., 1999).

2.3. Growth analysis

The mean length at age of all cohorts was used to estimate the parameters of the von Bertalanffy growth function proposed by Somers (1988) to take into account seasonal growth, i.e.

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

where L_i is the mean length at age i (year), L_∞ the asymptotic length (cm), K a growth coefficient (yr^{-1}), t_0 the hypothetical starting time at zero length if the adult and juveniles growth curve could be extrapolated back to the origin, C a dimensionless constant expressing the amplitude of a growth oscillation and t_s is the age at onset (with reference to $i = 0$) of a growth oscillation of period 1 year. 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 there is a period of no growth ($dL/dt = 0$). For practical purposes, the t_s was replaced by winter point (WP) ($= t_s + 0.5$) representing a WP that indicates the moment at which the growth rate is the slowest during the annual cycle. The parameters of Eq. (1) were estimated by non-linear regression using the Marquardt algorithm.

2.4. Catch in number

Catch in number was obtained by transforming total yield data, and catch at age i in month j ($C_{i,j}$) was obtained from catch in number of month j (C_j) multiplied by the proportion of each age of cohorts ($p_{i,j}$) estimated by MIX as following:

$$C_{i,j} = C_j \times p_{i,j} = \frac{Y_j}{W_j} \times p_{i,j}, \quad (2)$$

where Y_j is the yield (catch in weight) in month j and W_j the mean body weight in month j, i.e.

$$W_j = \frac{\sum_{l=1} w_l f_{l,j}}{\sum_{l=1} f_{l,j}}, \tag{3}$$

where $f_{l,j}$ is the number of individuals in the length class l in the sample of month j and w_l is the mean weight in the length class l, which was obtained by using the equation proposed by Beyer (1987), i.e.

$$w_l = a[L_{l+1} - L_l]^{-1}[b+1]^{-1}[L_{l+1}^{(b+1)} - L_l^{(b+1)}], \tag{4}$$

where a and b are the parameters of the length–weight relationship (LWR) and L the lower length of length class l. Parameters for the LWR were obtained monthly from weekly samples of length and weight of fishes.

2.5. Cohort analysis

The population model assumes that the abundance of cohorts is determined by a pulse of recruitment. After the pulse, the abundance of each cohort is diminished by natural and fishing mortality. According to the length–frequency data analysis and the growth analysis of cohorts (Fig. 3), recruitment occurs

in November in the common sardine population, and in January in the case of the anchovy population.

The matrix of catch in number was constructed by months $(1, 2, \ldots, J_{\max})$ and by cohorts $(1, 2, \ldots, K_{\max})$ for the 1990–1999 period. The month at recruitment was the same and, therefore, a single cohort enters the fishery every year (Fig. 3). We considered a maximum age of 36 months for every cohort in the population of common sardine, and a maximum of 40 months for the cohorts of anchovy (except for the more recent and incomplete cohorts). The abundance of cohorts was estimated backward, from the oldest to the youngest, using the equation of Pope (1972) as modified by MacCall (1986), i.e.

$$N_i = N_{i+1} \exp(M/12) + \frac{C_i(M/12)}{1 - \exp(-M/12)}, \tag{5}$$

where N_i is the abundance at age i, C_i the catch in number at age i and M the rate of natural mortality, which has been assumed to be constant. Following Cubillos et al. (1998b), a value of $M = 0.96 \, \text{yr}^{-1}$ ($=0.08 \, \text{month}^{-1}$) for common sardine, and $M = 0.69 \, \text{yr}^{-1}$ ($=0.0575 \, \text{month}^{-1}$) for anchovy were used. The estimates of natural mortality represent a weighted average by the inverse of the variance of
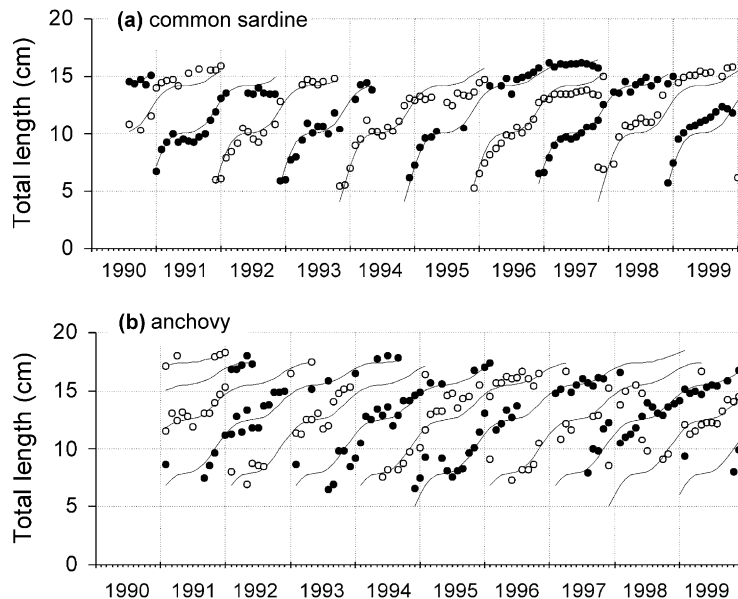

Fig. 3. Growth in length of the cohorts of *S. bentincki* and *E. ringens* in the 1990–1999 period. The average lengths at age of consecutive cohorts have been alternated with empty and full circles only for easier interpretation of the growth of each cohort.

alternative and equally probable values of M obtained from empirical models through a parametric bootstrap (Cubillos et al., 1998b).

Biomass of cohorts was estimated by multiplying the abundance in number at age by the average weight at age. Fishing mortality rate at age (F_i) of cohorts was estimated by

$$F_i = \ln\left(\frac{N_i}{N_{i+1}}\right) - \left(\frac{M}{12}\right), \tag{6}$$

and monthly fishing mortality, as required to be related to the fishing effort, was estimated by

$$F_j = \frac{\sum_{k=1}^{K_{max}} F_{k,j}\overline{B}_{k,j}}{\sum_{k=1}^{K_{max}} \overline{B}_{k,j}} = \frac{Y_j}{\overline{B}_j}, \tag{7}$$

where $\overline{B}_j$ is the average total biomass in month j, i.e.

$$\overline{B}_j = \sum_{k=1}^{K_{max}} B_{k,j} \frac{1 - \exp(-(F_{k,j} + (M/12)))}{F_{k,j} + (M/12)} \tag{8}$$

In the estimation process, the parameters to be estimated were the terminal abundance at maximum age (I_{max}) of the k cohorts ($N_{I_{max,k}}$), and the coefficient of catchability (q). The terminal abundance of cohorts was estimated by assuming a stochastic process about an average (geometric) value (N_0), i.e.

$$N_{I_{max,k}} = N_0 \exp(\tau_k), \tag{9}$$

where $\tau_k \approx N(0, \sigma_{N_{I_{max}}}^2)$ are the deviations (anomalies) of the average terminal abundance of all cohorts. Although terminal abundance of cohorts is not estimated directly for each cohort, the τ_k are unknown to be estimated. The advantage of this approach is that terminal abundance of cohorts will be always positive.

The estimation process was controlled by minimizing the following objective functions:

$$SSQ_{effort} = \sum_{y=1}^{Y_{max}} \sum_{j=1}^{12} \left[\left(\ln(E_{j,y}) - \ln\left(\frac{F_{j,y}}{q}\right) \right)^2 \right] \tag{10}$$

or

$$SSQ_{CPUE} = \sum_{y=1}^{Y_{max}} \sum_{j=1}^{12} [(\ln(CPUE_{j,y}) - \ln(q\overline{B}_{j,y}))^2] \tag{11}$$

where y indexes years and j indexes months; $CPUE_{j,y}$ the catch per unit effort (tons by standard trips) in the month j and year y; q the coefficient of catchability, assumed to be constant for all the period; $\overline{B}_{j,y}$ the average total biomass in month j and year y; $E_{j,y}$ the fishing effort in month j and year y; $F_{j,y}$ the fishing mortality rate in month j and year y. However, it is not necessary that the length of the time series of fishing effort or CPUE covers the whole period of study. The estimation process was implemented in the AD Model Builder$^{©}$ software of Otter Research (Fournier, 1996). The data and program template are available from the first author.

In the current analysis, we assumed that the coefficient of catchability was not affected by the biomass of the stock. This hypothesis can be wrong in schooling pelagic fish, because the shoaling behavior through which, even if in low abundance, pelagic fish would still tend to aggregate in shoals of a given size (Csirke, 1988, 1989; Fréon and Misund, 1999). This behavior could cause an increase in the catchability coefficient that allows the fleet to obtain relatively high catch rates in low abundance. We attempted to test the alternative hypothesis of a density-dependent catchability, by estimating the coefficient of catchability by

$$q_j = \frac{CPUE_j}{\overline{B}_j} \tag{12}$$

where j indexes months, CPUE the observed catch per unit effort, and $\overline{B}$ the average biomass (Eq. (8)). The model describing variation of q with the average biomass of the stock is that proposed by MacCall (1976), which has the form:

$$q = \alpha\overline{B}^{\beta} \tag{13}$$

where α and β are the parameters to be estimated. We assumed a multiplicative error structure for changes in catchability, therefore linear regression analysis of the log-transformed variables was used to test the nonlinear relationship.

3. Results

3.1. Cohort identification and growth analysis

The average length at age estimated by MIX for the cohorts of common sardine and anchovy are shown in Fig. 3. The seasonally oscillating growth curve

describing the growth of all cohorts (pooled data) of each species has been superimposed for ease of interpretation. A regular pattern of growth can be observed for the cohorts of both species, particularly the seasonal growth in length. Also, a regular process of recruitment can be observed for the cohorts, where the smaller mean length of common sardine usually enters into the fishery in November each year, and during January or May for anchovy.

The growth parameters describing the seasonally oscillating growth curve from pooled data of the cohorts of each species were: $L_\infty = 17.7$ cm, $K = 0.79$ yr^{-1}, $t_0 = -0.347$ yr, $C = 0.996$, and WP $= 0.373$ ($r^2 = 0.930$, $n = 207$, $P < 0.05$, SSQ $= 117.248$) for common sardine; $L_\infty = 20.8$ cm, $K = 0.444$ yr^{-1}, $t_0 = -0.392$ yr, $C = 0.849$, and WP $= 0.310$ ($r^2 = 0.906$, $n = 203$, $P < 0.05$, SSQ $= 169.535$) for anchovy. Asymptotic weight was estimated to be 49.9 and 63 g for common sardine and anchovy, respectively, by using the parameters of the LWR with $b = 3$ (see Cubillos et al., 1998b).

The growth of anchovy was lower than that of common sardine, and the asymptotic length of anchovy was greater than the asymptotic size of common sardine. In the case of the seasonal growth parameters, the amplitude of growth (C) was near unity for sardine, while the WP was similar in both species. The slowest growth rates tended to occur between April and May (winter time, Southern Hemisphere).

3.2. Catch, CPUE and fishing effort

There is a seasonal pattern in the catches of the two species, with greater catches during November–February every year. Usually, catches of common sardine are greater than catches of anchovy, especially at the beginning of the year (Fig. 4a). In 1999, total catches were higher because fishing effort was higher (Fig. 4b). However, the CPUE of common sardine was lower in 1999, and similar to the values observed between 1993 and 1994 (Fig. 5a). In contrast, the CPUE of anchovy was higher and similar to the values of CPUE observed between 1994 and 1995 (Fig. 5b).

3.3. Abundance, biomass and recruitment

In common sardine, the estimates of abundance and biomass were similar when CPUE or fishing effort
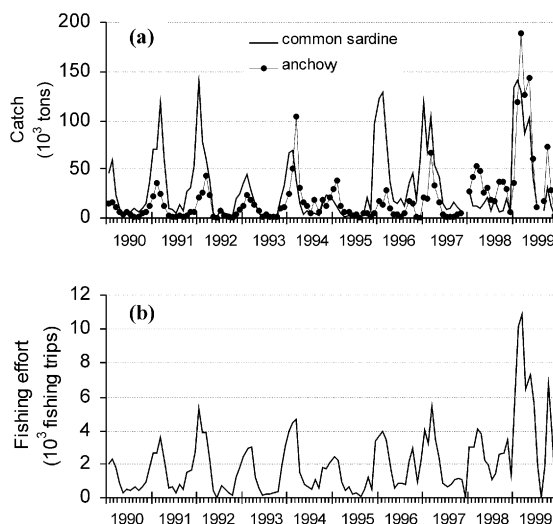

Fig. 4. Monthly catches of common sardine and anchovy (a) and standardized fishing effort (b) between January 1990 and November 1999.

data were used to control the estimation process of parameters, i.e. the coefficient of catchability and the terminal abundance of cohorts (Table 1). A value of -10.438 (natural logarithm scale) for the coefficient of catchability (q), and a value of 11.103 for the average terminal abundance (N_0) of the cohorts were estimated when CPUE was used. Instead, a log-value
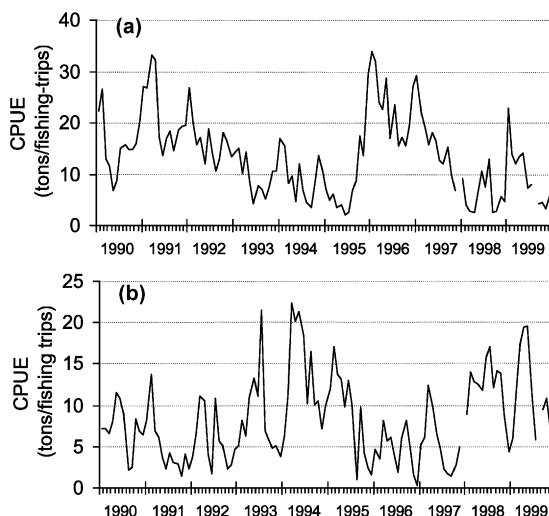

Fig. 5. CPUE of common sardine (a) and anchovy (b) between January 1990 and November 1999.

Table 1

S. bentincki, number, definition and value of the parameters (logarithms) to be estimated by using CPUE or fishing effort data as auxiliary information

Index	Parameter	CPUE-based	Effort-based
1	Coefficient of catchability	−10.438	−10.648
2	Average terminal abundance	11.103	12.855
3	Deviation for 1988 year-class terminal abundance	−4.6405	1.6548
4	Deviation for 1989 year-class terminal abundance	4.6821	3.0707
5	Deviation for 1990 year-class terminal abundance	4.0165	2.6228
6	Deviation for 1991 year-class terminal abundance	3.8604	2.1867
7	Deviation for 1992 year-class terminal abundance	2.5909	1.2861
8	Deviation for 1993 year-class terminal abundance	−4.5376	−1.9258
9	Deviation for 1994 year-class terminal abundance	−4.8519	−4.9612
10	Deviation for 1995 year-class terminal abundance	2.9464	2.2557
11	Deviation for 1996 year-class terminal abundance	−4.9543	−4.9778
12	Deviation for 1997 year-class terminal abundance	−3.1545	−4.9629
13	Deviation for 1998 year-class terminal abundance	4.0425	3.7508
	Objective function	101.55	19.7554

of −10.648 for q, and a log-value of 12.855 for N_0 were obtained by using the fishing effort data. The values of deviations of the terminal abundance of cohorts had the same trend between estimation processes, except in the case of the incomplete terminal cohort of 1988.

Abundance and biomass of anchovy were over-estimated because the coefficient of catchability tended to be very small, particularly when using fishing effort data. In fact, the log-estimates for q ranged between −23.460 and −12.107 for fishing effort and CPUE data, respectively (Table 2). However, although over-estimated, the relative changes in biomass and global fishing mortality followed the changes in the observed CPUE and fishing effort. The over-estimation of the abundance of anchovy was greater when fishing effort was used. In this way, we considered the estimation process that used CPUE by constraining the coefficient of catchability to $q = -11.2687$ (Table 2, last column), which was

Table 2

E. ringens, number, definition and value of the parameters (logarithms) to be estimated by using CPUE or fishing effort data as auxiliary information

Index	Parameter	CPUE-based	Effort-based	CPUE-based
1	Coefficient of catchability	−12.107	−23.460	−11.269[a]
2	Average terminal abundance	7.965	20.566	8.037
3	Deviation for 1987 year-class terminal abundance	7.786	6.646	6.616
4	Deviation for 1988 year-class terminal abundance	−8.867	−9.425	−8.432
5	Deviation for 1989 year-class terminal abundance	−2.319	3.937	−5.974
6	Deviation for 1990 year-class terminal abundance	−2.065	−8.954	−1.047
7	Deviation for 1991 year-class terminal abundance	8.080	6.547	6.928
8	Deviation for 1992 year-class terminal abundance	−5.276	6.522	4.610
9	Deviation for 1993 year-class terminal abundance	6.618	−5.574	−1.792
10	Deviation for 1994 year-class terminal abundance	−2.971	−8.919	−8.610
11	Deviation for 1995 year-class terminal abundance	−14.158	−5.424	−2.816
12	Deviation for 1996 year-class terminal abundance	1.143	7.830	−2.204
13	Deviation for 1997 year-class terminal abundance	9.462	8.595	3.450
14	Deviation for 1998 year-class terminal abundance	2.569	−1.779	9.272
	Objective function	129.447	36.8081	134.670

[a] This value was not estimated by the estimation process.

Fig. 6. Observed and estimated CPUE for common sardine (a) and anchovy (b).

Fig. 7. Coefficient of catchability against the average biomass of common sardine (a) and anchovy (b).
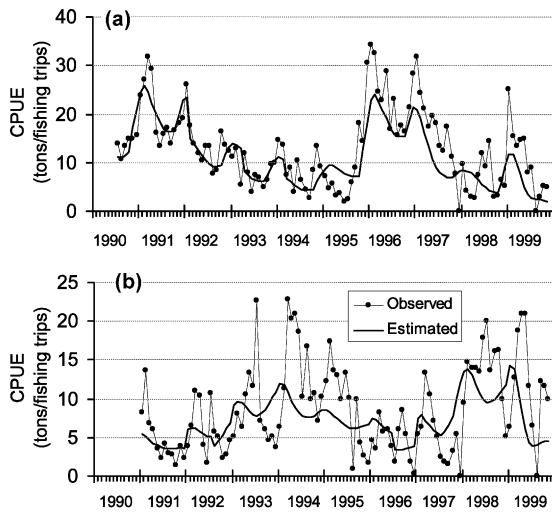
assumed to be the average between the q estimated for common sardine ($q = -10.4379$) and the q estimated freely for anchovy by using CPUE ($q = -12.1073$).

The final estimates of abundance for common sardine and anchovy were based on the estimation process that used CPUE data. There was a good agreement between the observed and estimated CPUE
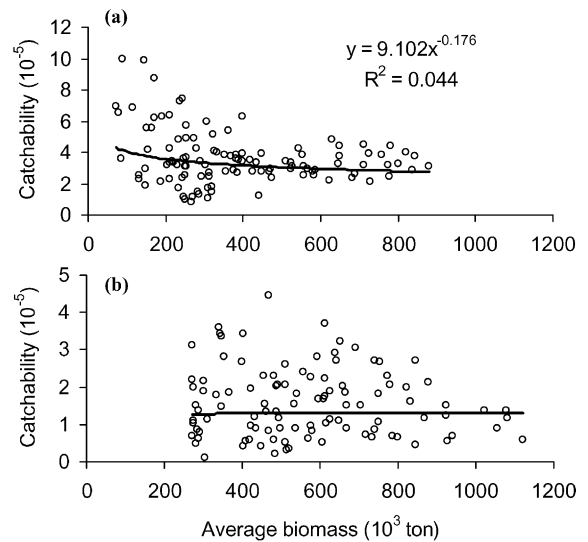
(Fig. 6). The CPUE residuals were significantly auto-correlated for each series. In the case of common sardine, the residuals at time t explained 58.6% of the residual at time $t + 1$ ($P < 0.05$), while in anchovy 52% was explained ($P < 0.05$).

The relationships between the coefficient of catchability and the average biomass of the stock are shown
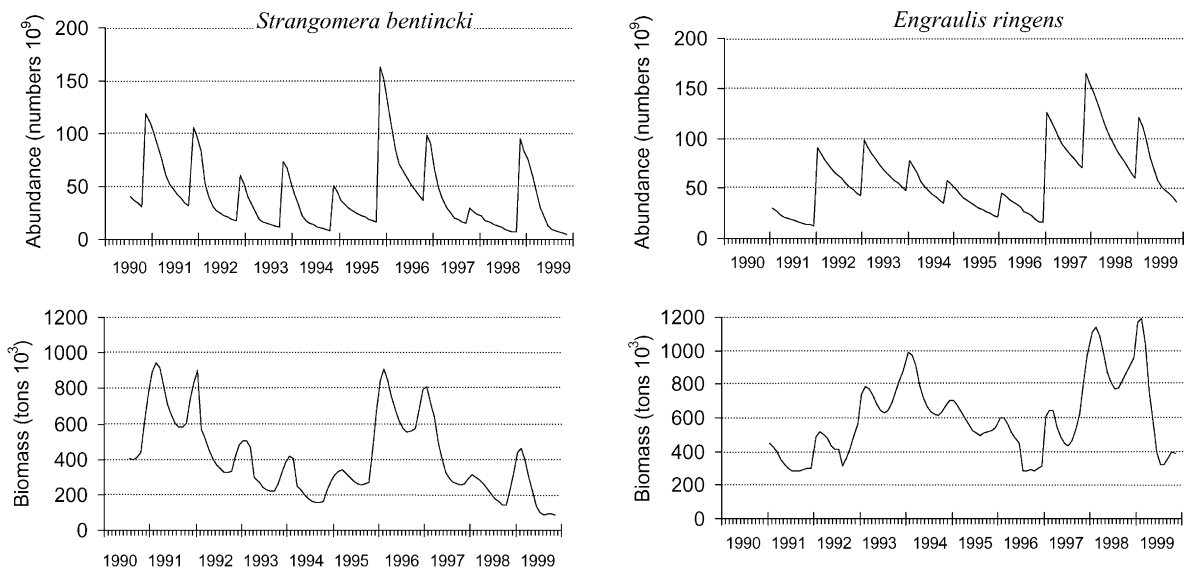

Fig. 8. Abundance and biomass time series estimated for common sardine (left) and anchovy (right).
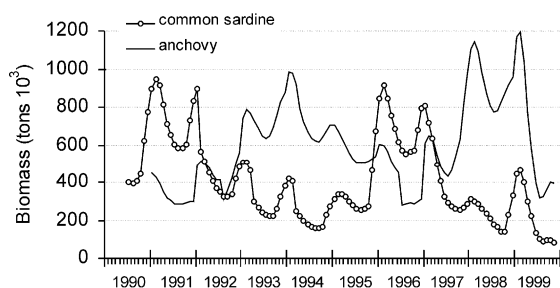
Fig. 9. Changes in biomass of common sardine and anchovy.

in Fig. 7. In the case of anchovy, q was constant as a function of average biomass. However, in the case of common sardine, q was inversely related to the average biomass ($P < 0.05$), particularly at biomasses less than 200,000 t. The exponent of the relationship was significantly different from zero, suggesting that the hypothesis of a density-dependent catchability cannot be rejected for common sardine.

The abundance of both species presents yearly pulses, which are related to recruitment, but in the biomass, the pulses are smoothed due to the growth in weight of cohorts (Fig. 8). The yearly pulses of recruitment produce a seasonal fluctuation in biomass, with higher values during January–March. The biomass of the two species tended to vary inversely in the 1990s (Fig. 9). At the beginning of 1991, 1992, 1996 and 1997, the biomass of common sardine was higher, while the biomass of anchovy was higher at the beginning of 1993–1995, 1998 and 1999.

The strongest cohort of common sardine occurred in 1995, while the 1997 cohort was the lowest in the 1990s. In the case of anchovy, the more abundant recruitments were due to the cohorts of 1991, 1996 and 1997 (Fig. 10). Because the 1998 cohort is incomplete, the recruitment estimate of this cohort could be affected by the higher catches of both species in 1999 (Fig. 2). Nevertheless, when the recruitment of common sardine tends to decline the recruitment of anchovy tend to increase, and vice versa. This pattern is producing the tendency to vary inversely in the abundance and biomass (Fig. 9). However, there was not a significant negative relationship between the recruitment of common sardine and of anchovy.

The recruitment is plotted against spawning stock biomass in Fig. 11. We used the biomass in August as the spawning stock biomass, because the major
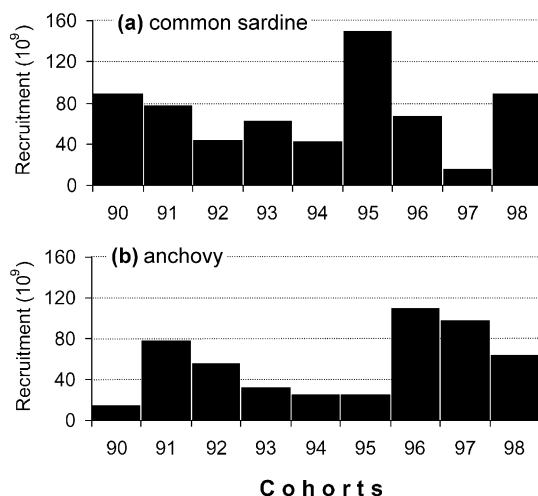

Fig. 10. Recruitment of common sardine and anchovy of the year-classes of 1990–1998.

spawning season begins in July and extends until September. Although the spawning stock biomass of the species has fluctuated in the 1990s, the stock–recruitment relationships were far from clear. Fluctuations in recruitment could be related to other causes than the spawning stock biomass.

Monthly estimates of the fishing mortality rate are summarized in Table 3 for both species. In the case of
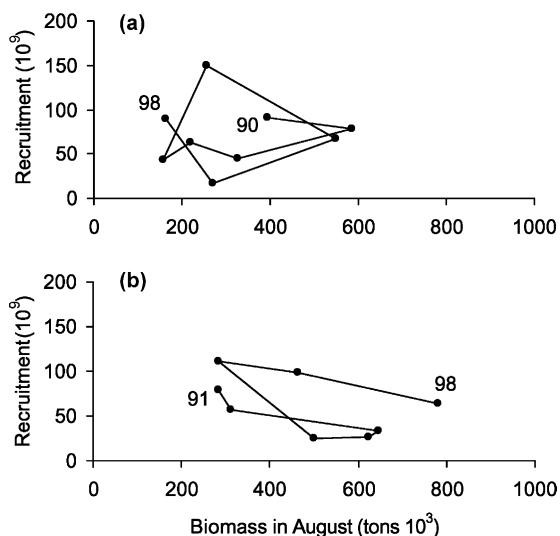

Fig. 11. Recruitment against spawning stock biomass for common sardine (a) and anchovy (b).

Table 3
Estimates of monthly fishing mortality for common sardine and anchovy in the central-southern area off Chile

Month	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
Common sardine										
January	–	0.075	0.172	0.058	0.151	0.058	0.158	0.171	0.095	0.347
February	–	0.081	0.137	0.080	0.164	0.031	0.156	0.114	0.042	0.366
March	–	0.136	0.117	0.036	0.147	0.016	0.107	0.196	0.043	0.405
April	–	0.075	0.064	0.053	0.065	0.004	0.051	0.122	0.039	0.345
May	–	0.014	0.011	0.018	0.017	0.008	0.026	0.118	0.065	0.597
June	–	0.014	0.001	0.002	0.039	0.001	0.026	0.047	0.107	0.359
July	0.014	0.009	0.028	0.006	0.022	0.003	0.037	0.030	0.050	0.170
August	0.019	0.024	0.012	0.008	0.032	0.002	0.023	0.037	0.124	0.000
September	0.015	0.013	0.008	0.006	0.011	0.017	0.068	0.068	0.051	0.058
October	0.022	0.045	0.008	0.009	0.096	0.088	0.085	0.047	0.056	0.404
November	0.023	0.044	0.041	0.059	0.106	0.016	0.028	0.030	0.094	0.179
December	0.039	0.066	0.049	0.085	0.074	0.156	0.080	0.000	0.019	–
Annual	0.133	0.595	0.648	0.420	0.923	0.401	0.845	0.980	0.784	3.231
Anchovy										
January	–	0.051	0.044	0.018	0.026	0.044	0.029	0.036	0.025	0.032
February	–	0.090	0.053	0.031	0.054	0.059	0.024	0.032	0.039	0.111
March	–	0.067	0.090	0.025	0.124	0.020	0.052	0.122	0.051	0.215
April	–	0.035	0.052	0.019	0.041	0.010	0.019	0.064	0.052	0.192
May	–	0.007	0.004	0.012	0.024	0.011	0.008	0.034	0.031	0.305
June	–	0.005	0.000	0.002	0.019	0.005	0.008	0.009	0.039	0.178
July	–	0.005	0.018	0.006	0.009	0.007	0.006	0.004	0.024	0.037
August	–	0.008	0.009	0.003	0.030	0.000	0.017	0.003	0.023	0.000
September	–	0.005	0.004	0.002	0.010	0.010	0.063	0.003	0.047	0.058
October	–	0.008	0.001	0.002	0.030	0.010	0.054	0.005	0.044	0.207
November	–	0.022	0.007	0.012	0.018	0.003	0.005	0.007	0.034	0.080
December	–	0.023	0.016	0.014	0.031	0.010	0.002	0.000	0.006	
Annual	–	0.326	0.298	0.146	0.416	0.188	0.288	0.319	0.416	1.415

common sardine, the annual fishing mortality fluctuated between 0.4 in 1995 and 3.2 in 1999. A similar trend was observed for anchovy, with the peak in 1999 (Fig. 12).
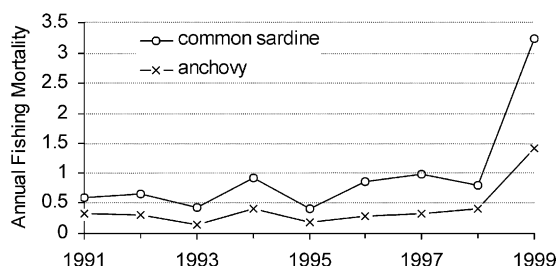

Fig. 12. Annual changes in the fishing mortality rate of common sardine and anchovy in central-southern Chile.

4. Discussion

Virtual population analysis is a standard method to estimate the abundance of fish stock (Gulland, 1965; Hilborn and Walters, 1992; Quinn and Deriso, 1999), but can be applied only if natural mortality and age composition of catches are known. Incorrect parameters might result in biased estimation of abundance (Ulltang, 1977; Sims, 1982, 1984; Hilden, 1988).

In this study, age composition was determined by analyzing length–frequency data in detail. Length–frequency analysis is considered reliable in fast-growing and short-life species, with a single reproductive season within the annual cycle. This is the case for common sardine and anchovy, where the progression of modes in length–frequency data can be followed easily after recruitment (Cubillos et al., 2001).

Furthermore, the effect of sample size can be considered negligible because a sufficient number of samples are obtained routinely from the fishery.

Cubillos et al. (2001) found similar growth regularity in both species. The notable similarity in the growth pattern of different cohorts is a consequence of the influence of seasonal upwelling in the life cycle of these small pelagics. According to the authors, the fastest growth rate during spring (October–November, Southern Hemisphere) is related to the productivity in the coastal waters as a consequence of upwelling events. In turn, the slowest winter growth rate may be related to the re-allocation of energy in the reproductive condition of the individual during July–September.

We used a constant natural mortality rate (M) for both species. Incorrect specification of natural mortality leads to incorrect trends in abundance and fishing mortality (Bradford and Peterman, 1989). Furthermore, the relationship between recruitment and oceanographic variables can be incorrectly determined when M is mis-specified (Lapointe and Peterman, 1991). However, natural mortality can be affected by many biological and environmental factors, and is hard to estimate accurately. We considered that the values used are consistent with the life-history parameters of the species because empirical models were used in the estimation (growth, maturity and longevity, see Cubillos et al., 1998b). However, numerous predators consume common sardine and anchovy in the central-southern Chile, particularly the hake (*Merluccius gayi*, Arancibia and Fuentealba, 1993), other fish, marine mammals and birds (Serra et al., 1979). Since natural mortality is an essential factor in stock assessment, it will be necessary to take into account the mortality by predation of these small pelagics. In the mean time, the M used for common sardine and anchovy can be considered adequate.

We did not use the annual age composition to carry out stock assessment on yearly time-scale due to the low number of age groups. Indeed, the convergence of fishing mortality across age classes could be affected in a virtual population analysis when applied to a small number of age classes. Furthermore, the fishery is highly seasonal and the assumption of a uniform fishing mortality within the year could bias the annual estimates of abundance (Sims, 1982). In this way, monthly estimation of cohort abundance can be con-

sidered better than an annual virtual population analysis, because the seasonal changes in fishing effort, catches and seasonal growth of the species are fully incorporated in the estimation of abundance. In addition, errors in terminal abundance should have less impact on recruitment due to the convergence of equations when working backward across monthly intervals covering at least 3 years for each cohort.

A cohort analysis requires good initial values of the terminal fishing mortality rate or the terminal abundance of the cohorts. Incorrect parameters might result in biased estimation of the abundance, so we used a formal statistical method of minimization estimation. This is an ADAPT (shorthand of "adaptive framework") approach of including auxiliary information into cohort analysis or VPA (Gavaris, 1988; Restrepo et al., 1992; Quinn and Deriso, 1999). In this approach, we assumed that error is only in the auxiliary indices (i.e. CPUE data), and therefore the trend in abundance are similar to the changes in CPUE or fishing effort. However, if other indices of abundance were available, they could easily be included in the estimation process. Unfortunately, the only relative abundance index available was CPUE.

It should be mentioned that CPUE may have several limitations as a relative abundance index (Gulland, 1974). In schooling pelagic fish species, the coefficient of catchability can vary inversely with the stock biomass (Csirke, 1988, 1989; Patterson et al., 1993; Fréon and Misund, 1999). We tested the hypothesis of a density-dependent catchability, and the results were not significant for anchovy. However, there is some indication that sardine biomass may have fallen to levels where there is some significant sign of density-dependence of catchability.

The estimation of absolute abundance of common sardine and anchovy in the central-southern area off Chile has not been attempted before on a monthly time-scale. In this way, the stock biomass of common sardine presented a declining trend in the last 2 years, while the fishing effort was growing. At present, the stock can be considered to be overfished, because the growing trend in the fishing effort would not be compensated by the productivity of the stock. The fishery is heavy dependent on the yearly pulse of recruitment, and growth overfishing is occurring. In the case of anchovy, the biomass of the stock was higher between 1998 and 1999 due to the occurrence

of two stronger year-classes. However, the perspectives for anchovy are far from certain, because recruitment would be lower in the short-term. In this way, although the status of the anchovy is better than the common sardine population, the productivity of anchovy would not compensate the growing trend in fishing effort. The growing trend in fishing effort is related to the status of the jack mackerel, *Trachurus symmetricus murphyi*, fishery. In fact, the jack mackerel fishery has been heavily regulated, because a high incidence of juveniles in the catches occurred between 1997 and 1999 (Arcos et al., 2001), and the industrial seiners had been oriented to fishing for common sardine and anchovy.

The advantage of the age-structured approach here developed is that the changes in recruitment have been estimated. The dynamics of the two species depends on the yearly pulse of recruitment, and it was observed that when recruitment of common sardine tend to be low, the recruitment of anchovy tend to be higher. Although the relationship between recruitment of the species was not statistically significant (may be due to the short time series), several hypotheses could be postulated if the abundance of year-classes of anchovy and common sardine are fluctuating inversely, particularly a probable interspecific competition (MacCall, 1983). However, in the catch history, a replacement between species is not observed, but the fluctuation in abundance of both species seems similar under different regimes of high or low abundance (Fig. 2). The competition hypothesis is difficult to test, but it has been postulated when analyzing the changes in abundance of the complex ''sardine–anchovy'' (Daan, 1980; Pauly, 1987; Serra and Tsukayama, 1988), as well as for other small pelagics (e.g. Cury and Fontana, 1988).

It is probable that the tendency of recruitment to vary inversely between sardine and anchovy can be related to the environmental variability during the reproductive season. Fonseca et al. (1986) found that an increased relative abundance of both species in a given year was related to warmer conditions in spring of the previous year. However, after years excessively warm and related to the El Niño, the abundance was lower. In the current study, the recruitment of the 1997 cohort of common sardine was the lowest in the 1990s, and probably related to the 1997–1998 El Niño event. In this context, the interannual climate variability and associated environmental changes would have profound effects on the species and the fishery. These aspects should not be overlooked, but more effort is needed to analyze the population dynamics of sardine and anchovy in the central-southern area off Chile, and the estimates of abundance here obtained are a starting point.

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