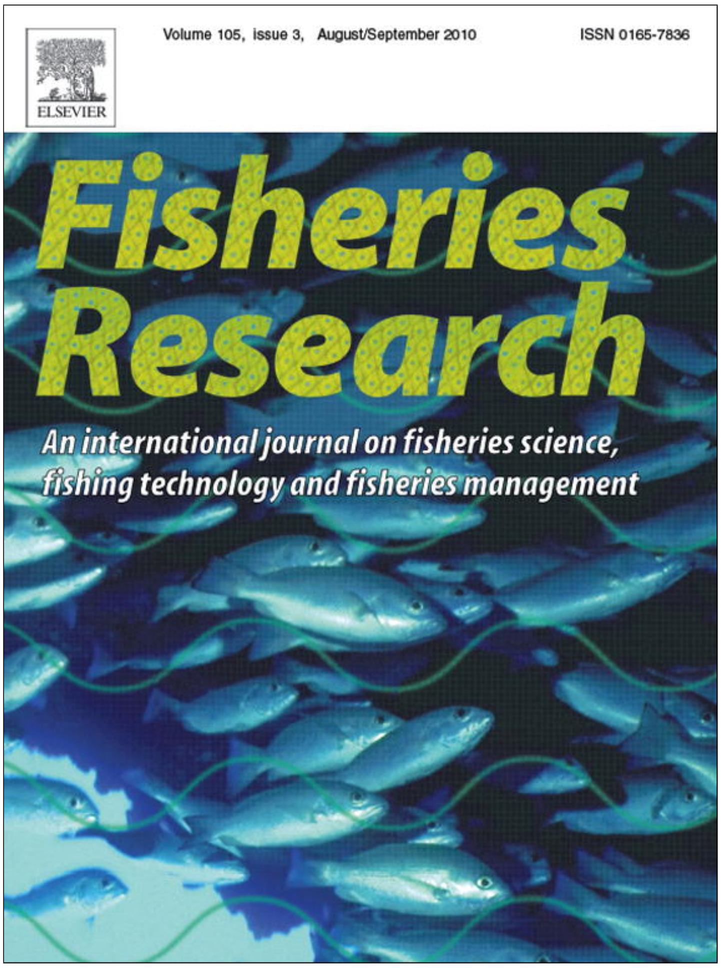
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Inter-cohort growth rate changes of common sardine (*Strangomera bentincki*) and their relationship with environmental conditions off central southern Chile

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ABSTRACT

The inter-cohort variability in the von Bertalanffy (VB) growth parameters of common sardine (*Strangomera bentincki*) was analyzed for the period between 1990 and 2007. Time series of monthly length–frequency data were used to study the growth of the species. The MIX software was used to separate normal components and modal progression analysis was used to identify cohorts that have recruited each year. The VB growth parameters were estimated using nonlinear mixed-effects model (NLME) by considering that the population growth parameters have a common distribution, and that cohort-specific parameters can be treated as random effects. A model that considered L_∞ (asymptotic length) and K (growth coefficient) as random effects was the best in explaining inter-cohort changes in body growth. The growth rate during the first fast-growing period of sardine cohorts exhibited a significant change after 1998. Cohorts recruited between 1990 and 1997 showed higher growth rates than cohorts recruited from 1999 to 2006. This significant change is coincident with a colder period established in the area after 1998, and with a significant increment in the Ekman transport. Sea surface temperature anomalies explained 46.2% of the variability observed in the early growth rate of the cohorts. It is concluded that environmental conditions encountered by the cohorts during the spawning period could modulate the growth rate of common sardine year to year, but the possibility of further intrinsic factors affecting the growth dynamics of common sardine could be also important and deserve to be considered in future studies.

1. Introduction

The variability in growth of marine fish, particularly in terms of changes in size at age, has been attributed to many factors, and can be classified into external factors (e.g. temperature, food, oxygen) or intrinsic factors (e.g. density-dependence, reproduction, size-selectivity mortality), or to combined effects of external and intrinsic factors (Sinclair et al., 2002; Swain et al., 2003; Brander et al., 2003; Watanabe and Yatsu, 2004; Mello and Rose, 2005; Kim et al., 2006; Martins, 2007). Also, geographic differences in growth rates over broad spatial scales have been used to identify growth patterns to infer size-specific migrations or stock structure (Begg, 2005; Silva et al., 2008).

It is known that somatic growth rate of fish is affected by temperature and food abundance (Brett, 1979). Usually growth studies are based on an aggregation of several cohorts, and the cohort effect on growth is often avoided. The cohort or year-class effect may be important when comparing growth curves (Dawson, 1986), and it cannot be detected when analyzing aggregated data (Martins, 2007). In fact, if a cohort experiences a significant increment in temperature, then it is expected that the growth rate of the cohort likely exhibits an increase, and vice versa (Brander, 1995; Dutil et al., 1999; Brander et al., 2003). Since individuals are originated under different environmental conditions, the growth rate during the early phase of a cohort could be expected to be determined during the spawning season (Ito et al., 2007; Mukai et al., 2007) and/or first period of enhancing food availability and the environmental conditions prevailing in the nursery habitat (e.g. Watanabe and Yatsu, 2004). Although the optimum temperature for growth declines as

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food ration declines (Woiwode and Adleman, 1991), generally a positive relationship between temperature and growth has been reported in most studies. Temperature can account a great fraction of the changes in length-at-age among North Atlantic cod (*Gadus morhua*) (Brander, 1995). However, effects on growth attributed to temperature may result to be spurious because the multiple interactions between temperature and other possible causal factors (Sinclair et al., 2002).

The common sardine (*Strangomera bentincki*) is a commercially important resource for both industrial and small-scale fisheries operating off central southern Chile (Cubillos et al., 1998), with catches that have fluctuated between 126,000 and 761,000 t in the period 2000–2007. The species is targeted by purse-seine gears, and in 2008 the landings of this species contributed with around 20% of the total fish landed in Chile. As other clupeids, common sardine is a fast growing species with relatively short life-span (~4 years; Aguayo and Soto, 1978; Cubillos et al., 2001), early maturation at the end of the first year of life (Cubillos et al., 1999), multiple spawner with indeterminate fecundity (Cubillos et al., 2007), and higher natural mortality rate (Cubillos et al., 2002). This small pelagic fish inhabits a highly productive environment (Daneri et al., 2000) due to the seasonal occurrence of upwelling events from middle September to March (austral spring–summer) (Arcos and Navarro, 1986; Sobarzo et al., 2007).

The growth in length of common sardine have been studied by reading annuli on whole otoliths (Aguayo and Soto, 1978), and also by detailed analysis of length–frequency data by Cubillos et al. (2001). The last authors have found a seasonal oscillation in the length growth rate, hypothesizing that the seasonal growth rate is a consequence of the reproductive strategy of this species to the seasonal upwelling. In addition, the reproductive strategy of common sardine is combined with an “energy storage strategy” during the upwelling period (September–March). The stored energy is metabolized for reproduction later, during the next Austral winter (July–August) when onshore transport (Sobarzo et al., 2007) increases coastal retention of eggs. In this way, the re-allocation of energy likely produces the seasonal fluctuation in the growth rate. Although the interannual variation in the mean length-at-age of different cohorts of common sardine have been low (Cubillos et al., 2001), it is probable that environmental changes could affect the growth rate of this species during the first growth phase in spring and summer (October–March), particularly when El Niño-Southern Oscillation events are impacting in the habitat of the species (Cubillos and Arcos, 2002). To do this, it is necessary to adequately estimate cohort-specific growth parameters before linking the growth changes to an environmental signal.

The objective of this paper is to investigate the inter-cohort body growth changes of common sardine and to determine the relationship with environmental conditions occurring during the first growth phase in spring and summer. The von Bertalanffy growth parameters of common sardine were estimated for cohorts recruited during the period 1990–2006. The length-at-age data used here come from length–frequency data in which the growth of the cohorts was identified, and updating the data reported by Cubillos et al. (2001, 2002). It was assumed that growth parameters of different cohorts come from a common distribution as random effects rather than treating growth parameters as cohort-specific values to be separately estimated. In statistical terms, nonlinear mixed-effects (NLME; Pinheiro and Bates, 2000) modeling provides a statistical framework for analyzing population growth parameters and the associated inter-cohort variations, even when individual cohort data sets are incomplete. Finally, interannual growth changes in the growth rate during the first growth period in spring are related with sea surface temperature, upwelling index, and chlorophyll-*a*.

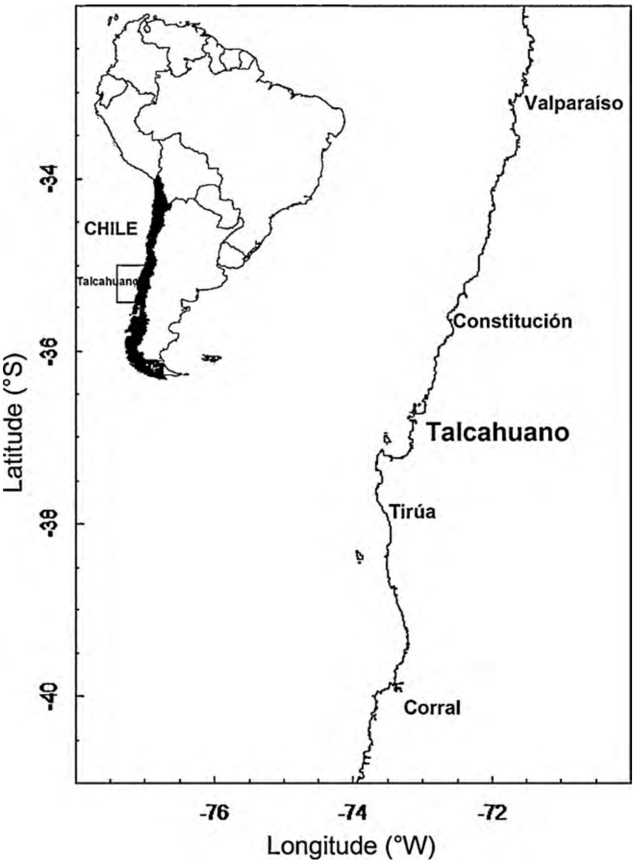

Fig. 1. Study area located off central southern Chile (33–40°S).

2. Materials and methods

2.1. Study area and data

The study area is located off central southern Chile (33–40°S), and the study covered the period from 1990 to 2007. During this period, length–frequency data have been collected from the fishery of common sardine in the main landings port, such as Talcahuano and Corral (Fig. 1). Each length–frequency data set corresponds to monthly summaries of random samples obtained from the catch of vessels operating in the fishery. Body size was measured as total length (TL) to the nearest 0.5 cm. Sampling details are described by Cubillos et al. (2001, 2002), and the number of fish that have been measured are shown in Table 1. Suitable monthly sample sizes were available for almost all the period under analysis.

Monthly time series of sea surface temperature and winds were constructed for the study area (34–40°S, Fig. 1), from January 1992 to December 2007. Instead, for chlorophyll-*a* the time series covered the period from September 1997 to December 2007. Time series of sea surface temperature anomalies (SSTA) were obtained from IRI/LDEO Climate Data Library (IGOSS, http://ingrid.ldeo.columbia.edu/) by considering a resolution of $1^\circ \times 1^\circ$. Wind data were obtained from ERS and QUIKSCAT (http://ifremer.fr/). In the case of wind data, the ERS-2 of mean wind product was used. This product had a spatial resolution of $1^\circ \times 1^\circ$ and a weekly temporal resolution. Instead, winds obtained from QuikScat had a spatial resolution of $0.25^\circ \times 0.25^\circ$ on a daily basis. The difference in the spatial resolution was resolved by interpolation of QuikScat data to obtain a resolution of $1^\circ \times 1^\circ$ on a weekly basis comparable to the ERS-2 data. In the case of chlorophyll-*a*, data correspond to daily Global Area Coverage SeaWiFS for the period 1997–2007, and obtained from the oceancolor

Table 1
Number of fish measured, mean and minimum–maximum length for *Strangomera bentincki* samples.

	January	February	March	April	May	June	July	August	September	October	November	December
1990												
n	–	–	–	–	–	–	1052	415	171	382	270	913
Mean	–	–	–	–	–	–	14.64	14.66	13.23	14.54	14.26	9.22
Min–max	–	–	–	–	–	–	8.5–17.5	10.5–17.5	9.0–17.0	11.5–17.5	9.5–17.5	3.0–17.0
1991												
n	2599	2043	2129	1863	783	1785	2520	2595	1803	3110	1994	2225
Mean	10.16	10.00	9.23	8.74	8.34	8.80	9.04	12.08	10.18	11.79	11.04	7.53
Min–max	4.0–18.0	5.5–17.5	5.0–17.0	5.0–18.0	4.5–15.5	5.0–17.0	5.0–16.0	5.5–19.0	7.0–16.5	4.5–17.5	5.0–17.5	3.5–17.5
1992												
n	2182	1922	1049	615	640	278	389	116	427	370	1086	808
Mean	8.67	8.65	9.40	10.72	11.17	10.38	12.62	11.82	13.75	13.35	6.36	6.20
Min–max	4.5–17.0	5.0–15.5	5.5–15.0	7.5–15.0	8.0–16.0	7.5–16.5	5.0–16.5	6.0–15.5	10.0–17.5	10.5–17.0	3.0–15.0	3.5–10.0
1993												
n	973	450	340	183	472	169	1048	966	642	839	2183	1129
Mean	7.99	8.25	9.95	11.96	10.09	11.27	10.13	7.62	10.35	7.49	5.62	7.22
Min–max	4.5–10.5	6.0–11.5	6.5–15.5	8.5–16.0	4.5–16.0	6.0–15.5	4.5–16.0	5.0–15.5	5.0–15.5	4.0–14.5	3.0–14.5	4.5–12.0
1994												
n	1479	677	71	246	338	851	852	842	455	1487	1795	1791
Mean	9.26	9.78	11.65	10.52	10.38	9.99	10.81	10.62	11.39	12.72	9.28	7.67
Min–max	5.5–14.5	7.0–14.5	9.0–15.0	7.5–15.5	7.5–13	7.5–17.0	7.5–15.5	8.5–15.5	5.5–14.5	4.5–16.0	4.0–16.0	4.0–15.5
1995												
n	1101	963	2757	1024	1994	617	1267	1873	1462	3258	2006	5447
Mean	9.11	11.72	12.63	10.46	11.74	10.78	12.36	13.65	12.40	13.52	13.85	8.14
Min–max	6.0–14.5	8.0–16.0	7.5–15.5	6.0–15.5	4.5–16.0	5.0–16.5	5.0–16.5	5.5–16.5	6.0–15.5	7.5–16.0	5.0–16.0	4.0–17.0
1996												
n	5003	4767	4523	3487	2409	2579	2961	2408	2462	2624	1006	2971
Mean	8.94	8.78	8.95	9.71	10.58	9.16	11.45	9.79	13.16	12.04	11.07	6.77
Min–max	4.0–17.0	5.0–16.5	6.0–16.0	6.0–16.5	4.0–17.0	5.0–16.0	5.0–17.0	4.5–17.0	6.5–17.0	6.0–17.0	5.0–17.0	4.0–16.5
1997												
n	4610	3831	2427	2036	1970	1633	2325	1627	2538	2975	4041	–
Mean	9.26	9.86	11.15	11.87	12.02	13.02	13.08	13.82	13.06	12.97	12.52	–
Min–max	4.0–17.0	4.5–17.0	5.5–17.0	5.5–18.0	5.0–17.5	7.5–17.5	8.0–17.0	8.5–17.5	7.0–17.5	5.0–17.5	4.0–17.0	–
1998												
n	4483	1636	1234	1450	1171	1282	301	2053	616	664	1737	1135
Mean	9.25	11.61	13.63	12.32	13.20	13.55	14.33	13.64	13.96	13.12	6.27	8.28
Min–max	4.5–17.0	7.0–17.0	7.5–18.0	6.5–16.0	9.0–16.5	6.5–17.0	8.5–17.5	9.5–17.0	7.5–17.0	8.5–16.5	4.0–16.5	5.0–17.0
1999												
n	5563	3989	3036	2541	2892	2025	1091	2049	1498	1513	1179	498
Mean	8.03	9.93	10.45	10.68	11.12	11.52	13.42	11.74	12.61	12.71	11.61	5.89
Min–max	4.0–15.5	4.5–16.5	5.0–17.0	7.5–16.5	8.0–17.0	8.5–17.0	8.0–17.5	8.5–16.5	6.0–17.0	7.0–18.0	5.5–16.5	5.0–12.0
2000												
n	4530	6162	2673	1715	1699	118	363	–	1285	1150	367	368
Mean	7.52	8.36	9.01	10.00	10.62	11.28	11.04	–	12.01	12.23	8.41	5.29
Min–max	4.0–16.0	4.0–18.0	6.5–17.5	6.0–16.5	7.5–16.5	9.0–15.0	4.5–18.0	–	5.5–16.0	6.5–16.0	5.0–17.5	3.5–7.0

Table 1 (*Continued*)

	January	February	March	April	May	June	July	August	September	October	November	December
2001												
n	6283	3442	4228	1876	356	530	–	–	1176	2027	227	–
Mean	7.43	7.31	8.84	8.94	9.14	9.95	–	–	9.70	13.11	11.83	–
Min–max	3.0–14.5	4.0–13.0	5.0–13.0	5.0–15.5	6.0–14.0	7.0–13.5	–	–	6.0–15.5	6.0–16.0	8.5–15.5	–
2002												
n	2934	4593	1896	741	370	287	147	–	899	–	–	–
Mean	7.78	7.97	8.46	9.25	8.81	9.13	8.62	–	12.31	–	–	–
Min–max	5.0–15.5	5.5–15.0	6.0–13.5	7.0–15.5	7.0–15.5	7.5–14.0	5.0–15.0	–	7.0–16.5	–	–	–
2003												
n	1124	3583	1282	689	378	84	117	–	398	–	414	883
Mean	7.40	7.53	7.82	8.15	8.96	8.48	7.76	–	10.17	–	6.40	6.39
Min–max	4.0–10.5	4.5–13.0	4.5–16.5	5.0–13.5	5.5–11.5	5.0–12.0	5.5–12.0	–	6.0–16.0	–	5.0–12.5	4.5–11.0
2004												
n	–	2980	785	653	189	–	–	1988	4110	87	344	282
Mean	–	7.97	11.37	12.06	10.89	–	–	11.03	11.03	12.61	5.90	5.46
Min–max	–	5.0–13.5	7.5–14.5	7.5–15.5	7.5–14.0	–	–	7.5–17.0	7.0–16.5	10.5–14.5	5.0–11.5	4.5–9.0
2005												
n	–	1909	2151	1229	122	457	87	3291	4126	1166	500	200
Mean	–	9.93	10.59	10.61	11.56	9.35	11.17	10.97	11.13	12.88	6.87	7.11
Min–max	–	5.5–17.5	6.0–16.5	7.0–13.0	9.0–14.0	6.0–14.5	6.5–15.0	7.0–17.5	7.0–16.5	7.5–16.5	5.0–15.5	4.0–13.5
2006												
n	2200	7078	10,051	2853	478	374	–	–	3987	7906	6900	191
Mean	6.91	7.38	8.48	8.55	8.95	9.72	–	–	10.40	11.18	7.11	12.73
Min–max	3.0–16.0	3.0–14.5	4.5–16.5	5.0–15.5	6.5–13.5	6.5–14.0	–	–	7.0–16.5	6.0–16.5	3.0–16.0	10.5–15.0
2007												
n	–	10,904	17,816	3733	2862	2679	3093	2086	4424	10,433	11,247	3911
Mean	–	11.04	11.65	12.70	12.85	11.04	12.38	12.42	13.73	13.62	11.91	12.72
Min–max	–	5.5–17.0	5.5–16.5	6.5–18.0	7.0–16.5	7.0–15.0	8.0–17.5	6.5–17.5	6.5–17.0	4.5–18.0	4.5–17.5	4.0–17.0

web site (http://oceancolor.gsfc.nasa.gov/ftp.html). Gaps in this data were caused by stratocumulus interference with satellite sensor, and were filled with three-dimensional kriging using a grid of 9 km × 9 km and 24 h of temporal resolution. The kriging was set with a search radius of 63 km and 7 days since the clouds interference in the region allows three images with over 50% area clouds free per week (Correa-Ramirez et al., 2007). Values of chlorophyll-*a* higher than a threshold of 0.1 mg m^{-3} and restricted to the shoreline were used to compute monthly average from daily values. The threshold of 0.1 mg m^{-3} is representative of values close to the most coastal distribution, and was considered as a proxy of the phytoplankton biomass available as food for common sardine.

2.2. Growth

Cubillos et al. (2001, 2002) analyzed the length–frequency data for the period between July 1990 and November 1999, and the data generated here must be considered an update of the previous results. The same methodology was used to analyze the length–frequency data. In fact, each monthly length–frequency data set was analyzed using the computer software MIX (MacDonald and Green, 1988). MIX considers a length–frequency data as a mixture of probability density functions (*pdf*), and uses maximum likelihood estimation to find unknown parameters describing each *pdf* in the mixture (MacDonald and Pitcher, 1979). We assumed length-at-age to have a normal *pdf* in the mixture. Thus, the parameters to be estimated were the total number of ages present in the mixture, times three parameters describing each normal *pdf*, i.e. the proportion in the mixture (p), the mean length (μ) and the standard deviation (σ) of length at age. The number of ages of the histogram by visual analysis, while parameters were estimated without constraints using maximum likelihoods according to MacDonald and Pitcher (1979), excepting few cases in which the standard deviation of length at age were constrained to be constant.

Once the mean, standard deviation and proportion of ages were estimated from each monthly length–frequency data, the growth of a cohort was 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 were linked (MacDonald and Green, 1988). Then, relative ages (in months) were assigned to the mean lengths belonging to each of the cohorts by considering July 1 as a fixed birthday date. This assumption was done because spawning season begins in July and extends until September (MacDonald and Pitcher, 1979; Arancibia et al., 1994; Cubillos et al., 1999). The age in months was transformed to years by dividing age in months by 12. The mean length-at-age data were used to estimate the parameters of the von Bertalanffy growth function modified by Somers (1988) to take into account seasonal growth, i.e.

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

where L_t is the mean length at age t (month as fraction of year), L_∞ the asymptotic length (cm), K is the growth coefficient (per year), t_0 is the hypothetical starting time at zero length if the adult and juveniles growth curve could be extrapolated back to the origin, C is a dimensionless constant expressing the amplitude of a growth oscillation and t_s is the age at onset (with reference to $t=0$) of a growth oscillation of period 1 year. Both parameters, C and t_s, should be in the interval [0,1]. When $C=0$, the growth is continuous, without seasonal oscillation; while $C=1$ implies a complete detention in the growth at some moment of the year. With practical purposes, the t_s parameter 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.

2.3. Inter-cohort variation in growth parameters

The growth parameters were estimated for each cohort recruited between 1990 and 2006 using nonlinear mixed-effects models because the parameters from specific cohorts come from noisy or incomplete measurements. The 'nlme' library of Pinheiro and Bates (2000) for the language and software R was used (Ihaka and Gentleman, 1996; http://cran.es.r-project.org/). Growth follows a seasonally oscillating von Bertalanffy growth curve by considering that: (a) L_∞, t_0, C and WP are the same for all cohorts in the population while the growth coefficient (K) differs among cohorts as a random effect; (b) K, t_0, C and WP are the same for all cohorts in the population while the asymptotic length (L_∞) differs among cohorts; and (c) both L_∞ and K are random while t_0, C and WP are the same for all cohorts in the population. The best model was chosen by examining the Akaike Information Criteria (AIC) (Akaike, 1974).

2.4. Linking growth rate to environmental variables

Once the best model was selected, the growth rate during the first fast growth period was computed according with the following expression (Roa and Tapia, 1998):

$$G = K\left(L_{\infty,i} - \frac{L_2^2 - L_1^2}{2(L_2 - L_1)}\right) \qquad (2)$$

where G is the average growth rate (cm year^{-1}) for ith cohort, L_1 and L_2 are the lower and upper length. The lower length (L_1) was estimated at November (age = 4 months) and L_2 was estimated at March (age = 8 months) for each cohort. Finally, K and L_∞ are the von Bertalanffy growth parameters, previously defined.

The wind stress was computed according with the algorithm of Large and Pond (1981), and the zonal Ekman transport (Ek) was computed using the local wind stress, i.e.

$$\text{Ek} = \frac{\tau_y}{f\rho} \qquad (3)$$

where τ_y is the local wind stress (Pa), f is the Coriolis parameter (per second), and ρ is the water density (1025 kg m^{-3}).

Since individuals are originated under different environmental conditions, the growth rate of a cohort could be determined during the spawning period or during the first period of enhancing food availability. With the aim of relating changes in G to environmental conditions, environmental variables were averaged for the spawning period, from July to September. Also, sea surface temperature anomalies (SSTA) and upwelling index were averaged for the first-growth period experienced by the cohorts, i.e. from October to March. Instead, the period October to December was considered for chlorophyll-*a*. In looking for significant relationships between the growth rate and environmental variables, ordinary linear regression analysis were carried out and tested through the significance of the coefficient of determination.

3. Results

3.1. Growth parameters

The mean lengths at age, as estimated by MIX, for the cohorts of common sardine during the period 1990–2007 are shown in Fig. 2, and the growth in length obtained for the entire data set is shown in Fig. 3. A notable regularity in the growth process of all cohorts can be observed, with the slowest length growth rate occurring between April and May, just before the austral winter.

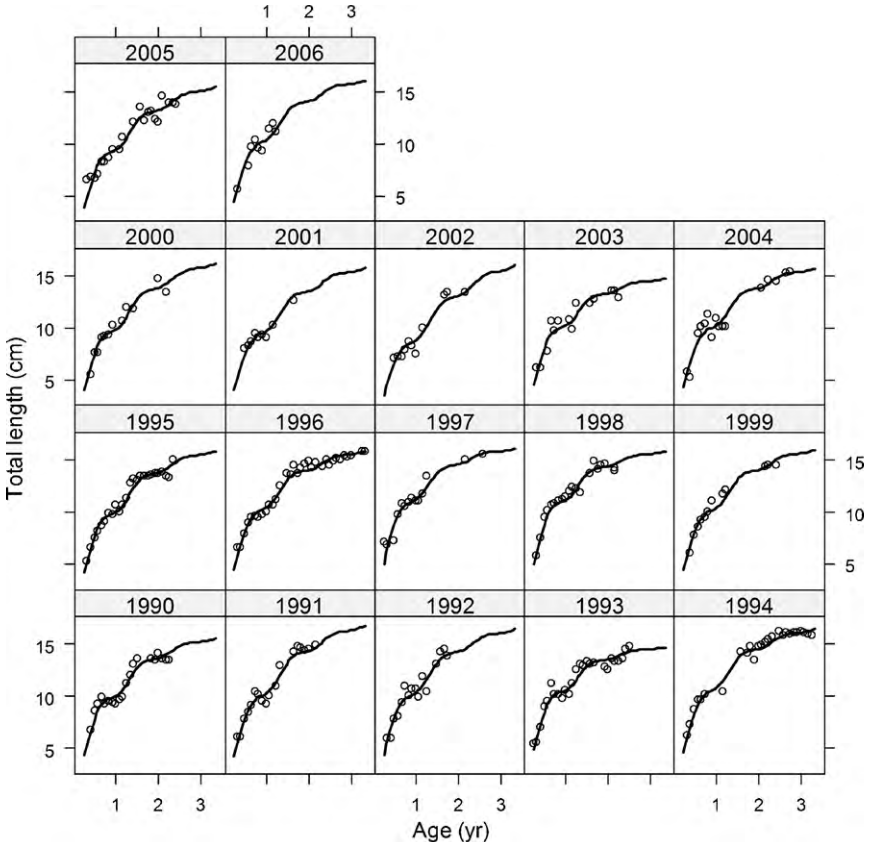

Fig. 2. Seasonally oscillating growth curve fitted for NLME whit the growth coefficient (K) and the asymptotic length (L_∞) as random parameters, and observed length-at-age data for the cohorts 1990–2006 of *Strangomera bentincki* off central southern Chile.

In terms of the growth parameters estimated with nonlinear mixed-effects models, and according with the AIC, the model that considered both L_∞ and K as random effects was chosen (Tables 2 and 3). It must be mentioned that neither the amplitude nor the phase of the oscillating growth was significant effects on the growth variability of the cohorts. The von Bertalanffy growth parameters (L_∞ and K) obtained for each cohort is shown in Table 3, observing higher values for K in 1993, 1997–1998, and 2003. Instead, lower K values were obtained for 1991, 1995, 2000–2001, and 2005. For the asymptotic length, lower values were obtained for 1993 and 2003 and higher values for 1992 and 2002.

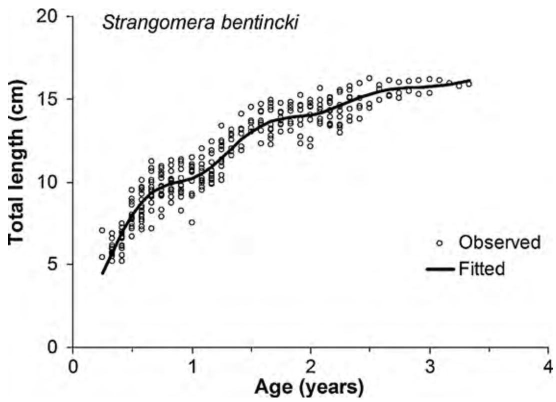

Fig. 3. Seasonally oscillating growth curve fitted to the observed length-at-age data of all cohorts of *Strangomera bentincki* off central southern Chile in the period 1990–2007.

3.2. Linking growth rate to environmental conditions

The changes in the growth rate, between March and November, for cohorts of sardine that have recruited between 1990 and 2006 are shown in Fig. 4a. To explore whether the growth rate of a cohort is determined during the spawning period or during the first period of enhancing food availability, the changes in growth rate are compared with annual changes in sea surface temperature anomalies (SSTA, Fig. 4b), Ekman transport (Ek, Fig. 4c), and Chlorophyll-*a* (Ch-a, Fig. 4d), for the spawning period (July–September) and for the first fast growing period (October–March).

The higher growth rate of sardine occurred for the cohorts of 1997 and 1998, and the lowest for the cohort of 2002. On average, the growth rate of sardine was higher for the cohorts recruited between 1990 and 1997 ($\bar{G} = 8.7\,\text{cm year}^{-1}$, $\text{Var}(G) = 0.32$, $n = 8$), and lower for the cohorts of 1999–2006 ($\bar{G} = 7.8\,\text{cm year}^{-1}$, $\text{Var}(G) = 0.39$, $n = 8$). The difference in the average growth rate was significant ($p = 0.018$, t-test for comparison of two mean), with the lowest G value occurring after 1998. This change in the growth rate of sardine is coincident with the persistent negative anomalies observed in the SSTA after 1998 (Fig. 4a), and also in the

Table 2
Selection of NLME models used for analyzing inter-cohort variability in the von Bertalanffy growth parameters of *Strangomera bentincki* off central southern Chile.

Model	Random effects	DF	Log-*L*	AIC
1	L_∞ and K	9	−304.10	626.21
2	K	7	−313.21	640.43
3	L_∞	7	−318.36	650.71
4	t_s	7	−334.28	682.56
5	t_0	7	−359.51	733.02
6	C	7	−359.51	733.02

Table 3
Growth parameters obtained with NLME for *Strangomera bentincki* as fitted to the von Bertalanffy growth function of all cohorts off central Chile, cohorts of 1990–2007.

Fixed effects	Value	Std. error	DF	*t*-Value	*p*-Value
L_∞	16.860	0.378	281	44.656	0
K	0.838	0.056	281	15.027	0
t_0	−0.305	0.045	281	−6.842	0
C	0.704	0.066	281	10.692	0
t_s	0.391	0.017	281	23.285	0
Random effects		Std. dev.			Correlation
L_∞		1.074			L_∞
K		0.139			−0.861
Residual		0.597			
Level: cohort		L_∞ (cm)			K (per year)
1990		16.4			0.843
1991		18.2			0.734
1992		17.5			0.789
1993		15.0			1.082
1994		17.3			0.862
1995		16.9			0.797
1996		16.7			0.866
1997		16.6			0.995
1998		16.2			1.027
1999		16.8			0.842
2000		17.6			0.729
2001		17.1			0.738
2002		18.7			0.566
2003		15.2			0.984
2004		16.7			0.843
2005		16.8			0.731
2006		17.1			0.823

change observed in the Ekman transport (Fig. 4b). Unfortunately, the chlorophyll-*a* time series only started in 1997 (Fig. 4c), and changes in this variable cannot be inferred.

The SSTA have similar fluctuations between the spawning period (July–September) and the first growth phase (October–March), excepting in 1998 in which conditions were rather warmer during the spawning period (Fig. 4b). The Ekman transport was lower and variable during the spawning period, and the chlorophyll-*a* was low and less variable during the spawning period (July–September).

During the spawning period (July–September), the growth rate was significant and positively related with SSTA (Table 4, Fig. 5a). Instead, the growth rate was not related with the Ekman transport neither with chlorophyll-*a* (Table 4). During the first fast growing phase, the inter-cohort changes in the growth rate were significant and negatively related with interannual changes in the Ekman transport. However, when the growth rate was related with the SSTA the relationship was not significant because the high growth rate of the 1998 cohort (Fig. 4a). In fact, only when this data-point (1998) was discarded from the regression, a positive and significant relationship between the growth rate and SSTA was found ($r^2 = 0.539$, Fig. 5b). Instead, the inter-cohort growth rate was not related with chlorophyll-*a* (Table 4).

Table 4
Coefficient of determination (r^2) between the early growth rate and the relationship with environmental variables during the spawning period (July–September) and during the first fast growing period (October–March) (***$p < 0.01$, **$p < 0.05$ and ns, non-significant).

Environmental variables	*G*	
	Spawning period	First fast growing period
SSTA	0.462*** ($n = 16$)	0.539*** ($n = 15$)
Ekman transport	0.117ns ($n = 15$)	0.279** ($n = 15$)
Ch-a	0.363ns ($n = 10$)	0.258ns ($n = 10$)

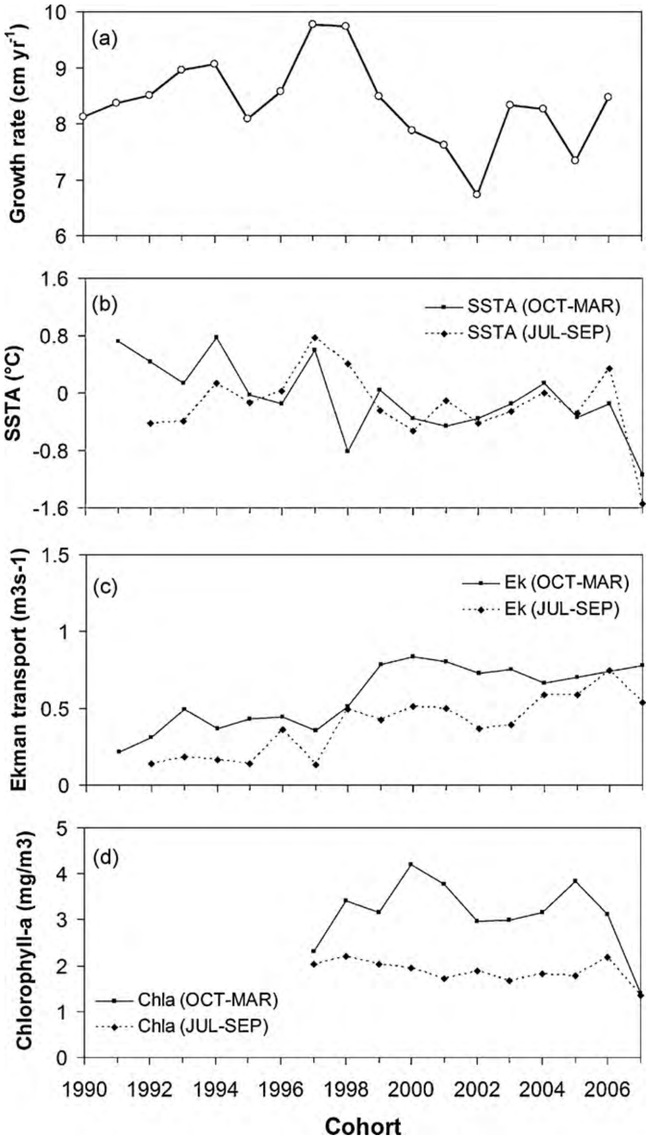

Fig. 4. Changes in the first fast-growth rate of the cohorts of *Strangomera bentincki* (a) and comparison with changes in the sea surface temperature anomalies (b), Ekman transport (c), and chlorophyll-*a* (d).

4. Discussion

The growth parameters of common sardine have been satisfactorily estimated on the basis of length–frequency data. Indeed, the modal progression analysis is better for fast growing fish with early recruitment, and particularly with one spawning peak per year, such as the case of common sardine. For all of the cohorts present in the study period, we found similar results to those obtained by Cubillos et al. (2001) for the period 1990–1997 (i.e. $L_\infty = 18.1$ cm, $K = 0.745$ year^{-1}, $t_0 = -0.330$ year, $C = 0.998$, $WP = 0.363$), excepting that we found a lower amplitude of the seasonal growth (see Table 3). Small differences could be due to the longer data set here analyzed, but the NLME results revealed that the seasonal growth parameters were not important in contributing to explain the inter-cohort growth variability.

According with Cubillos et al. (2001), average size-at-age of individuals born in different reproductive seasons had low interannual variation than intra-cohort variation. Nevertheless, the authors did not study the inter-cohort variability in growth parameters, or in the growth rate. Indeed, one of the main addresses of this paper was

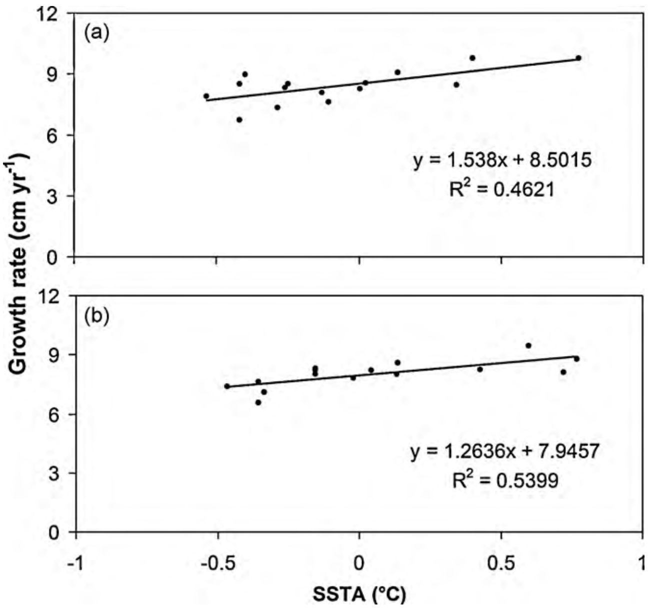

Fig. 5. Relationship between the growth rate and SSTA during spawning period (a) and during first fast growing phase (b).

how to estimate inter-cohort variability in von Bertalanffy growth parameters when data are incomplete or noisy for some cohorts. The advantages of NLME over the standard nonlinear (SNL) method are due to the assumption that growth parameters come from a distribution, as coming from a probability distribution with mean and variance to be estimated, i.e. as random effects. Instead the SNL method, although routinely used in growth studies (Roa and Ernst, 1996; Hernandez-Llamas and Ratkowsky, 2004; Silva et al., 2008), have the disadvantage that results could be affected by incomplete data or noise due to specific growth of cohorts or associated to errors related with length–frequency data analysis such as identifying older age groups (Cheung et al., 2008). Furthermore, the NLME has an advantage on the SNL method because we are assuming that the growth process of different cohorts is an average population process. This approach is similar to that suggested by Laslett et al. (2004), which consists of a two-stage procedure for fitting growth curves to length frequency data collected from commercial fisheries. Indeed, in the first stage length frequency distribution was decomposed into age groups using a Gaussian mixture model, while in the second stage the summary statistics for each cohort were used as raw data for growth modeling.

We might expect that some cohorts to growth faster (slower) than others, which was reflected in the asymptotic length and growth coefficient. Although there are some techniques to analyze directly the impact of environmental and density-dependent factors simultaneously in a growth model (Sinclair et al., 2002; Watanabe and Yatsu, 2004), our emphasis was to explore whether environmental variables, such as temperature, Ekman transport, and chlorophyll-*a* occurring during the spawning period or during the first fast growing phase were related with the changes in the inter-cohort growth variability detected. In this way, the inter-cohort growth rate of sardine during the spawning and the first-growth period was not related with chlorophyll-*a*, for cohorts 1997 onwards. If chlorophyll-*a* is considered a proxy for food availability then changes in growth rate could not be explained directly by food since zooplankton items are the main prey in stomach contents of larvae and juveniles of sardine off central southern Chile (Llanos et al., 1996; van der Lingen et al., 2009). One must bear in mind the short time series here used in looking for relationship with chlorophyll-*a*, and also that sometimes food availability is not a limiting factor in upwelling ecosystems. Furthermore, comparative studies on feeding of clupeoids are suggesting that the diet of most clupeoids in upwelling zones is primarily carnivorous in that most of their energy intake is derived from zooplankton (Cushing, 1978; James, 1988; James and Chiappa-Carrara, 1990; van der Lingen et al., 2009). In California, Fiedler et al. (1986) found that growth of juvenile and adults of northern anchovy (*Engraulis mordax*) decreased significantly during 1983, probably due to reduced availability of zooplankton prey. The authors discussed that the reduced growth rates of 1982 year-class fish adults, and juvenile fish during summer 1983 and summer 1984, were likely caused by El Niño's impact on the availability of appropriate zooplankton community during the 1982–1983 El Niño event. In the case of *Strangomera bentincki*, Arcos et al. (2004) found that residuals of length-at-age were significantly explained by SST during the first fast growth period of the cohorts, and the cohort generated during El Niño 1997–1998 reached larger size-at-age. This is consistent with our results since the 1997 and 1998 cohorts exhibited higher growth rates (Fig. 4a), reaching larger size-at-age. However, in 1998 the sea surface temperature anomalies were rather cold during the first fast-growth period (October 1998–March 1999) because environmental conditions were in transition toward the La Niña event of 1999. Instead, during the spawning period (July–September) sea surface temperatures were warmer and affected positively the growth rate of the 1998 cohort. In this way, perhaps cohorts of common sardine could be able to retain the growth from early life stages. A similar conclusion has been postulated for Pacific saury (*Cololabis saira*) by Ito et al. (2007) for the spring-spawned saury cohort to explain the differences of interannual growth variability between spawning seasons. In the case of common sardine, SSTA explained 46.2% of the variability observed in growth rate of cohorts during the spawning period. However, excepting the 1998 cohort, the SSTA during the first fast growing phase (October–March) explained almost 54% of the variability observed in the growth rate. In this way, environmental conditions encountered by the cohorts during this period could also modulate the growth rate of common sardine year to year.

From the point of view of a longer period, the inter-cohort growth rate of sardine exhibited a significant change after 1998, from higher growth rates in the period 1990–1997 ($G = 8.7\,\mathrm{cm\,year^{-1}}$) to lower values during 1999–2006 ($G = 7.8\,\mathrm{cm\,year^{-1}}$). This change is supported in the colder period registered in the SSTA after 1998 in the study area. This period is also coincident with more intense Ekman transport occurring after 1998. Furthermore, the changes in the growth rate of the cohorts of common sardine were significantly explained by the Ekman transport and the sea surface temperature anomalies during the first fast-growing period of the cohorts. Of course, SSTA and Ekman transport are correlated in that period and cannot be used to explain together the growth rate, but each one is explaining between 28 and 54% of the observed changes in the growth rate. Although environmental conditions are explaining a small but significant fraction of the observed variability, probably other intrinsic factors, such as density-dependence, changes in the timing of spawning or birth date, could be also important for inter-cohort growth of individuals of common sardine and deserve to be explored in future research.

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