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Inter-annual variability in somatic growth rates and mortality of coastal fishes off central Chile: an ENSO driven process?

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Abstract The effects of El Niño (EN) and La Niña (LN) events upon marine organisms inhabiting the Eastern Pacific coast have been widely studied in recent years, concentrating primarily on changes in species composition and on population size. In this study, using somatic growth rates as metabolic response variables, we evaluated the mortality rates of coastal fishes inhabiting a central Chilean upwelling marine ecosystem in the South Pacific between 1990 and 2003. Four coastal fish species belonging to different trophic levels (one herbivore, one omnivore, and two carnivores) were analyzed. In all species, the estimated cohort somatic growth rates were low for those recruited during EN and high for those recruited during LN events. Annual cohort mortality rates were highest during EN events and lower during LN and transitional years. We propose that productivity (as a bottom-up driver) acts as a primary exogenous factor upon annual cohort mortality rates. We also propose that a plausible mechanism underlying this process is the negative effect the low somatic growth rates may have on fish ecological attributes such as their competitive abilities, condition factors, and predation risks, which ultimately may affect their fitness.

Introduction

Today, most ecologists recognize that endogenous and exogenous factors interact in every process affecting natural populations. However, an understanding of how each factor acts directly and indirectly upon a given

ecological process is a critical goal to be determined (Lima 2001; Stenseth et al. 2002). Natural populations inhabiting marine ecosystems are strongly affected by a large ensemble of exogenous factors, which operate at all levels of ecological organization (Hayward 1997; Attrill and Power 2002; Walther et al. 2002). In this context, the El Niño Southern Oscillation (ENSO) phenomenon is a strong natural inter-annual climate fluctuation affecting natural populations in the coastal areas of the East Pacific Ocean (McPhaden 1999). The effects of EN on marine ecosystems have been widely documented, principally changes in population sizes and community structure (Jaksic 2001). For example, changes in abundance and structure of fish assemblages have been documented on the coast of California (Davis 2000), at Bahía Navidad, México (Godínez-Domínguez et al. 2000), and Bahía Ancón, Perú (Hoyos et al. 1985). Other organisms have also been reported to experience changes in their population abundance including algae, invertebrates, larval fish, seabirds, and marine mammals (Soto 1985; Tomicic 1985; Castilla and Camus 1992; Massey et al. 1992; Arntz and Fahrbach 1996; Tsai et al. 1997; Arcos et al. 2001; Riascos 2002; Fiedler 2002; Iriarte and González 2004), and changes also occur at ecosystemic and chemical levels (Chavez et al. 1999, 2002, 2003). The effects of LN events have been less well documented, for example, consisting in the augmentation of fish abundance (Godínez-Domínguez et al. 2000; Fiedler 2002) and increase in the survival rates during LN events (Hernández-Miranda 2006). Based on these findings, the question that naturally arises is why and how do these shifts in population size occur and are there any mechanistic explanations for the demographic processes occurring during EN and LN events?

When we analyze these issues from an organismal standpoint, two major factors appear to be important to the physiological conditions of individuals inhabiting a marine ecosystem: environmental temperature and food resources. Because fish, invertebrates, and algae are ectotherms, environmental temperature has been historically regarded as the principal factor influencing their

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metabolic rates, for example, directly affecting their somatic growth (Michalsen et al. 1998). Nevertheless, as the metabolic functioning of organisms also determines other physiologically based processes such as growth and reproduction, both the quantity and quality of available food are important factors. Therefore, the relationships between environmental temperature and food resources are key factors in the survival and reproduction of marine organisms (Calow 1985), which should be studied in tandem. In this sense, evaluating physiological responses of resident organisms by quantifying a variable that captures the effects of an exogenous factor on somatic growth rates of coastal fishes constitutes valuable evidence of how organisms respond to strong environmental variations, like those occurring during EN and LN events. This task may eventually

allow us to develop a mechanistic explanation as to why marine organisms of the Eastern Pacific coast (principally those in upwelling ecosystem) show high levels of mortality during EN and high levels of survival during LN. Studies of permanent resident species of areas affected by EN show strong somatic growth rate decreases in fish (Meekan et al. 1999; Woodbury 1999), marine iguanas (Wikelski et al. 1997), invertebrates, and macroalgae (Castilla and Camus 1992), which may through a variety of mechanisms explain the decline in population size observed during such periods. In contrast, the effects of LN on marine organisms remain poorly studied (Boersma 1998). Nevertheless, it is possible to hypothesize that because there is an increase in primary productivity during LN (acting as a bottom-up driver), somatic growth rates should be at their highest due to

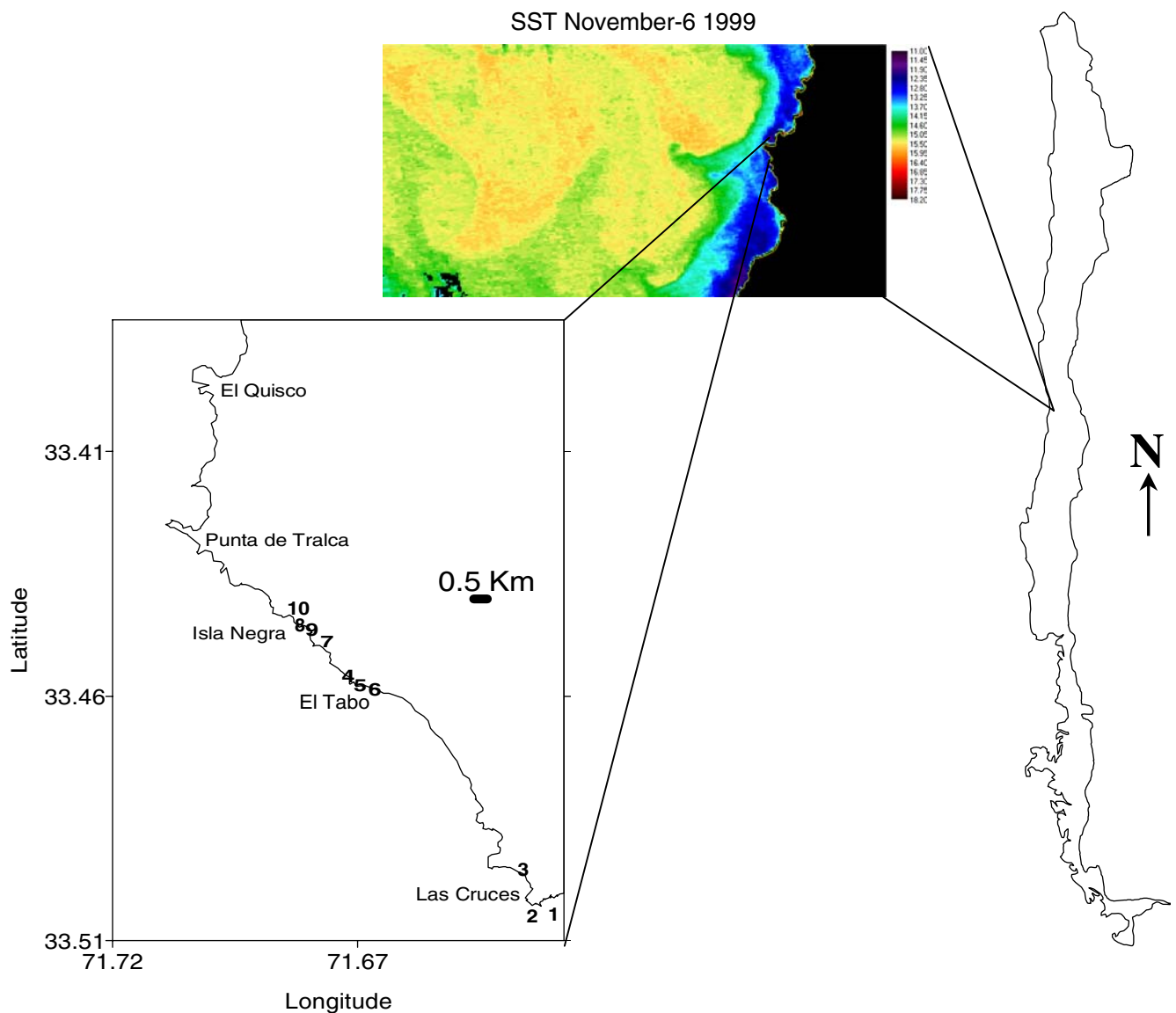


Fig. 1 Study area showing each rock pool sample: these sites are part of the upwelling ecosystem off central Chile. SST satellite image shows an upwelling event occurred during La Niña 1999

the increased levels of food availability in the coastal marine ecosystems. During LN scenarios it is, then, expected to observe lower levels of mortality of coastal organisms than those observed during EN events.

The present study evaluates the effects of EN and LN events on resident coastal marine fishes through an integrative approach, incorporating the somatic growth rates (as a response variable) estimated through combined size modal progression and capture-mark-recapture analysis at upwelling coastal sites of central Chile (Fonseca and Farias 1987; Strub et al. 1998). Our aims were: (1) to identify the annual cohort of four tide-pool fish species during a 13-year period, (2) to estimate the somatic growth and mortality rates of each cohort, (3) to estimate the degree of variability in growth and mortality rates for cohorts recruiting during EN, LN, and transition years, (4) to analyze the implications that shifts in cohort growth rates could have on the population size of tide-pool fish, and finally (5) to draw conclusions on how EN and LN events may differentially affect annual cohort growth and mortality rates of fishes belonging to different trophic categories, such as herbivores, omnivores, and carnivores.

Materials and methods

Fish sampling

Ten intertidal tidepools were selected in three localities along the central Chilean coast between 33° and 34° south latitude, four pools in Isla Negra (33.4°S), three at El Tabo (33.45°S), and three at Las Cruces (33.5°S) (Fig. 1). Tide pool temperatures were registered every 30 min and were obtained from loggers (Stow Away® Tidbits, Onset Computers Corp., with $\pm 0.3^\circ\text{C}$ precision) attached to the bottom of each pool. The pools were sampled every month from January 1997 to 2003 to estimate diversity, abundance, size distribution, and demographic parameters such as mobility, migration, and survival of these intertidal fish assemblages. Sampling consisted of suctioning off the water contained in the pools during the tidal ebb by means of portable water pump (Tecumseh 5 Hp). The nozzle of the hose was placed perpendicular to and at the bottom of the pool to prevent fishes from being sucked into the pump. Once the water was extracted, the fish anesthetic BZ 20 was applied under boulders and inside crevices, thereby facilitating their capture. Fishes were then collected with hand nets and placed in cooler tanks with fresh seawater and constant air supply. Individuals were identified, measured to the nearest mm and wet weighed. Variable proportions of individuals were marked for individual identification in future samplings. Once the pools had been replenished with seawater using the water pump, fishes were then returned to their original pool. Fish tagging was carried out with an electromagnetic device (PIT TAG, Fish Eagle Trading Co., 10 mm in length by 1 mm diameter) placed in the coelomic cavity of each

fish by means of a retractable implanter. Small individuals (< 5 cm long) were not tagged. Of the 15 species that comprise this fish assemblage (Varas and Ojeda 1990), 4 were marked: *Scartichthys viridis*, a strict herbivore (Ojeda and Muñoz 1999; Muñoz and Ojeda 2000; Quijada and Cáceres 2000), *Graus nigra* and *Auchenionchus microcirrhis*, both strict carnivores, and *Girella laevisfrons*, an omnivore (Muñoz and Ojeda 1997; 1998). These species are the dominant components of this assemblage representing about 70% of the total fish abundance. Each species reproduce once in a year, mostly at the end of winter or the beginning of spring (Hernández-Miranda et al. 2003).

Assessment of EN and LN

The regional incidence of EN and LN events along coastal zones of central Chile (33 to 34°S; 71.37°W) was

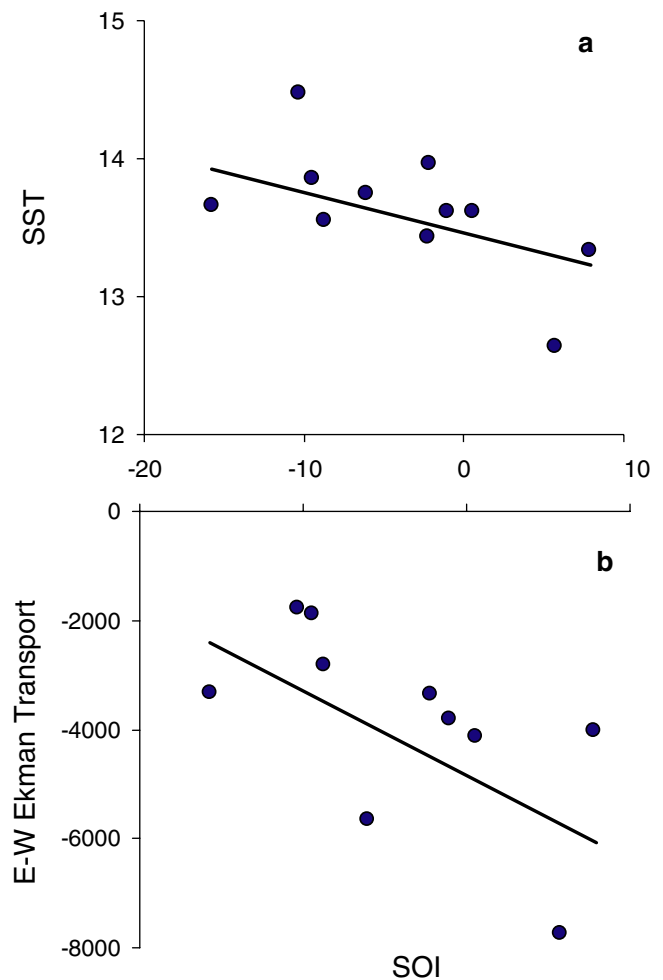
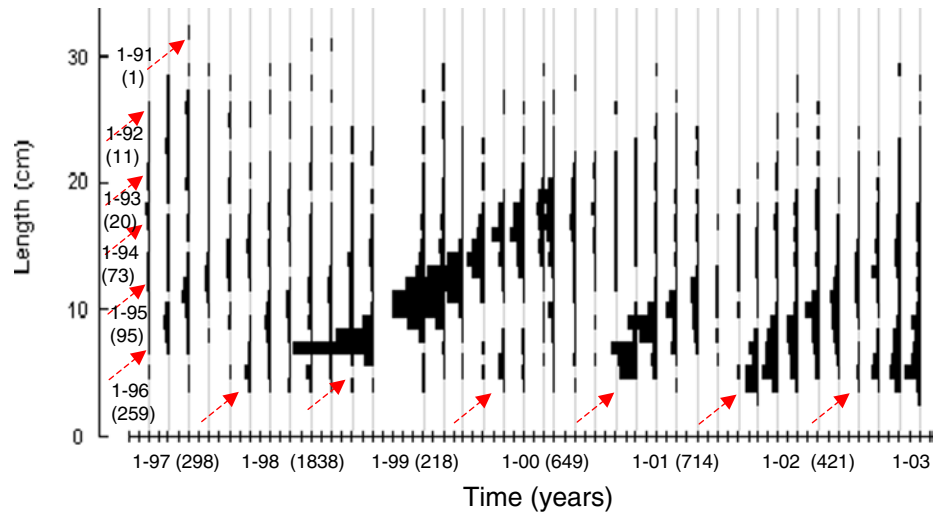


Fig. 2 **a** Regression analysis between mean yearly sea surface temperature ($^\circ\text{C}$) pooled SHOA and ECIM time series data and mean yearly Southern Oscillation index between January 1990 and 2003. **b** Regression analysis between mean yearly Ekman transport time series data and mean yearly Southern Oscillation index between January 1990 and 2003. *Negative values* indicate an increase of this oceanographic process

Fig 3 Size modal progression for *Scartichthys viridis* during entire period of sampling (January 1997–2003), each arrow corresponds to a different annual cohort indicating arrival of new recruits (*horizontally*) and pre-existent cohorts (*vertically*) that permit back-calculation of the von Bertalanffy growth parameter (k) and time from the beginning. Sample size is indicated for each cohort in bracket



monthly assessed by correlation between Southern Oscillation Index, SOI values (Global index), time series of sea surface temperature, SST and Ekman transport as a proxy of primary productivity (as local indexes). SST was obtained from two localities: San Antonio (January

1990–2003, data taken by Servicio Hidrográfico y Oceanográfico de la Armada de Chile, SHOA) and Las Cruces (April 1999–January 2003, data taken by Estación Costera de Investigaciones Marinas, ECIM). A correlation analysis was applied between the two sets of

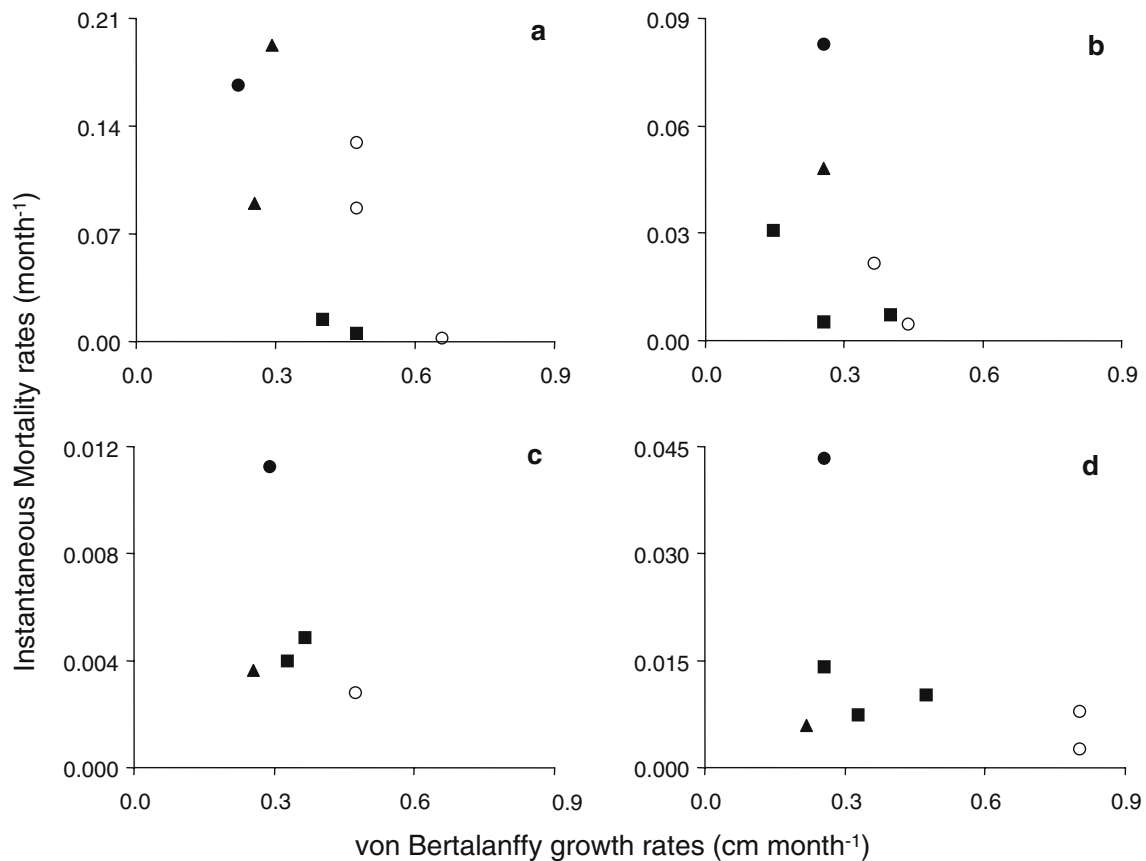


Fig. 4 Relationship between annual mortality rates of a cohort and its respective annual somatic growth. *Filled circles* correspond to annual cohort recruited during Strong El Niño events, *filled triangles* correspond to annual cohort recruited during weak

El Niño, *filled squares* correspond to annual cohort recruited during transitional years, and *open circles* correspond to annual cohort recruited during La Niña: **a** *S. viridis*, **b** *G. laevisfrons*, **c** *A. microcirrhis*, and **d** *G. nigra*

Table 1 Regression analysis of instantaneous mortality rate (month^{-1}) as a function of somatic growth rates (cm month^{-1})

Species	All data				Strong EI Niño and Niña events			
	Slope	<i>n</i>	r^2	<i>P</i>	Slope	<i>n</i>	r^2	<i>P</i>
<i>S. viridis</i>	-0.35	8	0.68	0.065	-0.36	4	0.92	0.078
<i>G. laevisfrons</i>	-0.13	7	0.48	0.273	-0.44	3	0.98	0.127
<i>A. microcirrhis</i>	-0.02	5	0.41	0.488				
<i>G. nigra</i>	-0.02	7	0.44	0.324	-0.07	3	0.99	0.075

temperature data during the overlapping period, with a significant correlation being found, (Cross correlation time series analysis: Lag=0 month, SHOA vs. ECIM=0.62, s.e.=0.122, $P<0.001$) showing that the

SST had an important regional consistency pattern. We therefore pooled the two time series for the purpose of this study. The final time series presented herein ($\text{SST}_{\text{pooled}}$) correspond to the mean monthly average for

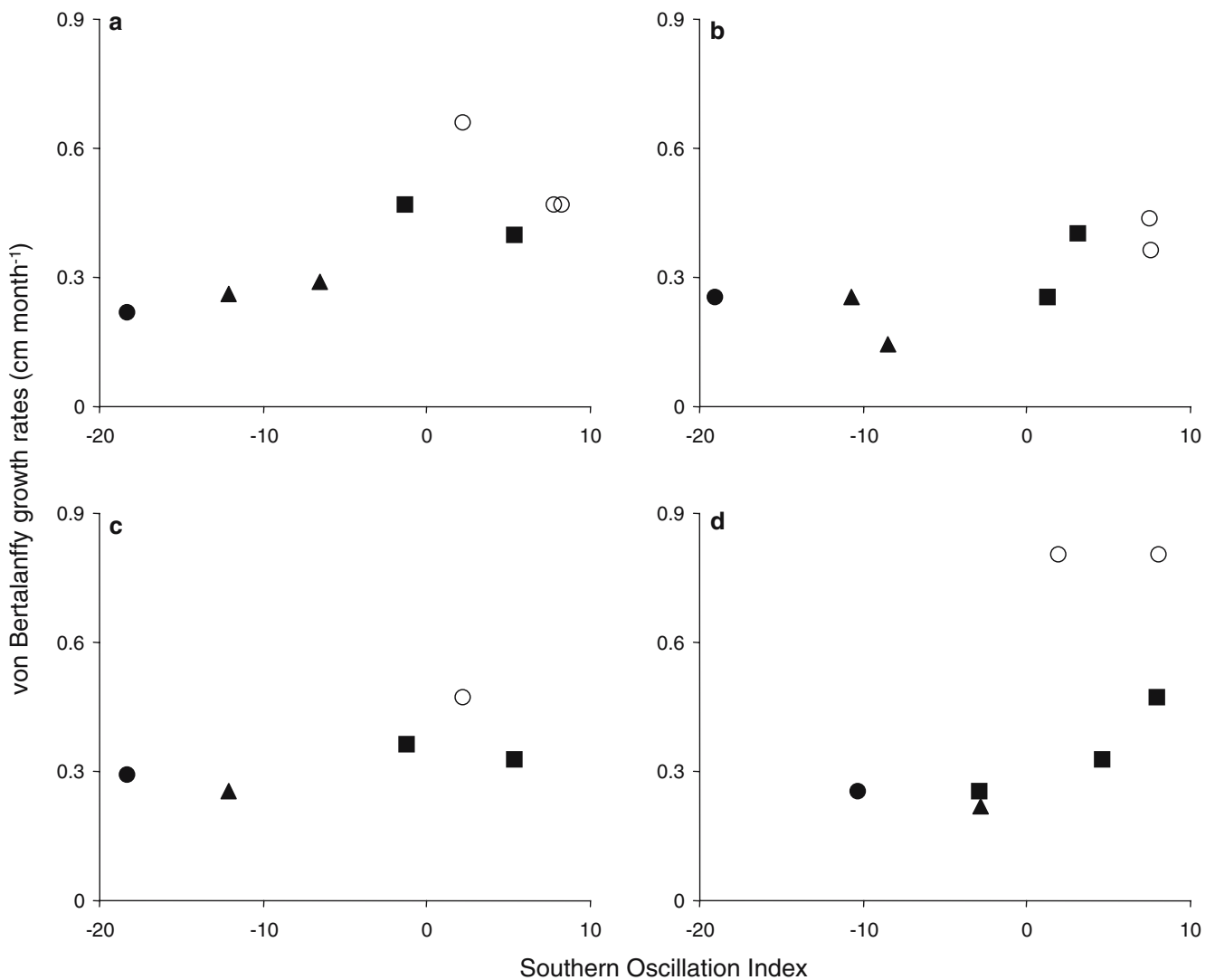


Fig. 5 Mean cohort somatic growth rates (cm month^{-1}) estimated by capture-mark-recapture methods for each cohort found between January 1990 and 2003 in four coastal fish species. *Filled circles* correspond to annual cohort recruited during strong El Niño events, *filled triangles* correspond to annual cohort recruited during

weak El Niño, *filled squares* correspond to annual cohort recruited during transitional years, and *open circles* correspond to annual cohort recruited during La Niña as a function of the 12 month mean of SOI after the time of recruitment of each cohort: **a** *S. viridis*, **b** *G. laevisfrons*, **c** *A. microcirrhis*, and **d** *G. nigra*

Table 2 Correlations between von Bertalanffy somatic growth rate (cm month⁻¹) and mean Southern Oscillation index

Species	SOI			
	1 month	3 months	6 months	12 months
<i>S. viridis</i>	0.43*	0.49**	0.66***	0.74****
<i>G. laevisfrons</i>	0.56	0.81	0.85**	0.81**
<i>A. microcirrhys</i>	0.14	0.31	0.71	0.77**
<i>G. nigra</i>	0.82**	0.76**	0.82**	0.73*

Significance levels: * $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$; **** $P < 0.005$

the entire period of study. The time series of Ekman transport correspond to east–west component obtained from FNMOC (Fleet Numerical Methodology and Oceanography Center), 144×72, 6 h pressure (kg/m) at 32.5°S–71.5°W.

The time series of the SOI indicate that between 1990 and 2003 the central Chilean coastal zone exhibited three macro-scale meteorological-oceanographic conditions: (1) EN events (1991–1992, 1997–1998 both strong and 1992–1993, 1994–1995, 2002–2003 all weak) coupled with a prolonged warm period in the Pacific during 1990–1994 (Wang et al. 1999), (2) LN events (1998–1999, 2000–2001), and (3) transition periods (1990–1991, 1993–1994, 1995–1997, 1999–2000, 2001–2002). Each

year was defined as a result of consensus criteria developed upon SOI, NINO3, and SST parameters (Null 2004). The occurrence and timing of these three meteorological–oceanographic conditions is further supported by: the SST between January 1990 and 2003 (Spearman rank correlation $R = -0.22$, $P < 0.05$; Fig. 2a) and Ekman transport ($R = -0.65$, $P < 0.05$; Fig. 2b).

Identification of annual cohorts, estimation of somatic growth parameters, annual cohort mortalities, and correlation analysis

For the entire study period (1990–2003), each species annual cohort number was identified by ELEFAN analysis (Gayanilo and Pauly 1997) using FISAT II FAO-ICLARM Fish Stock Assessment Tools Software (Fig. 3). The von Bertalanffy growth model ($l_t = l_{\infty}[1 - e^{-k(t-t_0)}]$, where l is standard length) was used to estimate the somatic growth rate parameter k for each identified cohort. The k value was estimated for the whole time period that the cohort was present and detectable. Analysis was carried out with individuals that were recaptured at least once after initial tagging (*S. viridis* = 887, *G. laevisfrons* = 394, *G. nigra* = 252, and *A. microcirrhys* = 153). These individuals were assigned to

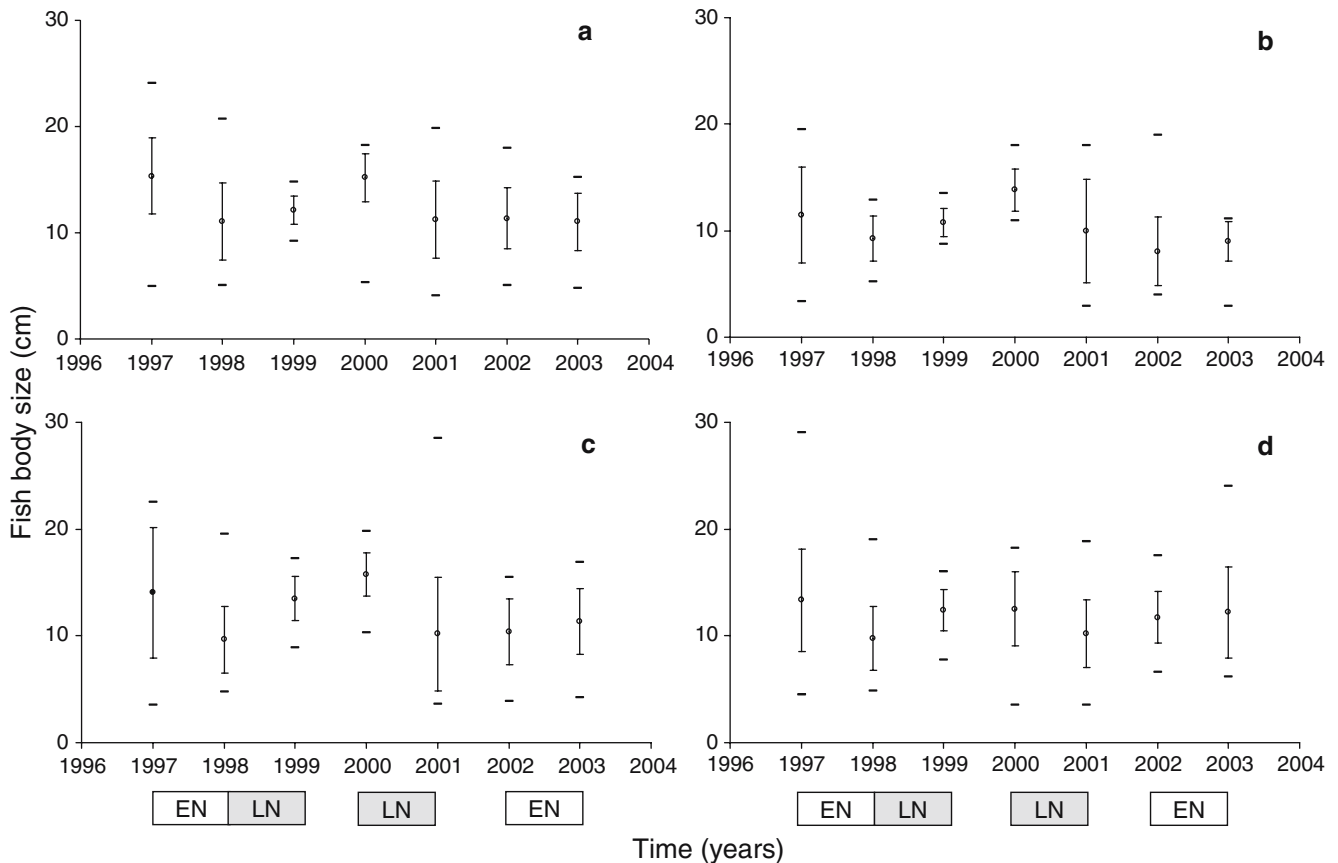


Fig. 6 Mean body size of all specimens sampled each year. Bars correspond to one S.D., and upper and lower horizontal bars indicate maximum and minimum body sizes found each year, respectively. **a** *S. viridis*, **b** *G. laevisfrons*, **c** *G. nigra*, **d** *A. microcirrhys*

each recognized annual cohort, depending on size at the time of tagging. Individuals that were never recaptured were not included in analyses. The growth increment method for k estimation from tagging/recapture experiments was applied (Gulland and Holt 1959). This consists of releasing many individuals at time 1, recapturing them at time 2, and then calculating the growth over that time period. The slope of simple linear regression permits us to describe the von Bertalanffy k for each observed cohort. Simple linear regression was also used to compute annual cohort mortality rates. This consisted of counting, during 1 year, the number of survivors of each cohort from the time of recruitment. The slope of the simple linear regression permits us to describe the instantaneous mortality rate z for each observed cohort. To evaluate the hypothesis that increase in fish somatic growth rates result in the decrease in mortality rates and that this process is driven by ENSO events, we use a correlational approach. Standard methods for correlation analysis depend on assumptions of normality and non-autocorrelation, which are seldom met by biological time series. To avoid the assumption of normality we apply Spearman's rank correlation. The second assumption was met by adjusting P -values. This method was proposed by Quenouille (1952) and has been used in a wide spectrum of science areas (e.g., Ottersen et al. 2002; Kristjánsson et al. 2002). To achieve this we applied the Quenouille formula: $N_e = N/(1 + 2a_1b_1 + 2a_2b_2)$,

where N_e is the effective number of independent observations, N is the number of data points common to the two series, a_1 and b_1 are the lag-one autocorrelation parameters, and a_2 and b_2 the lag-two autocorrelation parameters for the time series a and b .

Results

A total of 48 annual cohorts of coastal fish was identified by ELEFAN (see [Materials and methods](#)) analysis between January 1990 and 2003. Of these, 12 corresponded to *S. viridis*, 13 to *G. laevisfrons*, 11 to *G. nigra*, and 12 to *A. microcirrhis*. Due to insufficient data, it was possible to compute the von Bertalanffy k parameters by capture-mark-recapture in eight cohorts of *S. viridis*, seven cohorts of *G. laevisfrons*, seven cohorts of *G. nigra*, and five cohorts of *A. microcirrhis*. Estimates of cohort mortality rates were 11 for *S. viridis*, 9 for *G. laevisfrons*, 10 for *G. nigra*, and 9 for *A. microcirrhis*. There are apparent inverse relationships between the von Bertalanffy k parameters and cohort mortality rate z , but only for *S. viridis* marginal significant slopes are found (Fig. 4, Table 1). However, when a simple linear regression was only estimated for strong EN and LN year, marginal significant slopes were found for *S. viridis* and *G. nigra* (Fig. 4, Table 1).

Table 3 Parameters of the weight-size relationships estimated for each year and each species

Species	Year	b	a	r^2	k	S.D.	N	
<i>S. viridis</i>	1997	2.95	0.0149	0.94	0.135	0.048	321	
	1998	2.85	0.019	0.94	0.135	0.039	403	
	1999	3.04	0.0114	0.89	0.129	0.039	1073	
	2000	2.8	0.024	0.87	0.145	0.072	555	
	2001	3.11	0.0105	0.96	0.141	0.030	734	
	2002	2.99	0.015	0.92	0.152	0.044	801	
	2003	2.85	0.0181	0.96	0.130	0.066	544	
	<i>G. laevisfrons</i>	1997	2.73	0.0397	0.94	0.217	0.072	212
		1998	2.85	0.0237	0.78	0.179	0.060	294
		1999	3.05	0.0156	0.85	0.178	0.043	277
2000		2.94	0.0239	0.9	0.206	0.038	184	
2001		2.81	0.0353	0.96	0.241	0.066	413	
2002		3.04	0.0202	0.89	0.228	0.053	858	
2003		2.93	0.0214	0.91	0.187	0.036	387	
<i>G. nigra</i>	1997	3.12	0.0116	0.95	0.162	0.056	72	
	1998	2.87	0.0207	0.84	0.169	0.075	301	
	1999	3.35	0.0063	0.93	0.159	0.028	141	
	2000	2.9	0.0238	0.84	0.182	0.037	84	
	2001	2.84	0.0273	0.95	0.197	0.071	381	
	2002	3.03	0.017	0.91	0.189	0.046	536	
	2003	2.87	0.0205	0.96	0.152	0.028	544	
	<i>A. microcirrhis</i>	1997	3.29	0.0059	0.93	0.127	0.039	81
1998		2.64	0.0301	0.89	0.135	0.044	201	
1999		3.32	0.0055	0.91	0.129	0.033	207	
2000		2.84	0.0216	0.92	0.147	0.046	155	
2001		3.03	0.013	0.92	0.151	0.120	277	
2002		2.91	0.0186	0.89	0.156	0.045	271	
2003		2.77	0.208	0.86	0.121	0.040	186	

b slope, a intercept, r^2 Pearson's coefficient, k condition factor, S.D. standard deviation, N sample size

Annual cohort somatic growth rates (k) correlated positively with the SOI after 12 months of recruitment (Fig. 5, Table 2), although at 6, 3, and 1 months a significant positive correlation was also recorded (see Table 2 for Spearman's rank correlation coefficients). In this study, we used a 12-month period of SOI because it incorporates the first year of each annual cohort including the effect of seasonality. These results indicate that, for all four species, the estimated somatic growth rates were low during EN and high during LN. Furthermore, the somatic growth rate dynamics were species-specific. *S. viridis* showed the largest variability between EN and LN scenarios with growth rate differences nearing 3.0 times, *G. nigra* showed 3.2, *G. laevifrons* 1.8, and *A. microcirrhis* 1.6, when EN and LN events were compared. Despite these differences in somatic growth rates, mean body size of all four species studied showed the same pattern, i.e., a

decrease during EN events and an increase during LN events (Fig. 6). A similar pattern was also found when analyzing condition factors for these four species, characterized by low values during and after EN events and high values during and after LN events (Table 3).

In general, for the four species studied the highest annual cohort mortality rates occur during EN events and the lowest annual cohort mortality rates occur during LN events. These mortality rates correlated negatively with the SOI at 12 months (Fig. 7, Table 4 for Spearman's rank correlation coefficients). Furthermore, the mortality rate dynamics were species-specific. *S. viridis* showed the largest variability between EN and LN scenarios with mortality rate differences nearing twofold when both events were compared. *G. nigra*, *G. laevifrons*, and *A. microcirrhis* showed near onefold of variability.

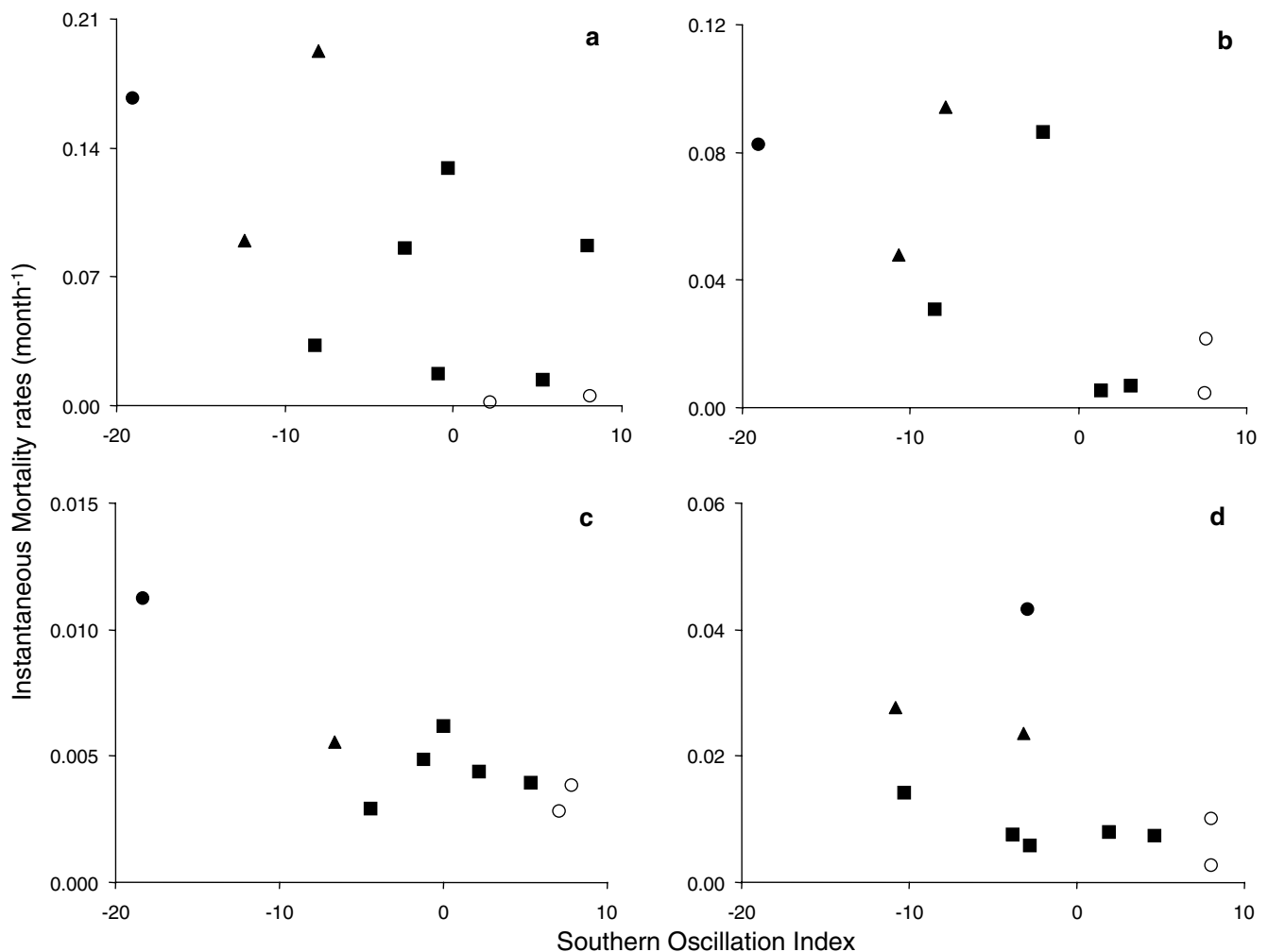


Fig. 7 Scatter plot of annual cohort mortality rates against the Southern Oscillation index between 1990 and 2003. The SOI corresponds to the mean of the first 12 months of each annual cohort. *Filled circles* correspond to annual cohort recruited during strong El Niño events, *filled triangles* correspond to annual cohort

recruited during weak El Niño, *filled squares* correspond to annual cohort recruited during transitional years, and *open circles* correspond to annual cohort recruited during La Niña. **a** *S. viridis*, **b** *G. laevifrons*, **c** *A. microcirrhis*, and **d** *G. nigra*

Discussion

In coastal central Chile, EN and LN events may be recognized by two principal signals. The first signal involves SST, which may increase (on average) 4 to 5°C during EN event and decrease nearly 2 to 3°C during LN. The second signal is related to nutrient enrichment of the coastal zone, principally in this upwelling ecosystem. In general, in tropical areas, productivity drops sharply during EN events causing oligotrophic conditions, while during LN events, this situation reverses and coastal zones become more productive (Davis 2000; Chavez et al. 2002). In Chilean coastal waters from the

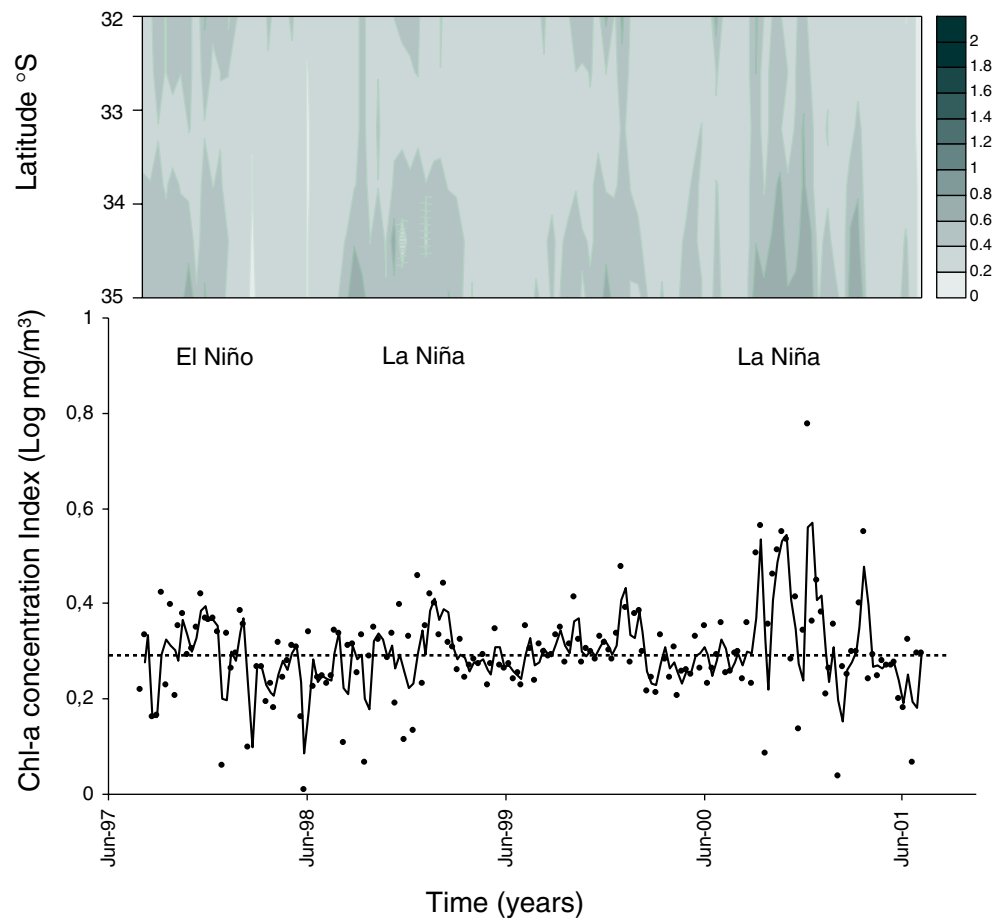
strong EN event of 1997–1998 to the LN event of 1999–2001, the index of standing stock of chlorophyll-*a* increased from 0.1 to 0.8 according to inferences from satellite images (Fig. 8, SeaWiFS data transformed to as a index between 0 and 1; for more details see original data from Thomas et al. 2001), suggesting an increase in phytoplankton biomass between the two opposite events. Also, Wieters et al. (2003) report a similar pattern in chlorophyll-*a* concentration. Further, Nielsen and Navarrete (2004) have recently shown that along the Chilean central coast upwelling intensity was strongly associated with increased abundance of intertidal macroalgae. Our results indicate that, irrespective of trophic level of fish (primary or secondary consumer), their

Table 4 Correlations between instantaneous mortality rate (month⁻¹) and mean Southern Oscillation index

Species	SOI			
	1 month	3 months	6 months	12 months
<i>S. viridis</i>	-0.17	-0.18	-0.28	-0.61**
<i>G. laevisfrons</i>	0.04	-0.63*	-0.54	-0.62*
<i>A. microcirrhis</i>	-0.37	-0.57	-0.70*	-0.56*
<i>G. nigra</i>	-0.18	-0.34	-0.46	-0.68**

Significance levels: * $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$; **** $P < 0.005$

Fig. 8 Monthly SeaWiFS chlorophyll (mg m⁻³) within 12 km of the coast contoured as a function of time (September 1997–August 2001) and latitude (between 32 and 35°S). Darker areas indicate highest levels (above). Same time series data show the mean (dotted line) and three-month moving average (continuous line), using the data between 33 and 34°S (below). Data in both figures were log-transformed and are presented herein as an index between 0 and 1



growth rates decreases with the EN scenario and increases during LN, which suggest that bottom-up effects of nutrients drive fish growth at multiple trophic levels. Interestingly, there is an apparent paradox in respect to the effect of temperature on growth: the highest somatic growth rates were found at the lowest SST (Fig. 9). A plausible explanation of this paradox might be found in the nature of intertidal environments, where fishes are exposed to water temperature that varies between 6 and 27°C within a 24 h period (Hernández et al. 2002), which represents a larger range than that recorded in the surface (SST ranged between 12.5 and 14.5°C from 1990 to 2003, Fig. 2). The unexpected relationships with temperature suggest that productivity rather than temperature is the key factor affecting the pattern of fish somatic growth that we report.

In recent years, the study of how organisms with indeterminate growth allocate energy that they obtain from their environment has become an important issue

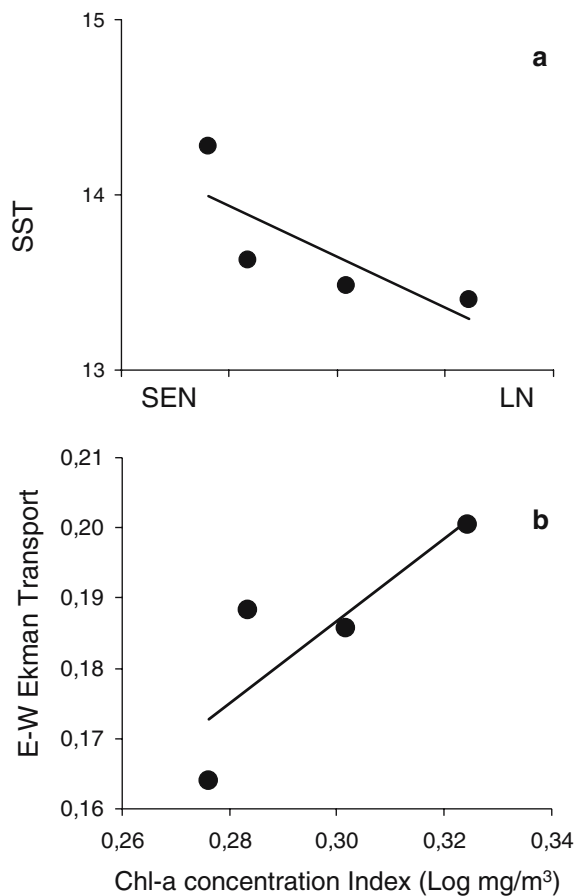


Fig. 9 **a** Scatter plot of annual average SeaWiFS chlorophyll (mg m^{-3}) against annual average sea surface temperature ($^{\circ}\text{C}$) pooled SHOA and ECIM time series data between September 1997 and August 2001. **b** Scatter plot of annual average SeaWiFS chlorophyll (mg m^{-3}) against annual average Ekman transport time series data between September 1997 and August 2001. *SEN* corresponds to 1997–1998 El Niño event. *LN* correspond to 2000–2001 La Niña event

in evolutionary biology, i.e., how much energy is allocated to maintenance, somatic growth, or reproduction. Heino and Kaitala (1999) outlined the basic pathways of resource allocation in a simple conceptual model. Their model proposes that maintenance has priority over other needs but when energy is in excess of maintenance needs, it can be allocated in to growth and reproduction. In light of our results, we propose to add the ENSO scenarios like an exogenous factor to this model. During an EN event, the total input of energy is limited, being primarily destined for maintenance of individuals. This reduction in energy results in a marked decrease in the allocation toward somatic growth, which in turn may produce low survival levels. During LN and transitional years, this situation is reversed with high levels of energy entering to ecosystem. These resources are then allocated to both somatic growth and reproduction, the former evident in our growth results. As an important consequence of Heino and Kaitala's model, body size should decrease under a low energy scenario, and increase under a high energy event. Indeed, mean body size of all four species studied decreased during EN events and increased during LN events (Fig. 6). The partial validation of this physiological-environmental conceptual model in our study suggests a novel mechanistic manner as to why marine organisms exhibit high mortality rates during EN. This idea presents an interesting view point in respect to the relationship between exogenous factors that affect natural populations and internal demographic processes. We propose that a plausible mechanism underlying this process is the negative effect the low growth rates may have on fish fitness such as their competitive abilities, condition factors, and predation risks. In this vein, Willette et al. (1999), for example, described changes in mortality rates of Pacific herring and walleye pollock as a function of intensity of spring blooms. They report that in this process, low somatic growth rates result in high cohort mortalities, similar pattern that we report in our study.

In this study, we have utilized, in terms of feeding strategies, at least three trophic levels, with the purpose of evaluating their potentially different physiological responses as a function of the high variability of resources present in the environment. Our results show that, despite differences in their somatic growth and mortality rates, the four species studied responded similarly to EN and LN scenarios. This suggests that during LN and transitional years, a bottom-up exogenous control effect acts upon species at different trophic levels inhabiting tide pools exposed to upwelling ecosystems and can be considered as a proximal mechanism (upward SOI, downward SST, upward resource availability, high somatic growth rates, high survival rates). This type of control is understood as a limitation in the input of food resources and associated physico-chemical factors that affect the higher trophic levels within food webs (Menge 1992). In this sense, our findings indicate that ENSO is a temporal high and low energy dynamic phenomenon that should be studied on a long-term basis. Finally, this

study represents, to our knowledge, a novel approach to understanding how environmental physical processes such as EN and LN may affect the demography of natural populations inhabiting marine ecosystems by altering energy allocation within individuals.

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