Simulating the effects of El Niño Southern Oscillation and fishing effort on the central Chile marine ecosystem

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Abstract

Community changes induced by bottom-up (El Niño Southern Oscillation, ENSO) and top-down (fishing) forcing in the central Chile marine ecosystem (CChME) are simulated using a 21-group ECOPATH model of the system in 1992 with the ECOPATH with ECOSIM software. Three 10-year dynamic scenarios are sketched: i) changes in phytoplankton biomass induced by sea surface temperature anomalies (ΔSST) at ENSO scale; ii) changes in mortality of fishing resources; and, iii) the combined effects of i) and ii). ENSO induces changes in phytoplankton biomass that are propagated in a cascade effect throughout the entire food web as oscillations. The intensity and duration of the oscillations decrease as the trophic level increases. Bottom-up forcing strongly affects the abundance of fishery resources such as horse mackerel, anchovy, common sardine, and Chilean hake. The fishing effort produces decreased anchovy and common sardine biomass, while oscillations in horse mackerel, Chilean hake, and sea lion biomass are observed. Although small, oscillations in phytoplankton biomass under top-down forcing suggest that cascade effects derived from the removal of target species by fishing could reach lower trophic levels. The interplay between ENSO and fishing indicates that both forcings could also affect horse mackerel, Chilean hake, and sea lion. Their effects on anchovy, common sardine, and phytoplankton could be weakened. It is concluded that both the environment (ΔSST) and fishing can play significant structuring roles in the CChME. This should be taken into account for fisheries management, since environmental forcing could accelerate, hinder, or mask the effect of fishing.

Key Words: Ecosystem modeling; physical forcing; ENSO; fisheries; ECOPATH with ECOSIM; central Chile
INTRODUCTION

Ecosystems change can be driven by internal (trophic structure) and external (environmental and exploitation) forcing. Therefore, the understanding of trophic relationships, environmental variability and fishing pressure on ecosystems is taking the attention of ecologists and resources managers around the world.

Environmental variability affects biological processes on different spatial-temporal scales (Steele, 1985). One oceanographic process affecting marine organisms is known as El Niño Southern Oscillation (ENSO). The intensity, phase (cold/warm), and length of ENSO affects primary production through variations in the sea surface temperature (SST) or reduced/intensified surface nutrient contributions (Barber and Chávez, 1983; Carr, 2002). The deepening of the mixed layer due to warm, nutrient-poor, equatorial waters suppresses fertilization in the surface layers (Morales et al., 1999). Lower concentrations of surface phytoplankton biomass (Chl a) are released (González et al., 2000; Rutllant and Montecinos, 2002), the flow of material to the bottom decreases (Sellanes, 2002), and changes are observed in the composition of the phytoplanktonic community (González et al., 1998; Ulloa et al., 2001). In the central Chile marine ecosystem (CChME), the interannual variability produced by ENSO is associated with the arrival of coastal-trapped waves or equatorial Kelvin waves (Hormazábal et al., 2001; Pizarro et al., 2002, Montecinos et al., 2003).

In general, the hypothesis that primary productivity decreases during warm El Niño events (positive ΔSST) and increases during cold La Niña events (negative ΔSST) is accepted (González et al., 1998; González et al., 2000; Carr, 2002; Rutllant and Montecinos, 2002). This bottom-up, ENSO-derived effect is transmitted through higher trophic levels, affecting even top predators (Barber and Chávez, 1983; Arntz and Fahrbach, 1996). Several studies show ENSO effects on the CChME at different trophic levels (see Escribano et al., 2004 for a review). For example, changes in the composition of benthic communities (Gutiérrez et al., 2000;
Sellanes, 2002) and modifications in feeding, reproductive behavior and recruitment of small- and medium-sized pelagic fish such as horse mackerel (*Trachurus symmetricus*), common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*) (Yáñez et al., 1992; Arcos et al., 2001; Cubillos and Arcos, 2002; Alheit and Niquen, 2004; Arcos et al., 2004; Cubillos et al., 2004).

However, living and non-living components of the ecosystem are also impacted by fishing. This top-down effect has been described and widely quantified (Jennings and Kaiser, 1998; Hall, 1999; ICES, 2000; Daskalov, 2002). Fishing removal of target and by-catch species impacts the whole community by altering trophic relationships between the latter species and their predators, prey, and competitors (Goñi, 1998; Hollingworth et al., 2000; Shannon et al., 2000; Harvey et al., 2003). It is also well known that fishing activities directly affect target species' population structure, growth, reproduction, and distribution and have indirect effects on non-target species and their habitats. In addition, the ecosystem structure in response to fishing, produce changes on the structural aspects and have indirect effects via predation processes. The extractions of elements from the intricate food web promote in the community structure serious impacts (Zabel et al., 2003). In fact, one example of these ecosystem-effects of fishing is the process called “fishing down marine food webs” (*sensu* Pauly et al., 1998), which has also been described for the CChME (Arancibia and Neira, 2005).

Although trophic relationships and community structure in the CChME has been recently modelled (Neira et al., 2004; Neira and Arancibia, 2004), the structuring roles of the oceanographic variability and fishing pressure on the ecosystem are not fully understood. Arancibia and Neira (2005), analyzed the trend in the mean trophic level of the catch showing that fisheries have been fishing down the food web as the result of fishery-induced changes more than environmental variability, since ENSO events do not seem to have induced a significant effect in this trend.
Considering the global call for an ecosystem-approach to fisheries (FAO, 2001), the evaluation of oceanographic (specifically $\Delta$SST) and fishing forcing on trophic links, specially those of targeted species, could provide valuable information for fisheries management by reducing the uncertainty in some fishing predictors, and then assuring species and ecosystem sustainability (Mercer, 1982; Shannon et al., 1988; Shelton, 1992; Botsford et al., 1997).

Therefore, the objectives of this paper are: i) to analyze the likely effects of bottom-up forcing on the CChME induced by changes in phytoplankton biomass in response to $\Delta$SST (ENSO event scale), with emphasis in fishery resources located on middle and upper trophic levels (Neira and Arancibia, 2004; Neira et al., 2004); and ii) to evaluate the top-down effects of CChME fisheries induces by changes in mortality of fishing resources; and, iii) the combined effects of i) and ii).

MATERIALS AND METHODS

Study area
The study area corresponded to the marine zone off central Chile: 33º S to 39º S and from the coast to 30 nm, i.e., approximately 50000 km2 (Fig. 1). This is the main fishing ground for the purse-seine and trawling industrial fishing fleets (Arancibia et al., 2003; Neira et al., 2004). According to Camus (2001), because of its oceanographic and bio-zoo-geographic characteristics, the area can be considered as an independent and intermediate unit – the Mediterranean District – between the Peruvian and Magallánica Province, respectively.

Effect of SST on phytoplankton biomass
Environmental data
The monthly SST data (precision 1º latitude x 1º longitude) from January 1982 to December 2003 were taken from http://ingrid.idgo.columbia.edu/sources/igoss (Reynolds and Smith, 1994). Then the annual average SST anomalies ($\Delta$SST)
were determined for the entire study area based on the long-term monthly average (1982 to 2003).

**Physical forcing on phytoplankton biomass**

The primary assumption of this work is that $\Delta$SST produces variations in the phytoplankton biomass (Chl a) within the CChME, which is consistent with results of Thomas et al. (2001) and Carr (2002), who found a positive and significant relationship between $\Delta$SST and surface Chl a on a large scale in the Humboldt Current ecosystem.

Satellite sea colour information (sensor SeaWiFS) was used as an indicator of biomass of phytoplankton in the study area, specifically images of Chl a concentration. Images of weekly Chl a averages were used for establishing monthly averages. The data were provided by the Programa Regional de Oceanografía Física y Clima (PROFC), Universidad de Concepción.

A Chl a series was constructed compared using the annual $\Delta$SST from the CChME and the empirical model developed by Watters *et al.* (2003). The relationship predicts that, on average, pigment concentrations (mg/m3) change in the North Pacific Ocean by around -0.183 per each °C of $\Delta$SST as follows:

$$B_t = B_{t=0} \times e^{(Chl\ a \ast \Delta\ SST)}$$

(1)

where: $B_t$ is the phytoplankton biomass over time $t$; $B_{t=0}$ is the phytoplankton biomass at time $t=0$ (September 1997), Chl a is the average value of the change in Chl a obtained in the 1997 to 2003 series for the study area (Chl a = -0.183), $\Delta$SST is the SST anomaly off CChME in the same period.
With the model of Watters et al., (2003), predicted values of phytoplankton biomass over time $t$ in the area of study were compared with observed values of Chl $a$ obtained from SeaWiFS by using lineal regression analysis.

**Simulations**

Dynamic scenarios we constructed using an Ecopath model built by Neira et al., (2004) and the ECOPATH with ECOSIM software version 5.0 (EwE, Walters et al., 1997). In EwE the change in biomass per unit of time for each model group occupying a trophic level higher than 1 is determined by the following equation:

\[
\frac{dB_i}{dt} = g_i \sum_{j=1}^{n} c_{ij}(B_i, B_j) M_i B_i - F_i B_i - \sum_{j=1}^{n} c_{ij}(B_i, B_j)
\]

(2)

where:

- $\frac{dt}{dB_i}$ is the biomass change in group $i$ during time interval $t$;
- $g_i$ is the net efficiency of group $i$;
- $c_{ij}(B_i, B_j)$ is the function that predicts the consumption of prey $i$ by predator $j$, which is influenced by environmental variations;
- $M_i$ is other mortalities;
- $F_i$ is mortality by fishing in group $i$.

A forcing function is defined as the effect of an environmental factor (physical forcing) or a human factor (fishing effort) over an ecotrophic group. The forcing function can modify the ecosystem structure through trophic interactions (Christensen et al., 2004). In the present study, changes in phytoplankton biomass are produced by $\Delta$SST, and changes in fishing resources are produced by $F$. According with the trophic control, the effects in a trophic group can be trespassed to other groups in the system.

In ECOSIM, each prey pool is viewed as a composite of biomass that is either available or unavailable to each consumer at any moment in time. The rate at which biomass changes state from unavailable to available to predators is a
function of a vulnerability ratio ($v=$ from 0 to 1), which is controlled by the modeller (see Walters et al., 1997, for details). Setting a low value of $v$ (i.e. 0) leads to bottom-up control of flow rates from prey to predators, while a high value ($v=1$) leads to top-down control and intermediate values ($v=0.3$) a mixed trophic control (Christensen & Walters, 2004).

**Scenario 1: Physical forcing**

A physical forcing function was built with Equation 1 using the annual values of $\Delta$SST in the CChME from 1992-2002. This was then applied to the phytoplankton biomass to evaluate the possible impact of warm (El Niño) and cold (La Niña) events on the phytoplankton biomass in the study area. The objective of this simulation is to analyze whether these effects are trespassed to groups located in higher trophic levels. In this scenario we assumed that the system is bottom-up controlled (i.e., $v=0$ for each group), since under this type of control, impacts on middle and higher tropic levels are considered to be indirect (Watters et al., 2003).

**Scenario 2: fishing force**

The effect of fishing was simulated using the coefficient of fishing mortality (F) as the forcing function for the biomass of fishery resources and by-catch species in the CChME from 1992 to 2002 (Table 2). F’s values were taken from Arancibia and Neira (2003) and Arancibia et al. (2003) and correspond to the official F’s during the same period. The purpose of this simulation is to evaluate the response of model groups under changes in F. The changes were analyzed under top-down control ($v=1$ for each group), that is, the direct effects are observed in the fishery resources and the indirect effects in prey and competitor organisms (Watters et al., 2003).

**Scenario 3: Interplay between physical forcing and fishing force**

This scenario combines scenarios 1 and 2. Changes in relative biomass were analyzed considering bottom-up control in phytoplankton and top-down control in fishery resources (sardine, anchovy, horse mackerel, and Chilean hake). For the
remaining components, the control was considered to be mixed (sensu Watters et al., 2003). The purpose of this mixed scenario is to reveal which of the two forcings has a greater effect on model groups and whether these are strengthened or weakened.

The effect of each scenario on the biomass of each trophic group was measured as the relative change between the biomass at the end of the simulation (Be) respect to the biomass at the beginning of the simulation (Bb). We considered significant impacts on group biomass as those higher or lower than 10% respect Bb. For significant impacts, the Magnitude of Change (MC) was measured in percentage since MC represents an attribute of system stability (Mackinson et al., 1997). Simulations representing each scenario (1 to 3) were run for ten years (1992-2002). Moreover, the biomass predicted by ECOSIM for the main fishery resources (anchovy, common sardine, Chilean hake, and horse mackerel) under the more realistic scenario (i.e. scenario 3) were compared with the observed biomass of the same groups in last 10 years, obtained from Arancibia et al., (2003), SubPesca (2004a, b, c).

The effects of three scenarios in the ecosystem’s structure were analyzed through the ratio of planktivorous fish biomass vs. zooplanktivorous fish biomass (PS/ZP). This index allows an evaluation of changes in the system considering only biological variations, oceanographic variation, fishing effort, or a combination thereof. This index has been used at different spatial and temporal scales, in a wide variety of ecosystems around the globe, permitting an evaluation of the state of health of the ecosystems being exploited by fishing (Caddy and Garibaldi, 2000).

The PS/ZP ratio (Caddy and Garibaldi, 2000) was quantified in the present study between the estimated biomass of the piscivorous fish (e.g. Chilean hake) and the estimated biomass of the zooplanktivorous fish (e.g. horse mackerel). All tendencies in each scenario were analyzed by Spearman correlations (rs).
RESULTS

Physical forcing on phytoplankton biomass
The analysis of the annual ΔSST time series shows a warm period (positive ΔSST) in the study area from 1992 to 1998, excepting 1996. Followed by cold period from 1999 to 2002 (Fig. 2a). The most elevated ΔSST (+0.77 °C) was observed in 1997, which is consistent with the largest ENSO of the last century (McPhaden, 1999) whereas the lowest negative ΔSST (-0.41 °C) appeared in 2000.

Observed Chl a values for the study area (SeaWiFS) and estimated Chl a values (empirical model; Equation 1) showed a highly significant correlation (r²= 0.94; P<0.01; Fig. 2b). The maximum Chl a values were observed in cold periods (2000 and 2001), whereas the lowest values occurred in warm periods, especially the 1997-98 El Niño, which is consistent with our assumption.

Simulations
Scenario 1: Physical forcing
When positive ΔSST occurs, a decrease is seen in the relative phytoplankton biomass (year 6 of the simulation, Fig. 3a). This decrease occurred in conjunction with the 1997-98 El Niño event and resulted in up to a 66% decrease in the initial phytoplankton biomass (1992) (Table 3). Negative ΔSST, however, have the opposite effect on the phytoplankton biomass (year 9 of the simulation), increasing it by up to 50%.

The relative phytoplankton biomass induced by changes in ΔSST is transmitted to higher trophic levels in the form of oscillations, which intensity and strength decreases as trophic increases (Table 3). Time lags are also observed between the oscillations of the phytoplankton and those of higher trophic groups; the lags increase as does the trophic level (Table 1). For example, the response was delayed one year for horse mackerel (TL=3.9), two years for Chilean hake (TL=3.5), and three years for sea lions (TL=4.23).
Scenario 2: Fishing forcing

Not all the functional trophic groups showed oscillations in this scenario (Fig. 3b), since the analysis involves target species that have different fishing mortality rates in the studied period (Fig. 3b). For example, the relative horse mackerel and Chilean hake biomass displayed oscillating tendencies. Small pelagic fishes (common sardine and anchovy) exhibited decreasing tendencies in their relative biomass throughout the entire simulation. Sea lions showed a decreasing trend in their relative biomass up to 16% with respect to the initial biomass (Table 3). Mild, slightly negative oscillations (< 10%) and significant increases (> 20%; Table 3) are seen in the relative phytoplankton biomass.

Scenario 3: Interplay between physical and fishing forcings

Under this scenario, the biomass of fishery resources (e.g. small pelagic fishes, Chilean hake, horse mackerel) and top predators oscillated (Fig. 3c). The phytoplankton biomass has irregular cycles that are milder than those in the first scenario (Fig. 3a). Horse mackerel shows wider oscillations, followed by the small pelagic fishes, Chilean hake, and sea lions. The largest magnitudes of change were observed in horse mackerel (Table 3).

In combination, the effects of $\Delta$SST and F are strengthened or weakened depending on the functional group and trophic level. In intermediate to high trophic levels (sea lions, Chilean hake, and horse mackerel) biomass changes are greater than those in the first and second scenarios. On the other hand, in intermediate to low trophic levels (i.e., small pelagic fishes and phytoplankton) biomass changes are smaller than those in the first scenario, but higher than those in the second scenario (Fig. 4).

Phytoplankton and small pelagic fishes has greater magnitudes of change with $\Delta$SST and decrease when considering the combination of $\Delta$SST and F. Unlike these first two cases, the combination of $\Delta$SST and F strengthen the MC for Chilean hake, horse mackerel, and sea lions (Table 3).
The biomass estimated by EwE for the main fishery resources (under scenario 3) showed dissimilar tendencies with respect to those observed; the latter are determined by hydroacoustics or swept area. Small pelagic fish biomass (Figs. 5a, b) oscillated, tending to decrease toward the end of the period. The oscillations in the EwE estimates were milder. Nevertheless, the EwE estimates of common sardine biomass did not agree with the drop in observed biomass. The tendency of the observed horse mackerel biomass to decrease was only reflected by EwE for the first years (Fig. 5c). Chilean hake biomass, however, increased in both observations and EwE, although EwE was more conservative (Fig. 5d).

**Changes on ecosystem structure**

The CChME's trophic structure, analyzed with PS/ZP in Scenario 1, tended to decrease significantly (rs= -0.75; P<0.01) reaching a minimum in 1998 (Fig. 6b). Under the influence of F, PS/ZP tended to decrease insignificantly (rs= -0.26; P>0.05), also lessening at the end of the period. However, when the forcings were combined (ΔSST and F), a marked oscillation was seen in the PS/SZ tendency, with a significant negative slope (rs= -0.60; P<0.05), especially as of 1997. This indicates a probable change in the CChME's structure.

**DISCUSSION**

Surprisingly, the empirical model developed by Watters et al. (2003), for the Equatorial Pacific Ocean, allows to satisfactorily predict the Chl a concentrations in the study area using ΔSST, which is demonstrated by the highly significant correlation between Chl a values obtained from the model and those from the SeaWiFS at a medium spatial scale. This is in accordance with Carr (2002) who informs the same correlation but in a bigger spatial scale, i.e., Humboldt Current System. Consequently, the bottom-up changes induced by ΔSST on the phytoplankton, and maybe on other groups, in CChME could be similar to those modelled here.
The effects of the environmental forcing function applied produced both direct and indirect effects on the trophic web of CChME, as inferred by Watters et al. (2003) for the Equatorial Pacific Ocean. Oscillations on phytoplankton biomass were trespassed to higher trophic levels through cascade effects indicating that predation and environment play important structuring roles in marine ecosystems (Herendeen, 2004).

Specifically, the results of this work indicate that such forcing could have repercussions on fishery resources (small pelagics). This is not surprising, since it has been informed that both, anchovy and common sardine are affected significantly by environmental variability, exhibiting high variability in recruitment (Cubillos and Arcos, 2002, Arcos et al., 2004), biomass and landings (Yáñez et al., 1992; SubPesca, 2004a). The explanation can be found in the strong trophic link between small pelagics and phytoplankton, characterized by fast responses of considerable magnitude (Fig. 3a) in this upwelling ecosystem of short trophic chains (Neira and Arancibia, 2004). This situation is not seen in ecosystems with longer trophic chains and several components, where a weaker coupling between lower trophic level is found (Micheli, 1999; Watters et al., 2003).

The simulation of the trajectory of horse mackerel and Chilean hake biomass indicate that these fishery resources can be sensitive to environmental variations ($\Delta$SST). Their observed biomass (hydroacoustics or swept area) and the EwE estimates do not show similar tendencies, which is probably due to other regulatory mechanisms. For example, horse mackerel biomass estimated with EwE (Fig. 5) tends to increase, probably due to interspecific interactions such as the increased euphausiid biomass. Euphausiids are the main prey of horse mackerel in the CChME (Arancibia and Aedo, in press). The greatest Chl a values registered in year 2000 (La Niña) would have allowed increased euphausiids biomass. Neira et al. (2004) show that the trophic structure of the CChME changes in year 1998, with euphausiids as the dominant prey in diet of both horse mackerel and Chilean hake.
This is consistent with observations in other upwelling areas (Barber and Chávez, 1983, 1986; Fiedler et al., 1992; Chávez et al., 2002). Daneri et al. (2000) reports that the CChME has one of the highest levels of primary production of the world’s oceans. The high phytoplankton biomass provides the ideal medium for the development of the other components of a bottom-up controlled ecosystem.

The combined forcing (ΔSST and F; scenario 3; Fig. 3c) hide the impact of fishing (i.e. horse mackerel), which is decreasing the observed biomass of the fishery resources. Daskalov (2002) showed that the combination of overexploitation of some fishery resources in the Black Sea (fishing forcing) and eutrophication (environmental forcing) had generated important changes in trophic structure, and that these changes were passed along through the trophic levels in a cascade effect.

On the other hand, the abundance of the horse mackerel stock in the CChME has declined due to overexploitation (Arancibia et al., 1998; Cubillos et al., 1999; SubPesca, 1999; Quiñones et al., 2003) and meso-scale oceanographic changes like ENSO (Arcos et al., 2001). Both the estimated and observed (hydroacoustics) Chilean hake biomass tended to increase. This is probably because the abundance and/or availability of demersal species increases after an El Niño event (Escribano et al., 2004), as found in Perú (Barber and Chávez, 1986) and South Africa (Shannon et al., 1988), where ecosystemic components respond to local, regional, and even large-scale environmental changes (Watters et al., 2003). In the present study, the simulated values were more conservative than the observed values (SubPesca, 2004b).

Nonetheless, Arancibia (unpublished) indicates that the Chilean hake biomass, estimated annually with hydroacoustics in central Chile, has been consistently overestimated (2000 to 2004). This author proposes that Chilean hake biomass was 50% less than officially reported by SubPesca in 2004 (SubPesca, 2004b).
The changes induced by F as top-down forcing on the biomass of fishery resources generated cascade effects of lesser magnitudes in lower tropic levels (phytoplankton) and of greater magnitudes in higher tropic levels (horse mackerel) (Fig. 3b).

Therefore, fishing promotes changes in the biomass of target species but can also indirectly affect phytoplanktonic biomass due to indirect trophic effects and the ecosystem’s structure, as reported by Daskalov (2002) and Harvey et al. (2003) for the Black Sea and the Baltic Sea, respectively.

The relative biomass of the CChME’s small pelagics tended to decrease, whereas that of horse mackerel and Chilean hake oscillated. This could be due to the control type and trophic interaction manifested in the systems, generating complex indirect responses in predator-prey interactions, as reported by Daskalov (2002) and Herendeen (2004). But, likely the biomass of Chilean hake has been over-estimated; meaning that that it's fishing mortality has been under-estimated.

Other factors to consider are generation times, lags in the response of each species to the forcings, resilience (sensu Mackinson et al., 1997), and life strategy (r, K) (sensu Micheli, 1999). The response times are fastest in short-lived organisms (phytoplankton, small pelagics) and slower in longer-living organisms (Chilean hake, sea lions, horse mackerel). All these factors can act together to weaken or strengthen coupling, a characteristic of marine environments (Micheli, 1999; Harvey et al., 2003; Watters et al., 2003; Herendeen, 2004).

The comparative analysis of the magnitude of change in relative biomass of fishery resources (anchovy, common sardine, horse mackerel, Chilean hake), phytoplankton and the top predator (sea lion), indicates that environmental forcing (ΔSST) is more important than fishing mortality (F). Arancibia & Neira (2005) shown that effects due to ENSO are lower than fishing effort effects on the ecosystem structure. Probably, these authors did not consider the importance of ΔSST as physical forcing on phytoplankton, which can also change highest trophic
levels, i.e. sea lion. This is supplied by the presence of short trophic webs and the strong connection between small pelagics and phytoplankton (Neira et al., 2004). However, the effect of both forcings on small pelagics leads to a slightly reduced change in relative biomass than the values derived from environmental forcing alone (Fig. 4).

Horse mackerel, a medium-sized pelagic fish, clearly exhibits larger changes in its relative biomass range when both forcing are operating than when only one is operating. This is due to horse mackerel is more sensitive to fishing pressure because it is in a higher trophic level, as seen indirectly by horse mackerel landings in central-southern Chile. In the mid-1990s, landings were at 3.6-4.0 million tons, decreasing drastically until reaching 1.1 million tons in 1999, a rate that is currently maintained. It should also be noted that the average size of the specimens has also decreased (SubPesca, 2004c).

It is readily apparent that the CChME’s structure has been changing, particularly in recent years, without discounting the fishing influence. Arancibia and Neira (2005) show that the process of fishing down the food webs clearly exists (sensu Pauly et al., 1998), which agrees with the PS/ZP ratio (sensu Caddy & Garibaldi, 2000; Fig. 6) in any of the three scenarios detailed here: environmental forcing, fishing forcing, or both simultaneously. This shift has occurred between 1999 and 2000.

In brief, this study showed that combination of fisheries and physical forcing can cause important alterations in the trophic structure in the CChME. These findings may provide insights for ecosystem management, suggesting that this type of studies could provide better understanding of fisheries dynamics in a holistic context.
Acknowledgements

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### Tables

Table 1. Trophic groups and trophic levels of the CChME, modified from Neira et al. (2004) (j-juveniles; a-adults).

<table>
<thead>
<tr>
<th>Common name</th>
<th>Scientific name (age group)</th>
<th>TLi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sea lion</td>
<td><em>Otaria flavescens</em></td>
<td>4.23</td>
</tr>
<tr>
<td>Chilean hake (j)</td>
<td><em>Merluccius gayi</em> (0-3)</td>
<td>3.4</td>
</tr>
<tr>
<td>Chilean hake (a)</td>
<td><em>Merluccius gayi</em> (4+)</td>
<td>3.5</td>
</tr>
<tr>
<td>Common sardine (j)</td>
<td><em>Strangomera bentincki</em> (0)</td>
<td>2.0</td>
</tr>
<tr>
<td>Common sardine (a)</td>
<td><em>Strangomera bentincki</em> (1+)</td>
<td>2.2</td>
</tr>
<tr>
<td>Anchovy (j)</td>
<td><em>Engraulis ringens</em> (0)</td>
<td>2.0</td>
</tr>
<tr>
<td>Anchovy (a)</td>
<td><em>Engraulis ringens</em> (1+)</td>
<td>2.2</td>
</tr>
<tr>
<td>Carrot prawn (j)</td>
<td><em>Pleuroncodes monodon</em> (0)</td>
<td>2.0</td>
</tr>
<tr>
<td>Carrot prawn (a)</td>
<td><em>Pleuroncodes monodon</em> (1+)</td>
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<tr>
<td>Yellow prawn</td>
<td><em>Cervimunida johni</em></td>
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<td><em>Genypterus maculatus</em></td>
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<td>Rattail fish</td>
<td><em>Caelorinchus aconcagua</em></td>
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</tr>
<tr>
<td>Big-eye flounder</td>
<td><em>Hipoglossina marmor</em></td>
<td>3.0</td>
</tr>
<tr>
<td>Cardinal fish</td>
<td><em>Epigonus crassicaudus</em></td>
<td>3.5</td>
</tr>
<tr>
<td>Pacific sand perch</td>
<td><em>Prolatifius jugularis</em></td>
<td>3.6</td>
</tr>
<tr>
<td>Skates</td>
<td><em>Raja spp.</em></td>
<td>3.0</td>
</tr>
<tr>
<td>Euphausiids</td>
<td><em>Euphausia spp.</em></td>
<td>2.5</td>
</tr>
<tr>
<td>Copepods</td>
<td><em>Calanus spp.</em></td>
<td>2.1</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td><em>Diatoms</em></td>
<td>1.0</td>
</tr>
<tr>
<td>Detritus</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Mortality by fishing ($F$, year$^{-1}$) for the main CChME fishery resources, from Arancibia and Neira (2003) and Arancibia et al. (2003).

<table>
<thead>
<tr>
<th>Year</th>
<th>Chilean Hake</th>
<th>Common sardine</th>
<th>Anchovy</th>
<th>Horse mackerel</th>
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</thead>
<tbody>
<tr>
<td>1992</td>
<td>0.18</td>
<td>1.58</td>
<td>0.46</td>
<td>1.00</td>
</tr>
<tr>
<td>1993</td>
<td>0.17</td>
<td>0.75</td>
<td>0.26</td>
<td>1.08</td>
</tr>
<tr>
<td>1994</td>
<td>0.11</td>
<td>0.23</td>
<td>0.76</td>
<td>1.35</td>
</tr>
<tr>
<td>1995</td>
<td>0.10</td>
<td>0.35</td>
<td>0.46</td>
<td>1.45</td>
</tr>
<tr>
<td>1996</td>
<td>0.11</td>
<td>0.88</td>
<td>0.90</td>
<td>1.58</td>
</tr>
<tr>
<td>1997</td>
<td>0.17</td>
<td>0.46</td>
<td>0.59</td>
<td>2.41</td>
</tr>
<tr>
<td>1998</td>
<td>0.18</td>
<td>1.40</td>
<td>0.27</td>
<td>1.36</td>
</tr>
<tr>
<td>1999</td>
<td>0.56</td>
<td>0.93</td>
<td>1.31</td>
<td>0.60</td>
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<tr>
<td>2000</td>
<td>0.43</td>
<td>0.84</td>
<td>1.42</td>
<td>0.60</td>
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<tr>
<td>2001</td>
<td>0.22</td>
<td>1.07</td>
<td>0.67</td>
<td>0.60</td>
</tr>
<tr>
<td>2002</td>
<td>0.06</td>
<td>1.01</td>
<td>0.64</td>
<td>0.52</td>
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</table>
Table 3. Magnitudes of change (%) in the biomass of the main CChME groups in the three simulation scenarios. Max: maximum magnitudes of change; Min: minimum magnitudes of change.

<table>
<thead>
<tr>
<th>Group</th>
<th>Scenario 1</th>
<th>Scenario 2</th>
<th>Scenario 3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Max</td>
<td>Min</td>
<td>Max</td>
</tr>
<tr>
<td>Phytoplankton</td>
<td>50</td>
<td>-66</td>
<td>22</td>
</tr>
<tr>
<td>Anchovy</td>
<td>55</td>
<td>-70</td>
<td>00</td>
</tr>
<tr>
<td>Common sardine</td>
<td>55</td>
<td>-70</td>
<td>00</td>
</tr>
<tr>
<td>Horse mackerel</td>
<td>47</td>
<td>-51</td>
<td>58</td>
</tr>
<tr>
<td>Chilean hake</td>
<td>29</td>
<td>-44</td>
<td>15</td>
</tr>
<tr>
<td>Sea lion</td>
<td>26</td>
<td>-40</td>
<td>29</td>
</tr>
</tbody>
</table>
Figure Captions

Fig. 1. Study area in the central Chile marine ecosystem (CChME). The stars (*) indicate positions used for estimating sea surface temperature anomalies (ΔSST).

Fig. 2. a) Sea surface temperature anomalies (ΔSST) in the CChME, 1992-2002; b) observed Chl a values (mg/m⁻³) from satellite images (SeaWiFS) and estimated values from an empirical model (equation 1).

Fig. 3. Ten-year simulations, using ECOSIM, of the biomass of the main groups making up the CChME. a) Scenario using ΔSST as a forcing function; b) scenario considering fishing mortalities (F) from 1992-2002; and c) scenario including both variables (ΔSST and F). In order to simplify the interpretation, only the following are shown: phytoplankton (TL= 1), common sardine (TL= 2.2), anchovy (TL= 2.2), Chilean hake (TL= 3.5), horse mackerel (TL= 3.9), and sea lion (TL= 4.23).

Fig. 4. Relative values expressed as a percentage of change in the biomass of the main trophic groups of the CChME’s marine ecosystem in the three simulated scenarios (-scenario 1; -scenario 2; -scenario 3).

Fig. 5. Relative biomass estimated by EwE (dotted line) and observations (solid line) for the main CChME fishery resources, 1992-2002: (a) anchovy, (b) common sardine, (c) horse mackerel, (d) Chilean hake.

Fig. 6. The PS/ZP ratio for the central Chile marine ecosystem (CChME) under three simulated scenarios. (Symbols: -scenario 1; ○-scenario 2; ●-scenario 3).
Figure 1.
Figure 2.

The top graph (a) shows the variation of ΔSST (°C) over time from 1992 to 2002, highlighting the El Niño 97-98 and La Niña 99-00 events.

The bottom graph (b) illustrates the observed and estimated chlorophyll a (mg/m³) levels from September 1997 to September 2002.
Figure 3.
Figure 4.
Figure 5.
Figure 6.