Analysing changes in the southern Humboldt ecosystem for the period 1970–2004 by means of dynamic food web modelling

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\section*{A B S T R A C T}

A 22-group Ecopath model representing the southern Humboldt (SH) upwelling system in the year 1970 is constructed. The model is projected forward in time and fitted to available time series of relative biomass, catch and fishing mortality for the main fishery resources. The time series cover the period 1970 to 2004 and the fitting is conducted using the Ecopath with Ecosim (EwE) software version 5.1. The aim is to explore the relative importance of internal (trophic control) and external (fishing, physical variability) forcing on the dynamics of commercial stocks and the Southern Chilean food web. Wide decadal oscillations are observed in the biomass of commercial stocks during the analyzed period. Fishing mortality explains 21% of the variability in the time series, whereas vulnerability (\nu) parameters estimated using EwE explain an additional 20%. When a function affecting primary production (PP) is calculated by Ecosim to minimize the sum of squares of the time series, a further 28% of variability is explained. The best fit is obtained by using the fishing mortality time series and by searching for the best combination of \nu parameters and the PP function simultaneously, accounting for 60% of total variability in the time series. The PP function obtained from the best fit significantly correlates with independent time series of an upwelling index (UI; \rho = 0.47, \ p < 0.05) and sea surface temperature (SST; \rho = 0.45, \ p < 0.05), representing environmental conditions in the study area during the same period of time. These results suggest that the SH ecosystem experienced at least two different environmentally distinct periods in the last three decades: (i) from 1970 to 1985 a relatively warm period with low levels of upwelling and PP, and (ii) from 1985 to 2004 a relatively cold period with increased upwelling and PP. This environmental variability can explain some of the changes in the food webs. Fishing (catch rate) and the environment (bottom-up anomaly in PP) appear to have affected the SH both at the stock and at the food web level between 1970 and 2004. The vulnerability setting indicates that the effects of external forcing factors may have been mediated by trophic controls operating in the food web.

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1. Introduction

Fishing is a partly managed human activity that often represents a major threat to marine ecosystems (Jackson et al., 2001; Halpern et al., 2008). Technology applied to shipping, navigation, stock detection, and fishing devices (Valdermarsen, 2001) transformed human abilities, so humans could become efficient and dangerous predators, able to capture almost anything that is abundant and/or valuable in the sea (Pauly et al., 2002). This behaviour has disrupted many ecosystems through changes in marine food webs and destruction of physical habitat (Jennings and Kaiser, 1998; Pauly et al., 1998; Daan et al., 2005). Although worldwide decreases in fish stocks are strongly correlated with the start of the industrial fishing era (Hutchings, 2000; Myers and Worm, 2003; Christensen et al., 2003), physical factors are widely recognized to play an important role in fish population dynamics (Cushing, 1982). Marine populations showed fluctuations even before the start of
fishing, revealing a strong link between their dynamics and environmental variability (Shackleton, 1987; Schwartzlose et al., 1999). Marine ecosystems also undergo large-scale, decadal fluctuations and regime shifts, which seem to be driven by climate forcing (Hare and Mantua, 2000; Stenseth et al., 2002; Chavez et al., 2003; Steel, 2004), but some have been also related to overfishing (Curry and Shannon, 2004; Lees et al., 2006; Daskalov et al., 2007).

In some marine ecosystems predation mortality is the main source of total mortality (Bax, 1991; 1998) and fishery removal of predatory species has revealed putative trophic cascades (top-down control) in the ocean (Steneck, 1998: Dulvy et al., 2004; Frank et al., 2005; Daskalov et al., 2007). On the other hand, wasp-waist control exerted by small pelagic fish (sensu Curry et al., 2000) seems to be a characteristic feature in upwelling ecosystems (Curry et al., 2005). This suggests that in such ecosystems, marine populations are often also regulated by the behaviour of predators, total consumption and prey availability. Therefore, the effects of fishing and physical forcing on living groups and food web structure can strongly depend on who eats whom, and more significantly on who controls whom (Shannon et al., 2000; Hunt and McKinnell, 2006).

Upwelling ecosystems are productive areas of the world’s oceans where fishing, environmental shifts and trophic controls are key processes (Schwartzlose et al., 1999; Chavez et al., 2003; Curry et al., 2005; Fréon et al., 2009). However, the relative importance of each factor on food web dynamics is poorly understood and quantified. In particular, the southern section of the Humboldt system – off central Chile – is one of the least studied upwelling systems of the world (Morales and Lange, 2004). Although species replacement, trophic controls and fishery-induced changes at the ecosystem level are likely to affect the whole ecosystem (Yáñez et al., 1992; Neira et al., 2004; Arancibia and Neira, 2005; Alheit and Niñuen, 2004), single-species approaches dominate fisheries management in Chile.

The global call for an ecosystem approach to fisheries (FAO, 2003) implies the adoption of a wider and holistic view in management, necessitating consideration of multi-species and climate effects. Ecopath with Ecosim (EwE; Walters et al., 1997; Christensen and Walters, 2004) is a family of models that has been applied to many different regions around the world (see www.ecopath.org), allowing global and local assessments of aquatic food webs and ecosystem effects of fishing (e.g., Pauly and Christensen, 1995; Pauly et al., 1998, 2002; Christensen et al., 2003; Neira and Arancibia, 2004; Neira et al., 2004). The dynamic Ecosim model allows users to fit food web models to observed data and, in the process, evaluate the relative effects of fishing, trophic relationships and bottom-up forcing on observed dynamics (Christensen and Walters, 2004; Christensen et al., 2005).

Shannon et al. (2008) used three EwE models representing the Benguela Current and the northern (Peru) and southern (central Chile) subssections of the Humboldt Current, with the aims of comparing internal and external forcing in these three ecosystems, with focus on environmental forcing in different trophic levels. The fitting process revealed that changes in the sum of squares were sensitive to, among others, trophic relationships involving common sardine and anchovy as predators and prey (Shannon et al., 2008). Unfortunately, these authors did not analyze further the dynamics of other functional groups that are of economic or ecological value in the Southern Humboldt. However, the above authors indicated that food web dynamics in the Southern Humboldt may be different from the other upwelling systems due to unique features.

Comparing marine ecosystems using inter-calibrated models is important in understanding ecosystem effects of fishing and the environment worldwide. This endeavour requires relatively detailed understanding of the different ecosystems and models. Previous publications describing the EwE model of the Southern Humboldt are not readily available (Neira, 2008) and/or not present all details regarding model parameterization and findings (Shannon et al., 2008). Thus, we consider important to fully introduce the dynamic simulation for the southern Humboldt in order to allow future comparisons of marine ecosystems affected by environmental variation and fishing. Therefore, in this paper we further investigate the southern Humboldt system introducing an Ecopath model representing the upwelling system off central Chile in 1970 that is constructed and projected forward in time using the Ecosim routines. The model simulations are fit to available time series of biomass, landings and fishing mortality for the main commercial fish stocks. Our aim is to analyze the relative importance of fishing mortality, predator–prey interactions (through prey vulnerability) and bottom-up forces (through changes in primary productivity) on observed stocks and food web dynamics.

2. Methods

The study area corresponds to the southern section of the Humboldt (SH) system off central Chile, from 33° S to 39° S and from the coast to 30 nautical miles offshore, covering a total area of 50000 km² (Fig. 1). The geographic, oceanographic, ecological and fishing features of this sub-system have been described in Camus (2001), Strub et al. (1998), Daneri et al. (2000), Escribano et al. (2003) and Neira et al. (2004). The area consists of a narrow
continental shelf, seasonal upwelling and high primary, secondary and fish production. As a consequence, the main Chilean purse seine and trawling fleets operate in this area, supporting most of the landings in Chile. As described by Neira et al. (2004), pelagic fish stocks of anchovy (Engraulis ringens), Araucanian herring (Strongamogena bentincki) and horse mackerel (Trachurus symmetricus) dominate the pelagic fish community, both in biomass and landings. Important flows are also present in the demersal and benthic domains mainly associated with Chilean hake (Merluccius gayi), the main demersal fish component. Chilean hake has strong trophic interactions in the system, mediated by cannibalism and including predation on anchovy, Araucanian herring, euphausiids, benthic invertebrates (mainly red squat lobster Pleuroncodes monodon) and other demersal fish (Neira et al., 2004).

2.1. Southern Humboldt ecosystem model

An Ecopath model (Christensen and Pauly, 1992) representing the SH system in 1970 was constructed by Neira (2008) as an updated version of the model constructed by Neira and Arancibia (2004). The year 1970 was chosen because it represents the starting point for the longer time series of biomass estimates of the main fishery resources in central Chile. The model comprises 22 functional groups, including all the main trophic components of the system with emphasis on pelagic, demersal and benthic fish species (target and non-target species), plus their main prey (zooplankton and phytoplankton) and predators (marine birds, sea lions and cetaceans). Considering the strong ontogenetic changes in the diet of Chilean hake, the model includes age structure in this species as follows: juvenile Chilean hake includes the age group 0–3 years old, whereas adult Chilean hake consists of age groups 4+ years (for details see Neira and Arancibia, 2004). Input parameters for model groups are fully described in Neira and Arancibia (2004), Neira (2008) and Neira et al. (submitted for publication). For Araucanian herring, anchovy, macrobenthos (red squat lobster), horse mackerel and Chilean hake, biomass (B) and landings (Y) were set at values for 1970. These data correspond to official statistics on stock biomass estimated by using direct (i.e., survey) or indirect (i.e., single-species stock assessment models) assessments methods and landings (see Table 1).

No changes were required to balance this Ecopath model. Routines in the EwE software version 5.1 were used to project the model variables forward in time, forced by data series representing intensity of fishing (Table 1). The model was fitted using available time series of estimates for relative biomass (Table 1).

2.2. The modelling approach

Ecopath is the time-dynamic version of the Ecopath model and uses mass-balance results from Ecopath for parameter estimation. Differential and difference equations are used in Ecopath to simulate the dynamics of fast and slow growing groups (Walters et al., 1997; 2000). The model explicitly incorporates the effects of trophic controls and allows for size/age structure.

In Ecopath, the biomass changes for functional groups are a function of biomass, harvest rate, predator consumption and other mortalities (for more detailed equations see Walters et al., 1997; Pauly et al., 2000; Christensen and Walters, 2004; Christensen et al., 2005).

\[
\frac{dB_i}{dt} = f(B_i) - M_0 B_i - F_i B_i - \sum_{j=1}^{n} c_{ij}(B_i, B_j)
\]

where \(f(B_i)\) is a positive function of biomass \(B\) for each group \(i\) in the model, \(M_0\) is a non-predator mortality rate, \(F_i\) is the fishing mortality rate, and \(c_{ij}(B_i, B_j)\) is a function that predicts consumption of prey \(i\) by predator \(j\). In the case of primary producers, a simple saturation production relationship is used:

\[
f(B_i) = \frac{r_i B_i}{1 + B_i h_i}
\]

where \(r_i\) is the maximum \(P/B\) that \(i\) can exhibit when \(B_i\) is low and \(r_i/h_i\) is the maximum net primary production rate for pool \(i\) when biomass is not limiting to production \((B_i, h_i)\). Assuming the Ecopath parameters an estimate of the ratio of maximum to initial or base \(P/B\) (ratio of \(r_i\) to \((P/B)\) entered for Ecopath estimation), \(r_i\) can then be computed from this ratio, and \(h_i\) from the Ecopath base estimates of primary production rate \((P/B)\) and biomass.

Ontogenetic shifts in juveniles and adult components of Chilean hake were modelled using a Deriso–Schnute delay difference model (Deriso, 1980; Schnute, 1987), for details see Walters et al. (2000).

Predator prey interactions are assumed to be moderated by prey behaviour to limit exposure to predation (Walters et al., 1997; Christensen et al., 2005).
Consumption ($Q_i$) of each group $i$ by their predator $j$ is estimated by:

$$Q_{ij} = \frac{a_{ij} \times v_{ij} \times B_j \times T_i \times T_j \times S_{ij} \times (M_{ij}/D_j)}{v_{ij} + (v_{ij} \times T_i \times M_{ij}) + a_{ij} \times (M_{ij} \times B_j \times S_{ij} \times (T_j/D_j))}$$

(3)

where $a_{ij}$ is the rate of effective search for $i$ by $j$, $v_{ij}$ is the exchange rate for prey biomass between a vulnerable and non-vulnerable state, $T_i$ represents prey relative feeding time, $T_j$ the predator relative feeding time, $S_{ij}$ a user-defined seasonal or long term forcing effect, $M_{ij}$ a mediation forcing effect, and $D_j$ the effects of handling time as a limit to consumption rate. In the absence of further information, the model was run assuming Ecosim default values for all parameters in Eq. (2). The only exception was $v_{ij}$, which is allowed to change during the process of fitting the model to time series, see below.

The parameter $v$ (vulnerability) is a key feature of Ecopath with Ecosim since it allows for incorporation of density-dependence. The vulnerabilities represent the factor by which a large increase in predator biomass ($B_j$) will affect predation mortality for a given prey ($M_{ij}$). Low vulnerability means that an increase in $B_j$ will not cause any noticeable increase in $M_{ij}$. A high vulnerability indicates that if $B_j$ is for example doubled, it will cause close to a doubling in $M_{ij}$. This means that the dynamics of the biomasses will be stable when close to carrying capacity (where vs. are low), and unstable when far below carrying capacity (where vs. are high).

Ecosim models this aspect of predator prey interactions by re-expressing Ecopath base biomass in terms of two components: one vulnerable or available biomass ($V$), the other invulnerable or unavailable biomass ($B-V$) to predators. Further, it is assumed that there is a flow ($v_{ij}$) of organisms from ($B-V$) to $V$. In Ecosim, $v$ distributes from 1 to $+\infty$, with a default value of 2 (also termed mixed control). Therefore when $v$ is high ($v \gg 2$), the consumption will be proportional to the amount of predators, and thus predation control will be top-down. Conversely, if $v$ is low ($1 < v \ll 2$), replacement of depleted biomass from ($B-V$) to $V$ will be slow, and the control will be bottom-up (Walters et al., 1997; Christensen et al., 2005).

Ecosim uses an iterative fitting procedure to match predicted biomasses to time series data. Following Shannon et al. (2004) and Christensen et al. (2005), the following steps were used to explore the relative roles of fishing, predator–prey interactions and anomalies in primary productivity (PP) in explaining variability in the abundance time series data:

1. The time series data file was read from an Excel file and stored in the EwE database.
2. The model was projected forward in a null case, using the catches and fishing mortalities in the balanced Ecopath model for 1970 and default vulnerabilities for all $i$. This allowed estimation of a baseline goodness-of-fit value (sums of squares, SS) which Christensen and Walters (2004) define as the sums of log ratios of observed and predicted biomasses, observed and predicted fishing mortalities and observed and predicted fishing mortality rates, and the log ratios of observed and predicted catches (using all the series listed in Table 1).
3. The fishing rates (fishing forcing) were set to the observed values from the time series (Table 1) and the model was run using default vulnerabilities for all $i$.
4. The 15 $v$ values to which EwE was most sensitive were calculated by slightly changing each $v$ parameter (by 1%) and rerunning the model to assess how much the SS changed. This simplifies what was previously undertaken for cross-system comparisons of internal vs. external forcing in upwelling systems, in which 25 $v$ parameters were fitted (Shannon et al., 2008). Unlike Shannon et al. (2008), we present the obtained values for the $v$ parameter, so allowing potential users to perform simulations and/or inter-model comparisons.
5. A vulnerability search based on (4) was used to estimate $v$ values that would minimize SS.
6. A search was conducted for time series values of annual relative PP that may represent historical productivity shifts impacting biomasses through the food web (for details of this routine see Christensen et al., 2005). This step included the analysis of a probability distribution for the null hypothesis that all of the deviations between model and predicted abundances are due to chance alone, i.e., under the hypothesis that there are no real PP anomalies.
7. A final search was carried out to minimize the SS for a combination of $v$ values and a relative PP time series simultaneously, based on (4) and (6). Unlike Shannon et al. (2008), no external forcing function was applied to search rates of interactions involving predator prey interactions.

We stress that steps (6) and (7) do not fit model predictions to a time series of observed PP values or yearly mean phytoplankton concentrations, but generate model-based yearly PP anomalies.

3. Results

Fishing mortality time series contributed 21% to explain observed trends in commercial stocks and zooplankton in the SH system for the period 1970–2004. The vulnerability tuning indicated that the 15 interactions for which the $v$ parameters had the strongest impact on the SS included phytoplankton with zooplankton III, anchovy and Araucanian herring; zooplankton I with zooplankton II; zooplankton III with mesopelagic fish, horse mackerel and small Chilean hake; macrobenthos with large Chilean hake; anchovy with small Chilean hake; Araucanian herring with large Chilean hake and small Chilean hake; horse mackerel with sea lion; large Chilean hake with sea lion; small Chilean hake and large Chilean hake; and detritus with macrobenthos (Table 2).

The estimated vulnerability settings reduced the baseline SS by 14% (in addition to the 21% explained by fishing). The search for time series values of annual relative PP that may represent historical productivity shifts impacting biomasses through the food web resulted in a further 28% decrease in the SS when vulnerabilities had been tuned, and 28% also when the anomaly in PP was estimated using default $v$ values ($v=2$) for all model groups. A vulnerability setting run over fishing and the anomaly of PP (see step 7 in Methods section) reduced the baseline SS by a further 20% (in addition to the 21% explained by fishing and the 28% explained by the anomaly in PP). This last result gave the best fit to the time series (Figs. 2 and 3), decreasing the baseline SS by 69%.

This fitting scenario resulted in a fair representation of the biomass and catches of model groups for which the time series are long, e.g., macrobenthos, Araucanian herring and Chilean hake (adults) (Fig. 2). However, the fit between EwE estimates and observed macrobenthos biomass is not good before 1980. The model is not as good at reproducing the biomass trends for anchovy, mesozooplankton and macrozooplankton (Fig. 2). The model explains the biomass trend for horse mackerel until the end of the 1980s, underestimates horse mackerel biomass until the 1990s and then overestimates biomass from the early 1990s onwards (Fig. 2).

The model reproduces the catches fairly well for all groups for which series are available, i.e., macrobenthos, anchovy, Araucanian herring, horse mackerel and Chilean hake (Fig. 3). However, the catches predicted by EwE for macrobenthos are overestimated post-1980. In the case of anchovy, catches are underestimated after
Table 2
Vulnerability parameter setting obtained from the best fitting scenario. Shaded interactions are those 15 values to which Ecosim model is most sensitive (measure as change is sum of squares). The colour significance scale is: red, very sensitive; cyan, moderately sensitive; yellow, slightly sensitive; green, sensitive; light blue, less sensitive.

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1985. For horse mackerel, EwE predicted a peak in catches approximately five years later than observed catches.

The PP function obtained from the best fit significantly correlates with independent time series of an upwelling index (UI; rho = 0.47, p < 0.05) and sea surface temperature (SST; rho = −0.45, p < 0.05), representing environmental conditions in the study area during the same period of time (Fig. 4).

4. Discussion

Although the percentage of total variability explained by fishing in the analyzed time series of the SH could be considered low (21%), fishing impacts in the southern Humboldt are larger than or similar to those found in another upwelling systems where a similar analysis has been conducted. Shannon et al. (2004) found that reported fishing patterns explained 2–3% of total variability when fitting an EwE model to available time series for trophic groups in the southern Benguela system. On the other hand, Taylor et al. (2008) and Shannon et al. (2008) indicated that fishing patterns explained 22% and 21% of variability in a model of the Northern Humboldt Current (Peru). Arancibia and Neira (2005) found that fishing has affected community structure in the SH system by causing a significant decrease in the mean trophic level of the catch. Likewise, Neira (2008) and Neira et al. (submitted for publication) showed that fishing mortality increased across snapshot models representing past to present periods of the system. However, the information on fishing catches and fishing mortality is not complete for the Southern Humboldt for all species during the span of this study (Table 1), and time series are needed that include data for more species and more years to improve model quality.

4.1. Internal flow control

It has been estimated that, for some periods, predators removed most of the production of commercial stocks and, therefore, predation mortality could be considered the main cause of mortality in the SH system (Neira and Arancibia, 2004; Neira et al., 2004, submitted for publication; Neira, 2008). However, vulnerability to predation (trophic control) was found to explain 14–21% of the variability in the time series analyzed here. This indicates that, in marine ecosystems, the answers to questions such as “who eats whom (and how much)?” do not necessarily provide answers to the question of “who controls whom?”

The explanatory power of vulnerability parameters is low in this study when compared with results in Shannon et al. (2004) and Shannon et al. (2008) for the southern Benguela, where changes in the most sensitive ρ parameters reduced baseline SS by up to 50%. In turn, Taylor et al. (2008) reported a 40% decrease in variability of time series analysis when vulnerability parameters are tuned. This can be partly explained by the lack of time series for top predators and the shortness of the time series for zooplankton in the southern Humboldt system. These groups are important because they can constrain fish dynamics in food web models (Christensen et al., 2005). Therefore, it is recommended that studies aimed at reconstructing population levels for top predators and plankton groups in the southern Humboldt system should be conducted, because they can potentially increase our understanding of the dynamics of commercial stocks and the whole food web. Stock reduction analysis (Walters et al., 2006), fish scales, and silicates can be good alternatives to reconstruct abundances of top predators, fish species and plankton, respectively.

The search procedure revealed that changes in the SS are sensitive to trophic relationships involving Araucanian herring and
These anchovies (S. of Chilean small) such as the hake, were foraging on small pelagic fish and plankton. These results partially agree with the hypothesis of wasp-waist control in upwelling ecosystems, i.e., small pelagic fish exerting top-down control on prey and bottom-up control on predators (Cury et al., 2000, 2005). However, the wasp-waist architecture of food webs in upwelling ecosystems has been disputed more recently (Fréon et al., 2009), which may help explain why the combination of \( \nu \) values for the best fit model did not indicate a clear pattern in terms of wasp-waist control. It is also important to note that wasp-waist control is likely to depend on the spatial scale of the analysis – i.e., more likely to occur at smaller spatial scales (see Ayón et al., 2008; Taylor et al., 2008). This is an important consideration for inter-Eastern Boundary Current Systems comparisons, via dynamic trophic model fitting or other methods.

On the other hand, the vulnerability of small pelagic fish to Chilean hake deviated from mixed control (\( \nu < 2 \)), suggesting a tendency for bottom-up control although Araucanian herring and small Chilean hake had \( \nu \geq 2 \), indicating top-down control.

These results could be related, again, to the lack of knowledge about the dynamics of trophic groups located at both higher and lower trophic levels of the food web. For example, Shannon et al. (2004) found that a wasp-waist control pattern emerged when fitting an EwE model of the southern Benguela to time series data including good representations of the dynamics of top predators such as seals and marine birds. Therefore, a more robust conclusion about wasp-waist, top-down or bottom-up control between prey and predators in the SH system, at least from this modelling perspective, should be possible when these kinds of data become available.

The foraging arena model (Walters et al., 1997) depicts the relationship between per-capita consumption by a predator as decreasing with the overall abundance of that predator. Therefore, an alternative way of interpreting vulnerability values is that high and low values of \( \nu \) indicate how far or close to carrying capacity predators were at the beginning of the simulation. High \( \nu \) values indicate that predators were far from their carrying capacity change with predator abundance indicating that there is little density dependence, while low \( \nu \) values indicate that predators were close to carrying capacity because their consumption is proportional to prey productivity indicating strong density dependence (Christensen et al., 2005). The high and low \( \nu \) values obtained from the best fitting scenario (e.g., in the case of hake and mesopelagic as predators) could be interpreted in this way. From the time series we know that the biomass of hake at the beginning of the time simulation was very low compared to the late 1990s (likely far from its carrying capacity). Unfortunately, no abundance data are available for mesopelagic fish.

The model is also sensitive to the \( \nu \) parameter of horse mackerel (as predator) and zooplankton III (as prey). However, this interaction appears to be best represented as a mixed control, rather than top-down or bottom-up.

The sums of squares were also sensitive to changes in macrobenthos vulnerability (Table 2). Specifically, high vulnerability was observed for macrobenthos to predation by Chilean hake, which could either indicate top-down control by Chilean hake (in the traditional way of interpreting \( \nu \) values) or that hake was far from its carrying capacity with respect to macrobenthos at the beginning of the time series. This result illustrates the important role of Chilean

**Fig. 2.** Best fit of Ecosim predicted biomass (line) to time series of observed biomass (dots) or CPUE (hake) for model groups in the southern Humboldt ecosystem off central Chile, period 1970–2004. Biomass is plotted relative to biomass in the first year of simulations, i.e., 1970. Additional symbols: macrobenthos cross and triangles = surveys; hake cross = spawning biomass, triangles = acoustic surveys.

**Fig. 3.** Best fit of Ecosim predicted catches (line) to time series of observed catches (dots) for several commercial stocks in the southern Humboldt ecosystem off central Chile, period 1970–2004. Catches are plotted relative to the catch in the first year of simulations, i.e., 1970.
hake as a predator in the benthic-demersal realm as already noted by Neira et al. (2004).

### 4.2. Environmental forcing

The best fit indicated that a long-term change in PP might have affected the dynamics of groups in the SH system. No statistical evidence was found to support the null hypothesis that all of the deviations between model and predicted abundances are due to chance alone (p value < 0.05), indicating that there is a consistent pattern in the deviations. This result is reinforced when the proposed anomaly in PP is compared with independent time series of sea surface temperature (SST) and an upwelling index (UI) in the SH system for the period 1970–2000 (Fig. 4). This information leads to the development of a hypothesis that there has been a change in the system, affecting all trophic levels, in the last three decades. Likely, the relationship between upwelling intensity/sea surface temperature and primary production is not linear. However, in this paper we are not aiming at establishing the right form of this relationship or its parameters. Instead, we are interested in relating model predictions to environmental series as a first step in understanding bottom-up forcing on trophic interactions, stock and food web dynamics in the Southern Humboldt.

Previous studies have documented switches in pelagic species in the SH system (Yáñez et al., 1992) and also a regime shift affecting the northern Humboldt system (Alheit and Niñcq, 2004). This “regime shift” is supported here for the southern Humboldt by analysing observed trends of relative biomass and catches of the main stocks, the proposed anomaly in PP and physical variables in the SH system in the last 35 years. From 1970 to 1985 the system appeared to be characterized by a relatively warm period of reduced upwelling and PP. From 1985 to the early 2000s the system appeared to be characterized by a relatively cold period with increased upwelling and PP (Fig. 4).

The switch between these two periods in the SH system occurred approximately during 1985–1986, which is coincident with a proposed regime shift affecting the northern Humboldt system (Alheit and Niñcq, 2004). This could indicate that the dynamics of the sub-systems of the Humboldt Current have been synchronized in the past three decades. In fact, Cubillos et al. (2007) reported that the catch in three anchovy fisheries from the North central Peru, South Peru – Northern Chile and Central-South Chile display large and synchronous interdecadal changes during the period 1962–2002. The same authors propose that long-term climate variability seems to be the main cause for interdecadal fluctuations in anchovy fisheries in the Humboldt Current System, although available time series are too short to prove this link and exclude the hypothesis of non-environmental forcing (Cubillos et al., 2007).

### 4.3. Combination of drivers of ecosystem dynamics

Overall, the combination of fishing, vulnerability to predation and environmental variability affecting primary production accounted for more than two thirds of total variability in the time series (a reduction of 69% in baseline SS). These results could be indicative of the dynamics of the whole SH system since available time series correspond to groups that dominate the system both in biomass and landings (Neira et al., 2004). The relative importance of each forcing as well as the overall sum of squares found in this paper are comparable to those informed by Neira (2008) and Shannon et al. (2008). This is somehow surprising since the searching procedures used in each paper differ as they are intended to approach different questions. For example, Shannon et al. (2008) explored the extent models from different upwelling systems support the wasp-waist hypothesis, thus focusing mostly on the dynamic of small pelagic fish. On the other hand, here we are more interested in understanding the importance of fishing, predator–prey and bottom-up forces in the dynamics of all stocks as well the whole food web in the SH. In doing so, we have identified a switch in system productivity that has not been previously documented for the SH system.

Even though we obtained a good overall fit of the Ecosim predictions to observations, this does not necessarily means that we have found the best Ecosim parameters (Walters et al., 2000). We are aware that aspect such model validation and the exploration of error analysis as well as parametric uncertainty in model predictions are lacking for the Ecosim model representing the SH. However, this is also true for many ecosystem simulation models currently in use worldwide. Therefore, we warn potential users of this model to be careful when interpreting model outputs as well as we encourage future research in model validation and error analysis. Future modelling exercises should be conducted as soon as longer and more accurate data become available, to improve

**Fig. 4.** Independent time series of sea surface temperature and upwelling index measured off Talcahuanco, Chile (36°42'17" S; 73°06'44" W) for the period 1970–2000 compared to the anomaly in primary production (PP) estimated by Ecosim to decrease the sum of squares between predicted and observed biomasses, catches and fishing mortality for the groups in Table 1. Key: dots = yearly observations/estimates; continuous line = 5-year running mean; punctuated line = long-term average. Spearman rank correlations: anomaly in PP vs. sea surface temperature $r = -0.45$, $p < 0.05$; anomaly in PP vs. upwelling index $r = 0.47$, $p < 0.05$. 

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understanding of how individual and synergistic effects of the main forcing factors act on stocks and food web dynamics in the SH system. Specifically, future research efforts should be directed to try and model the functional group horse mackerel in a more realistic way. As seen in Fig. 2, the biomass of this group is poorly represented by the current configuration of the model. It is possible that the dynamics of this group is influenced by fishing vulnerabilities and PP in the study area, but also by processes occurring offshore. The spawning and recruitment of this species occur outside the study area and oceanic processes may be as important for horse mackerel dynamics as coastal ones. An alternative to model this group in the future is to apply individual forcing functions under the hypothesis that they have an effect on the biomass of this group (e.g., recruitment series and or environmental signals) and observe the gains in the model fitting as explored by Field et al. (2006) and Shannon et al. (2008) for model groups in Ecosim modelling conducted for the California and Benguela systems, respectively.

The kind of holistic approach presented here should be considered when planning long-term strategies for sustainable fisheries in the SH system. At present, the advice for management is based almost exclusively on traditional single-species approaches that do not take into account fishing impacts on ecosystem components (other than target species) and rarely, if ever, include predation mortality and environmental variability when projecting the effects of different management scenarios on exploited populations. The EwE software can be used not only as an academic tool for hypothesis testing, but as a management tool that should complement, together with other multi–species and ecosystem models, single–species advice in guiding fisheries management in the SH system.

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