

Research Article

Modelling fishery-induced impacts on the food web of the continental shelf off central-south Chile using a size-based network approach

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ABSTRACT. The continental shelf off central-south Chile sustains highly productive fisheries. The sustainability of these resources is nevertheless in jeopardy since many of them are either overexploited or collapsed. Using an allometrically (size-based) parameterized model of the shelf's food web, we analyze the likely ecosystem effects of fishing in this system by measuring the response of several ecological indicators to changes in fishing pressure. Indicators performed as follows: i) insensitive (community biomass stability, clustering coefficient), ii) varying directly (number of species going "extinct") or inversely (Normalized biomass size spectra (NBSS) coefficient of determination), and iii) abrupt inverse change, but then insensitive beyond a threshold (Fishing in Balance (FiB) index, Mean Trophic Level of the Catch, NBSS slope, and total community biomass). The latter four indicators seem less informative for management once a fishery has developed. Simulations showed that fishing any single species affected several species through food web-mediated mechanisms, then making difficult to predict the effects of fishing on the abundance of target and non-target species. Therefore, conservation measures should not rely exclusively on reducing fishing mortality for a given target species, but also take into account the status of interacting species.

Keywords: allometry, bio-energetic modeling, ecological indicators, fishing pressure, food webs, central-south Chile.

INTRODUCTION

In the last two decades scientists have been increasingly concerned with the possibility of an imminent collapse of world fisheries (Casey & Myers, 1998; Pauly *et al.*, 1998; Jackson *et al.*, 2001; Worm *et al.*, 2006). However, recent analysis indicates that this is not necessarily happening, at least in the short term. Worm *et al.* (2009) assessed fishery management in areas where restoration practices have been both successful and unsuccessfully and concluded that a small change in fishing practices can have strong effects on the fisheries sustainability; concluding that "More successful forms of governance have involved local communities in a co-management arrangement with government or nongovernmental organizations". Despite a long history

of overexploitation, certain marine fish stocks can recover when one or several of the following factors are present: i) exploitation rates are substantially reduced, ii) commercial species are included in restoration measurement, or iii) protected areas are established in fishing grounds (*e.g.*, Micheli *et al.*, 2004; Worm *et al.*, 2006). For example, it is known that stock recovery is not simple or without short-term socioeconomic and political costs (Beddington *et al.*, 2007). The time required for recovery appears to be substantial in duration and highly dependent on the life history of the fishing stocks (Hutchings, 2000).

The effects of fishing extend well beyond target species, impacting the entire food web and habitats (Jennings & Kaiser, 1998; Hall, 2001). In addition, fisheries management needs to incorporate ecosystem

information in each step of the decision making process. Such as environmental variability, bycatch and incidental catch levels of the fishery, trophic interactions. Thus, the potential ecological impacts of different management scenarios could be assessed in order to support responsible fishing and sustainability. In fact, decisions must be based on the best information, and tools for analyzing the range of possible consequences derived from alternative fisheries management scenario are required (FAO, 1996; García, 1996; González-Laxe, 2005).

To determine the extent to which communities and ecosystems have been altered by fishing, as well as the reversibility of these changes, a range of models (Plagányi, 2007) and ecological indicators (Link, 2005; Rice & Rochet, 2005; Methratta & Link, 2006; Shin *et al.*, 2010) have been applied. Several indicators that focus on different processes, observations or branches of ecology are available, and the approximations based on organism size on the one hand and the organism taxonomy on the other hand, are complementary rather than redundant (Strayer, 1991; Rodríguez & Magnan, 1993). Thus, the combination of taxon-based and size-based approaches in the study of community structure leads to a better understanding of the ecological functioning of aquatic ecosystems. However, to date, analyzes comparing and/or using both approaches (size-based and taxonomy-based), have been limited almost exclusively to planktonic communities (Brucet *et al.*, 2006; Quintana *et al.*, 2006; Basedow *et al.*, 2010; Poulin & Franks, 2010; Manríquez *et al.*, 2012) and soil (Rall *et al.*, 2011).

The structure and trophic dynamics of the Humboldt Current Ecosystem off central-south Chile, one of the most productive upwelling ecosystems of the world's oceans (Fossing *et al.*, 1995; Daneri *et al.*, 2000, 2012), have been described using taxonomic models (*i.e.*, ECOPATH; Neira *et al.*, 2004; Neira, 2008), in particular including temporal variability (Neira *et al.*, 2004; Arancibia & Neira, 2005), the El Niño Southern Oscillation (Neira *et al.*, 2009), and the population outbreaks of predators such as jumbo squid (*Dosidicus gigas*) (Arancibia & Neira, 2008; Neira & Arancibia, 2013). A description based on the size structure approach, however, is still missing for this pelagic ecosystem. The effects of fishing on the size structure of marine communities have been shown to be pervasive. The emerging patterns seem to indicate that both size structure and production are affected by fishing, as indicated by changes in both the slope and intercept of the size spectrum (Rice & Gislason, 1996; Bianchi *et al.*, 2000; Daan *et al.*, 2005; Gómez-Canchong *et al.*, 2011).

Based on the trophic description of the pelagic community in the upwelling ecosystem off central-south Chile developed by Neira *et al.* (2004), which incorporates the main fishing stocks in the system (*i.e.*, common hake *Merluccius gayi gayi*, jack mackerel *Trachurus symmetricus murphyi*, common sardine *Strangomera bentincki* and anchovy *Engraulis ringens*, among others) and the main trophic components in the study area in terms of biomass (*i.e.*, euphausiids, copepods, phytoplankton), we use a bioenergetic model (Brose *et al.*, 2005, 2006) in which the characteristics of nodes (*i.e.*, functional groups) and links (*i.e.*, trophic interactions) are calculated or parameterized by means of allometric functions (*i.e.*, size-based approach as production, predation and metabolic rates). This study is intended to understand the effect of fishing on ecological indicators such as trophodynamics, size spectra and complex networks indicators, from the pelagic community in the upwelling ecosystem off central-south Chile, and to determine which indicators are best showing these effects.

MATERIALS AND METHODS

Study area

The study area corresponds to the continental shelf off central-south Chile (33°-39°S) and extends to 30 nautical miles offshore, covering an area of around 50,000 km² (Fig. 1). This zone is part of a typical eastern boundary current system or upwelling ecosystem, the Humboldt Current.

The levels of primary production reported for this upwelling system, which are among the highest for the world's oceans (Fossing *et al.*, 1995; Daneri *et al.*, 2000, 2012), support a remarkably large fish biomass, which in turn sustains one of the most productive fisheries worldwide (Bakun & Broad, 2003; FAO, 2014). Total landings in central-south Chile reached 1.4 million ton in 2011, representing 31% of total Chilean landings (SERNAPESCA, 2013). Maximum historical landings were 4,5 million ton in 1997. Currently, the main target species in the area are considered to be collapsed (common hake and anchovy) or overexploited (jack mackerel) by the Chilean Fishing Authority (SUBPESCA, 2016). The stock of common sardine was considered to be fully exploited in the 2015 annual report on the status of the main Chilean fisheries published in March 2016 by the Chilean fisheries authority (SUBPESCA, 2016), then sustaining most of the fish meal production in central-south Chile. However, important fluctuations observed the last five years in recruitment levels (SUBPESCA, 2016) implies that the fishery needs to be managed with caution, and

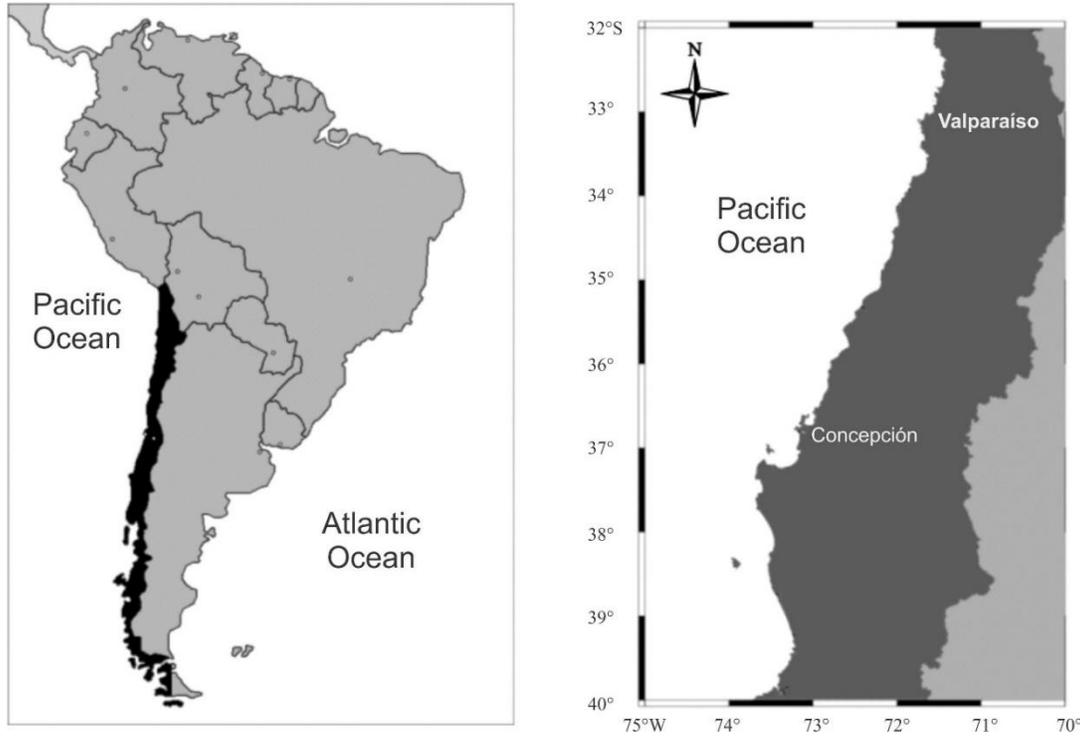


Figure 1. Study area, the marine zone off central Chile (33°-39°S).

consequently reproductive closure have been longer in time each year.

Model description

In order to simulate the temporal dynamics of individual stocks and food web within the marine ecosystem off central-south Chile, a bioenergetics consumer-resource model of species biomass over time was developed, based on the model of Yodzis & Innes (1992), where a consumer-resource system with two species, one of which eats members of the other, and where most of the parameters were determined by the body sizes and metabolic categories (endotherm, vertebrate ectotherm, invertebrate ectotherm, or plant) of the populations in question. The Yodzis & Innes (1992) model was later extended to multispecies systems by Williams & Martinez (2004), and updated by Brose *et al.* (2005, 2006) with new allometric coefficients (Brown *et al.*, 2004). We added a fishing mortality term in this model in order to carry out simulations.

The model encompasses 21 functional groups, including the main trophic components in the study area in terms of biomass (Table 1). In those functional groups where data indicate strong ontogenetic changes in diet among adults and juvenile individuals (Chilean hake), or where the fishery is strongly sustained by juvenile individuals (*e.g.*, anchovy, common sardine,

and squat lobster), we split the species into juvenile and adult stages. The structure of the food web off central-south Chile and its main components were obtained from Neira *et al.* (2004). However, given that most of the information is only available for species of commercial value, our analysis is focused on, although not necessarily limited to, functional groups that are target and by-catch species and incidental catch.

The population dynamics within the food web follows a model based on bioenergetics and allometric reasoning, which involves parameterizing the model using power functions of individual body mass. Changes in relative biomass densities of primary producer (Eq. 1) and consumer (Eq. 2) species are described by the following equations:

$$B_i' = r_i(M_i)G_iB_i - \sum_{j=consumers} \frac{x_j(M_j)y_jB_jF_{ji}(B)}{e_{ji}f_{ji}} \tag{1}$$

$$B_i' = -x_i(M_i)B_i + \sum_{j=resources} x_j(M_j)y_jB_jF_{ji}(B) - \left(\sum_{j=consumers} \frac{x_j(M_j)y_jB_jF_{ji}(B)}{e_{ji}f_{ji}} \right) + B_i \left(1 + R_{jm}/nm \right) \tag{2}$$

In these equations, B_i is the i^{th} population density; r_i is i^{th} mass-specific maximum growth rate; M_i is the body mass of individuals within population i ; G_i is the logistic net growth rate of each of the producer species,

Table 1. Input parameters for functional groups of the model from the food web of the continental shelf off central-south Chile. j: juveniles; a: adults (Data taken from Neira *et al.*, 2004). Bi: Biomass, TLi: Trophic level. Column “Use” indicates if the functional group is being targeted by a fishery (Target), caught as bycatch (Bycatch), is targeted by a fishery but is also bycatch in another fishery (Both), or is not directly affected by fishing process (-).

| Functional group | Scientific name (age group in years) | B_i (ton km ⁻²) | TL_i | Use |
|--------------------|--------------------------------------|-------------------------------|--------|----------|
| Sea lion | <i>Otaria flavescens</i> | 0.030 | 4.23 | - |
| Jack mackerel | <i>Trachurus symmetricus murphyi</i> | 13.790 | 3.99 | Target |
| Pacific sand perch | <i>Prolatilus jugularis</i> | 0.759 | 3.90 | Boht |
| Cardinal fish | <i>Epigonus crassicaudus</i> | 0.780 | 3.84 | Both |
| Chilean hake (a) | <i>Merluccius gayi gayi</i> (4+) | 4.487 | 3.54 | Target |
| Chilean hake (j) | <i>Merluccius gayi gayi</i> (0–3) | 4.827 | 3.40 | By-catch |
| Blackling | <i>Genypterus maculatus</i> | 0.212 | 3.05 | Both |
| Rattail fish | <i>Coelorhynchus aconcagua</i> | 0.256 | 3.05 | By-catch |
| Big-eye flounder | <i>Hipoglossina macrops</i> | 0.286 | 3.05 | Both |
| Skates | <i>Raja</i> spp. | 0.436 | 3.00 | Both |
| Euphausiids | | 73.627 | 2.98 | - |
| Copepods | | 48.956 | 2.62 | - |
| Common sardine (a) | <i>Strangomera bentincki</i> (1+) | 6.970 | 2.14 | Target |
| Common sardine (j) | <i>Strangomera bentincki</i> (0) | 4.620 | 2.14 | Target |
| Anchovy (a) | <i>Engraulis ringens</i> (1+) | 5.230 | 2.14 | Target |
| Anchovy (j) | <i>Engraulis ringens</i> (0) | 3.120 | 2.14 | Target |
| Yellow prawn | <i>Cervimunida johni</i> | 0.416 | 2.00 | Target |
| Squat lobster (a) | <i>Pleuroncodes monodon</i> (1+) | 0.799 | 2.00 | Target |
| Squat lobster (j) | <i>Pleuroncodes monodon</i> (0) | 0.665 | 2.00 | Target |
| Phytoplankton | | 112.107 | 1.00 | - |
| Detritus | | 100.000 | 1.00 | - |

where $G_i = 1 - (B_i/K_i)$ and K_i is i^{th} carrying capacity; x_i is i^{th} mass-specific metabolic rate; y_i is i^{th} maximum consumption rate relative to its metabolic rate; e_{ij} is the j^{th} assimilation efficiency when consuming population i ; f_{ji} is the fraction of the biomass removed from the resource population i that is actually eaten by population j ; F_{ij} is the functional response which describes the realized fraction of i 's maximum rate of consumption achieved when consuming population j ; $R_{fm/nm}$ corresponds to the fishing pressure ratio, which is calculated as the ratio of fishing mortality to natural mortality. The functional response F_{ij} is described as follows:

$$F_{ij} = \frac{\omega_{ij} B_j^h}{B_0^h + c_i B_i B_0^h + \sum_{k=\text{resources}} \omega_{ik} B_k^h} \quad (3)$$

where ω_{ij} is the weight factor representing the proportion of i 's attack rate targeting prey j , B_0 is the half-saturation density, h is the Hill coefficient (Real, 1977) and c quantifies predator interference. The predator interference term quantifies the degree to which individuals within population i interfere with each other consumption activities, which reduces i 's per capita consumption if $c > 0$ (Beddington, 1975; De Angelis *et al.*, 1975; Skalski & Gilliam, 2001). We determined the initial biomass, the body mass and the

weight factors for consumers according to data and diet described by Neira *et al.* (2004). We modified F_{ij} between type II ($h = 1$), type III ($h = 2$) and intermediate values (*i.e.*, systematic variation between 1.0 and 2.0 in steps of 0.1).

The biological rates of production, R , metabolism, X , and maximum consumption, Y , follow a negative quarter-power law relationships with the species' body mass (Yodzis & Innes, 1992):

$$R_p = a_r M_p^{-0.25} \quad (4)$$

$$X_c = a_x M_c^{-0.25} \quad (5)$$

$$Y_c = a_y M_c^{-0.25} \quad (6)$$

where a_r , a_x and a_y are allometric constants and the subscripts C and P indicate consumer and producer parameters, respectively (Yodzis & Innes, 1992). The time scale of the system was defined by normalizing all rates according to the growth rate of the primary producers, and the maximum consumption rates were normalized by the metabolic rates as follows:

$$r_i = 1 \quad (7)$$

$$x_i = \frac{X_c}{R_p} = \frac{a_x}{a_r} \left(\frac{M_c}{M_p} \right)^{-0.25} \quad (8)$$

$$y_i = \frac{Y_C}{X_C} = \frac{a_y}{a_x} \quad (9)$$

Inserting Eqs. (7), (8) and (9) into Eqs. (1) and (2) yields a population dynamics model with allometrically scaled parameters.

The average body masses (M) of each functional group was calculated depending on their trophic level (TL) according to (Gómez-Canchong *et al.*, 2013):

$$\log_{10} M_i = TL^d + rsd \quad (10)$$

where d is the exponent of the relationship between the trophic level and the body mass of each functional group, and rsd is a stochastic variable that is randomly sampled from a normal distribution (mean = 1, SD = 2).

A complete list of the parameters and constants values used in the model is presented in Table 2.

Food-web simulations

A total of 1000 simulations were run with over 800 time steps each. A time step represents the turnover rate of a phytoplankton cell, which represents three days, approximately. Berlow *et al.* (2009) demonstrated that 800 time steps is an adequate time series length for obtaining stable mean biomass densities from populations that are independent from initial biomass densities. Simulations conducted with time steps up to $t = 2000$ (results not shown) indicating similar trend, with no changes after $t = 800$. The niche topological model (*sensu* Williams & Martinez, 2000) is used to simulate food webs. In each simulation, the structure of trophic relationships, trophic levels and initial biomass of populations were assigned based on information representative of year 1992 (Tables 1, 3).

It is important to consider that during 1992, almost all fisheries were under open access, or stocks were healthy and in full exploitation regime. The exception was red squat lobster (*Pleuroncodes monodon*), which was under a recovery regime (Arana *et al.*, 1993). Ensembles (*sensu* Baird, 2010) were defined as sets of experiments with small, but well-defined differences in initial conditions or in specific variables. Model simulations within an ensemble were set as identical. The following food web parameters were set as constant for all model runs of the ensembles: connectance, functional response type, strength of predator interference, the metabolic types of the populations (invertebrates or ectothermal vertebrates), and the resources carrying capacity.

In the first ensemble, $R_{fm/nm}$ was systematically increased in steps of 0.1 units, from 0.0 (no fishing activity or fishing mortality = 0.0 y^{-1}) to 4.0 (intensive fishing, in this case the fishing mortality is 4 times greater than natural mortality, causing 80 percent of

total mortality) in the exploited functional groups (i.e., all groups that were either historical target species or species that were recurrent by-catch in the commercial fisheries). In addition, system recovery time (Holling, 1996) for the main fishing stocks under each fishing scenario was assessed as a measure of system's resilience. Fishing closure ($R_{fm/nm} = 0.0$) and system recovery after an overfishing period were simulated ($R_{fm/nm} = 4.0$). Simulations were run for another 800 time steps to assess whether community biomass returned to the initial value.

In the second ensemble, fishing pressure was applied only to specific functional groups: i) adult anchovy (*E. ringens*) and common sardine (*S. bentincki*), ii) adult common hake (*M. gayi gayi*), iii) jack mackerel (*T. symmetricus murphyi*) or iv) sea lion (*Otaria flavescens*). The first three analyses were conducted to assess the fishery-induced impacts on the main stocks in central-south Chile, as well as the entire food web. Examination of the changes affecting sea lion biomass was aimed to assess the interaction of this group with the main fisheries in the area. For the above fishery resources, initial biomass was established based on existing information from 2009 (when the main fisheries were considered in critical status, SUBPESCA, 2011, 2012a, 2012b). In these simulations, two values for fishing pressure were used: $R_{fm/nm} = 0.0$ (no fishing) and $R_{fm/nm} = 4.0$ (intensive exploitation).

Ecological indicators

For the first ensemble, in order to analyze the effects of increasing fishing pressure on the community structure, we calculated a set of selected ecological indicators following each simulation. Thereafter, we assessed the indicators' responses to simulated changes in fishing pressure.

Community stability was calculated using the coefficient of variation of total biomass derived from the inverse of the temporal variability of total community biomass, considering the sum of the biomass of all the species in the model (Worm & Duffy, 2003). A second measure for community stability was calculated as the number of species reaching extinction (i.e., species biomass less than 1×10^{-30}) during community dynamic simulations. A community with more species that are likely to go extinct is considered to be less stable (Brose *et al.*, 2005).

The clustering coefficient is the average fraction of pairs of species which are one link away from a species that is also linked to each other (Watts & Strogatz, 1998). This parameter measures the degree of compartmentalization of an ecosystem (Camacho *et al.*, 2002), which is crucial to the propagation of ecological pertur-

Table 2. Summary of the variables and parameters used/calculated in the bioenergetics model. Constant: values obtained from bibliography. User: parameters set by the user before running the simulations. Model Structure: these variables are set automatically when the initial species abundances are generated according to the model structure. Simulation: these variables are constantly changing during the simulation.

| Variable | Abbreviation | Type | Value | Equation | Source |
|--|-------------------|-----------------|----------|----------|-----------------------------|
| Number of time steps | t | User | 800 | | Berlow <i>et al.</i> (2009) |
| Initial mean trophic level | TL ₀ | Model Structure | | | Neira <i>et al.</i> (2004) |
| Links between top and intermediate species | links ti | Model Structure | | | Neira <i>et al.</i> (2004) |
| Links between top and basal species | links tb | Model Structure | | | Neira <i>et al.</i> (2004) |
| Links between two intermediate species | links ii | Model Structure | | | Neira <i>et al.</i> (2004) |
| Links between intermediate and basal species | links ib | Model Structure | | | Neira <i>et al.</i> (2004) |
| Links per species | L/S | Model Structure | | | Neira <i>et al.</i> (2004) |
| Initial connectance | C ₀ | Model Structure | | | |
| Carrying capacity | K | User | 1-3 | 1 | |
| Fishing pressure ratio | R _{fish} | User | 0-4 | 2 | |
| Type of functional response | F | User | II - III | 1-3 | |
| Predator interference | c | User | 0-1 | 3 | Beddington (1975) |
| Half-saturation density | B ₀ | User | 0.5 | 3 | Brose <i>et al.</i> (2006) |
| Weight factor | □ _{ij} | User | | 3 | Neira <i>et al.</i> (2004) |
| Hill coefficient | h | User | 1-2 | 3 | Real (1977) |
| Allometric constant for production relationship | a _r | User | 1 | 4 & 8 | Brose <i>et al.</i> (2006) |
| Allometric constant for metabolism relationship for invertebrates | a _s | User | 0.314 | 5, 8 & 9 | Brose <i>et al.</i> (2006) |
| Allometric constant for metabolism relationship for ectotherm vertebrates | a _s | User | 0.88 | 5, 8 & 9 | Brose <i>et al.</i> (2006) |
| Allometric constant for maximum consumption relationship for invertebrates | a _y | User | 2.512 | 6 & 9 | Brose <i>et al.</i> (2006) |
| Allometric constant for maximum consumption relationship for ectotherm vertebrates | a _y | User | 3.52 | 6 & 9 | Brose <i>et al.</i> (2006) |
| Mass-specific maximum growth rate | r _i | User | 1 | 1 & 7 | Brose <i>et al.</i> (2006) |
| Mass-specific metabolic rate | x _i | User | | 1, 2 & 8 | Brose <i>et al.</i> (2006) |
| Maximum consumption rate relative to its metabolic rate for invertebrate predators | y _i | User | 8 | 1, 2 & 9 | Brose <i>et al.</i> (2006) |
| Maximum consumption rate relative to its metabolic rate for ectotherm vertebrates | y _i | User | 4 | 1, 2 & 9 | Brose <i>et al.</i> (2006) |
| Assimilation efficiency for carnivores | e _{ji} | User | 0.85 | 1 & 2 | Brose <i>et al.</i> (2006) |
| Assimilation efficiency for herbivores | e _{ji} | User | 0.45 | 1 & 2 | Brose <i>et al.</i> (2006) |
| Fraction of biomass removed from resource population that is actually eaten | f _{ji} | User | 1 | 1 & 2 | Brose <i>et al.</i> (2006) |
| Final number of species | S | Simulation | | | |
| Mean trophic level | TL | Simulation | | | |
| Standard deviation of trophic level | TL.SD | Simulation | | | |
| Maximum trophic level | TLmax | Simulation | | | |
| Final connectance | C | Simulation | | | |
| Links | L | Simulation | | | |
| Standard deviation of linkedness | LinkSD | Simulation | | | |
| Clustering coefficient | Cl | Simulation | | | |
| Standard deviation of generality | GenSD | Simulation | | | |
| Standard deviation of vulnerability | VulSD | Simulation | | | |
| Mean chain length | ChLen | Simulation | | | |
| Standard deviation of chain length | ChSD | Simulation | | | |
| Maximum chain length | ChMax | Simulation | | | |
| Mean amplitude | Ampli | Simulation | | | |
| Mean biomass | Biom | Simulation | | | |
| Mean standard deviation | StdV | Simulation | | | |
| Mean variance | Var | Simulation | | | |
| Mean covariance | CoVar | Simulation | | | |

bations in the system (Pimm, 1979). As Krause *et al.* (2003) has stated, “the clustering coefficient refers to the existence of groups of species that have a higher probability of interacting with one another than with other species in the food web”. A food web consists of a set of species V and a set of trophic links E between them. A link e_{ij} is a trophic link where species i feeds or preys on species j . The neighborhood N_i for a species v_i is defined as its immediately connected neighbors as follows:

$$N_i = \{v_j : e_{ij} \in E \wedge e_{ji} \in E\} \quad (11)$$

Suppose that a species v_i has k_i neighbors; then at most $k_i(k_i - 1)/2$ links can exist between them (this occurs when every neighbor of v_i is connected to every other neighbor of v_i). C_i denotes the fraction of potential trophic links that are functional:

$$c_i = \frac{|\{e_{jk}\}|}{k_i(k_i - 1)} : v_j, v_k \in N_i, e_{jk} \in E \quad (12)$$

The clustering coefficient (\bar{C}) for the whole network is given by Watts & Strogatz (1998) as the average of the local clustering coefficients of all the n species:

$$\bar{C} = \frac{1}{n} \sum_{i=1}^n C_i \quad (13)$$

The mean trophic level of the catch (mTL_k) is an indicator of fishing impacts (Pauly *et al.*, 1998; Piet & Panovi, 2005) which is used for detecting shifts in community dominance from high trophic level predators to low trophic level invertebrates and planktonic feeders (Branch *et al.*, 2010). The mTL_k was estimated by weighting the trophic level (TL) of the caught species (K_i) by their proportion in total catches (K):

$$mTL_k = \frac{\sum (K_i TL_i)}{\sum K_i} \quad (14)$$

The Fishing in Balance (*FiB*) Index represents the ratio between the energy required to sustain the fishery landings and a baseline value; it was proposed to assess whether a certain level of exploitation of a given marine ecosystem can be sustainable and to detect bottom-up effects (Pauly *et al.*, 2000; Pauly & Palomares, 2005). The *FiB* is estimated for the time series of landings using the first year as a reference; it takes into account both catch and mean trophic level (Piet & Panovi, 2005). The *FiB* Index was calculated as follows:

$$FiB_k = \log \left(\frac{Y_k \left(\frac{1}{TE} \right)^{mTL_k}}{Y_0 \left(\frac{1}{TE} \right)^{mTL_0}} \right) \quad (15)$$

where: Y_k represents total catch for time k ; TE is the trophic transfer efficiency, specific to an ecosystem, set by default at 0.1. Negative values of *FiB* indicate an impaired fishery, where fishing in lower and more productive trophic levels is not compensated by higher catches (Pauly & Palomares, 2005).

Normalized biomass size spectra (NBSS) were constructed following Platt & Denman (1977) and Blanco *et al.* (1994), summing the biomass of all species whose average body mass falls in the same size class, on a geometric size scale. The normalized size spectrum was obtained by averaging the biomass of each species across all time steps and then dividing the biomass of each size class (M) by its amplitude (AM). To calculate the NBSS parameters (slope, intercept and coefficient of determination) we used linear least squares regressions (Zar, 2010) on the log-transformed values of aggregated biomass of species against the mean body mass for each size class. Total biomass of the community for each run was calculated directly as the sum of the biomass of each species from the model output. Total biomass was also estimated from the area under the normalized biomass-size spectra from arbitrarily chosen \log_{10} body sizes between one and five by means of the integral under the curve, as follows:

$$TotalBiomass(wl, wu) = \int_{wl=1}^{wu=5} aw^b dw = \left[\frac{a}{b+1} w^{b+1} \right]_1^5 \quad (16)$$

where a and b represent the intercept and slope of the NBSS and w is body mass. The area under the curve method assumes a linear size spectrum (Platt *et al.*, 1984; Blanco *et al.*, 1994). In order to evaluate whether the NBSS adequately represents the size structure of the community, the goodness of fit was tested between the community biomass calculated using the two approaches.

In order to evaluate the fishing impacts on the different size ranges, cumulative relative biomass spectra along the trophic level gradient (Sosa-López *et al.*, 2005) were obtained by summing the biomass of each species after ordering the entire set of species by trophic level.

For the second ensemble of simulations, we calculated the mixed trophic impact (MTI) as a way to evaluate direct and indirect trophic impacts derived from the exploitation of a single stock on other species of the central-south Chile food web. The MTI is a measure of the relative impact of a change in the biomass of one component on other components of the system (Ulanowicz & Pucia, 1990). When an increase in the abundance of the component takes place, it is referred to as a positive impact; the opposite case is termed negative impact. In this analysis, we used MTI to compare the relative change in trophic impacts between a continuous fishing scenario and a closed fishery. Therefore q_{ij} , the net impact that fishing group j will have on each component i of the food web, can be calculated as follows:

$$q_{ij} = \frac{(b_{i0} - b_{ij})}{b_{i0}} \quad (17)$$

where b_{i0} represents i 's biomass when none of the species is being fished and b_{ij} represents i 's biomass when species j is being fished.

RESULTS

Most of the ecological indicators calculated were responsive to fishing pressure (Fig. 2), with the exception of the community biomass stability (Fig. 2a) and the clustering coefficient (Fig. 2c), which were insensitive to fishing pressure, at least within the range of simulated values.

Although the stability of community biomass was unresponsive to fishing, the biomass fluctuations of the functional groups (Fig. 3) increased the probability in the simulated food webs (Fig. 2b), therefore showing that the community biomass stability is not a suitable indicator of fishing. Ecological indicators displayed a response to fishing pressure, which can be classified

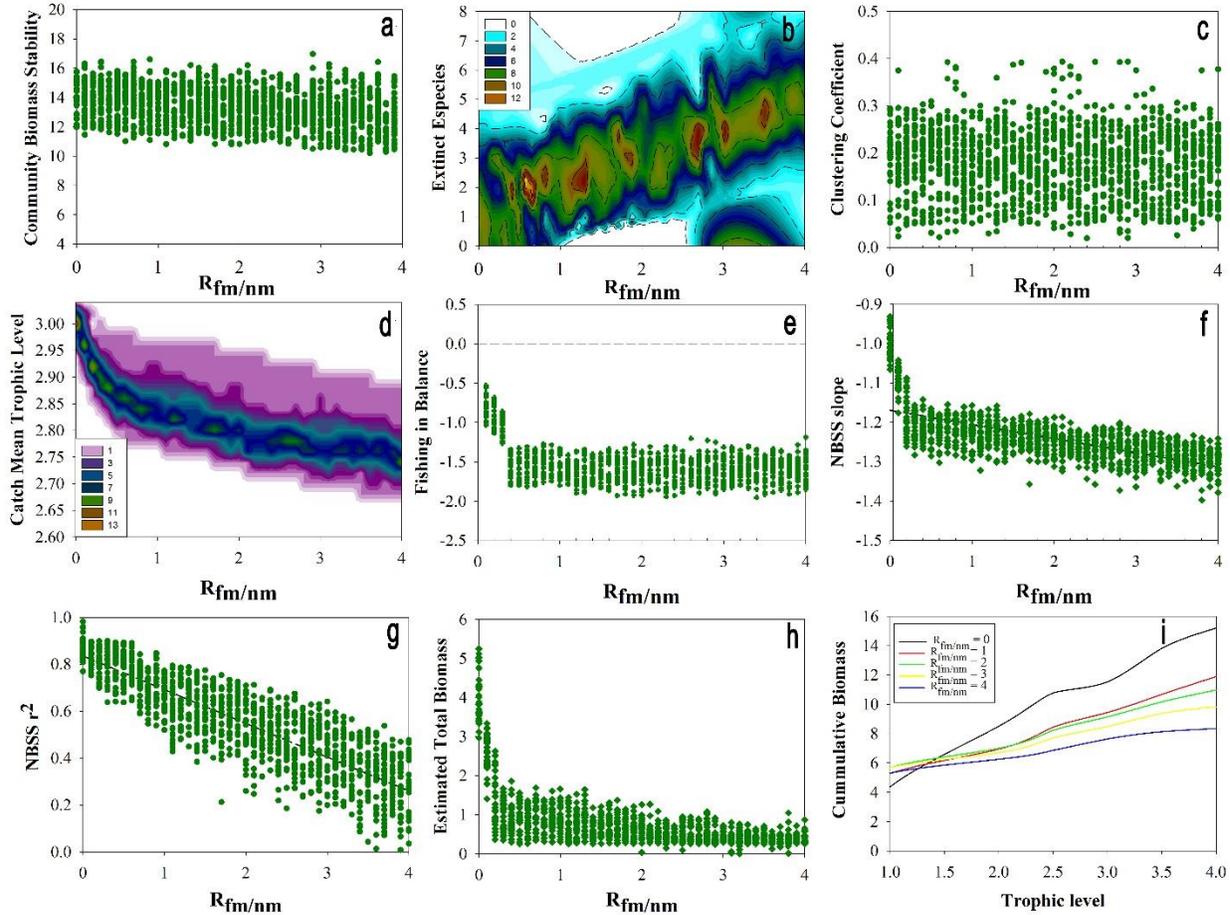


Figure 2. Behavior of the various indicators when the fishing pressure ratio $R_{fm/nm}$ applied to the food web of the marine zone off Central Chile was increased. a) Community biomass stability, b) Number of “extinct” species, c) cluster coefficient, d) mean trophic level of the catch, e) Fishing in Balance index, f) slope and g) coefficient of determination of the Normalized Biomass Size-Spectrum (NBSS), h) estimated total community biomass and i) cumulative relative biomass spectra along the gradient of trophic level. Lines were smoothed using the least squares method, each line represents a level of the fishing pressure ratio ($R_{fm/nm}$). Initial biomasses correspond to the biomass of each functional group in 1992, when almost all resources were healthy (with the exception of red squat lobster, that was under a recovery regime). In panels b) and d) the color represent the number of simulations where a specific outcome occurs.

into two groups: i) those that vary directly (number of species going extinct, Fig. 2b) or inversely (NBSS coefficient of determination, Fig. 2g) with fishing pressure, and ii) those that initially respond abruptly to fishing pressure, but becomes insensitive after a threshold is reached (FiB index, Mean Trophic Level of the Catch, NBSS slope and estimated total community biomass, Figs. 2d, 2f, 2h). NBSS intercept exhibited an inverse trend than NBSS slope, therefore, further analysis were not performed.

The catch mean trophic level (Fig. 2d) and the FiB index (Fig. 2e) decreased when fishing mortality increased. FiB index remained within values under the -0.4 threshold. The increase in fishing pressure resulted in the steepening of the NBSS slope (greater negative

values for the slope) (Fig. 2f), and a reduction in both the coefficient of determination (Fig. 2g) and the total community biomass estimated as the area under the NBSS curve (Fig. 2h).

Total community biomass decreased with increasing fishing pressure. However, this reduction was size-dependent meaning that it did not affect all size ranges equally. In this case, smaller size groups (phytoplankton, TL = 1.0) showed a slight increase in biomass (Fig. 2i), the predation release by a decrease in biomass of their predators is a possible explanation for this observation, suggesting a trophic cascade process (Pace *et al.*, 1999). This size-dependent response can also be observed as the constant drop in the biomass of the main target species during the first 800 time steps

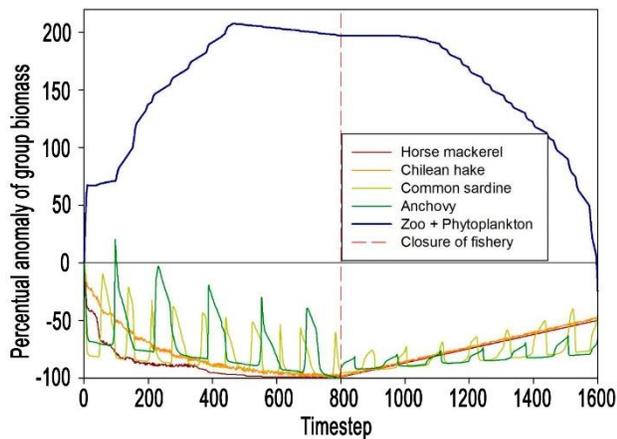


Figure 3. Time series showing the trend for the biomass of the main functional groups (target species and plankton) during a period of intense fishing ($t = 1$ to 800 ; $R_{fm/nm} = 4.0$), followed by a no-fishing period ($t = 800$ to 1600 ; $R_{fm/nm} = 0.0$). The initial biomasses correspond to 1992, when all resources were healthy. Each time step represents approximately one day.

(Fig. 3), while at the same time there was an increase in planktonic biomass. Thereafter, during the fisheries closure (*i.e.*, second 800 time steps, approx. 7 years) biomass recovery was observed in all of the main fishing resources, as well as a reduction in planktonic biomass.

The speed of recovery was slightly slower than the rate of depletion, thus final biomass did not reach initial simulation values. In the case of the simulation of fishing impact on small pelagic fishes, a decrease in the oscillation amplitude of the abundance was observed, increasing the extinction probability and decreasing the biomass stability of these species.

When the fishing pressure targeted one or two resources, the abundance of all species (target and non-target species) in the model was affected. The majority of species were negatively affected (*i.e.*, the biomass level was lower in this scenario compared to the non-fishing scenario), and the negative effects were of greater magnitude than the positive effects (Fig. 4).

DISCUSSION

This paper focused on: i) trophic interactions between different size groups, such as predation (bigger individuals preying on smaller individuals of other species), competition (similar size species sharing preys), and cannibalism (individuals preying on smaller individuals of their own species), and ii) the effects of fishing on ecological indicators as trophodynamics, size spectra and complex networks indicators. Other

important factors that modulate food webs structure and dynamics (*e.g.*, climate/oceanographic variability, discards and the effects of fishing gear on benthic biota and habitats), were not assessed due to lack of information on how these factors can modify the allometric parameters of the model or the community size structure. It is important to clarify that the recommendations for fisheries management that arise from our work are focused on exploring which ecological indicators are able to summarize the state of the resources being exploited and the communities impacted by fishing. Our model, have never been intended to forecast future abundance levels of the resources and/or set fishing quotas.

Fisheries can have a variety of impacts on ecosystems, such as: i) the reduction in total community stability (Jennings & Kaiser, 1998), ii) reduction in the trophic level of catch (Pauly *et al.*, 1998), iii) lower value of the NBSS slope (Gislason & Rice, 1998; Bianchi *et al.*, 2000), and iv) the reduction of total community biomass, particularly in populations of larger sized individuals (Steele & Schumacher, 2000). Almost all the indicators analyzed in this study (*e.g.*, Mean Trophic Level of Catch, Fishing in Balance, NBSS slope) behaved in accordance to what is expected when fishing pressure is increased (Table 4), corroborating that the model is adequate for being used for testing hypotheses (Caswell, 1988). Total community biomass (Fig. 2a) was rather stable over time regardless of the fishing scenario simulated; however, the number of possible extinctions did increase over time (Fig. 2b). This seemingly contradictory result of total community biomass stability may be explained by two mechanisms: 1) a high degree of functional redundancy (Walker, 1992) among the functional groups considered in the models (*i.e.*, remaining species in the food web have a similar ecological niche to the species that disappear) can mask the disappearance of a species by increasing the abundance of the redundant species; and/or 2) trophic cascades occur when predators in a food web suppress the abundance of their prey (Pace *et al.*, 1999); the removal of predators by the fishing activity, releases from predation many other functional groups. The biomass increase of those functional groups can compensate the biomass loses of predators, keeping the total community biomass approximately constant. In our model, one functional group can be replaced by any other functional group provided that they are similar in terms of mean body size or trophic level, and belong to the same metabolic type. The common sardine could be replaced by anchovy (Pedraza-Garcia & Cubillos, 2008) and the red squat lobster by the yellow squat lobster (Thiel *et al.*, 2007; Ahumada *et al.*, 2013), and vice versa. Both proposed mechanisms, under a fishing

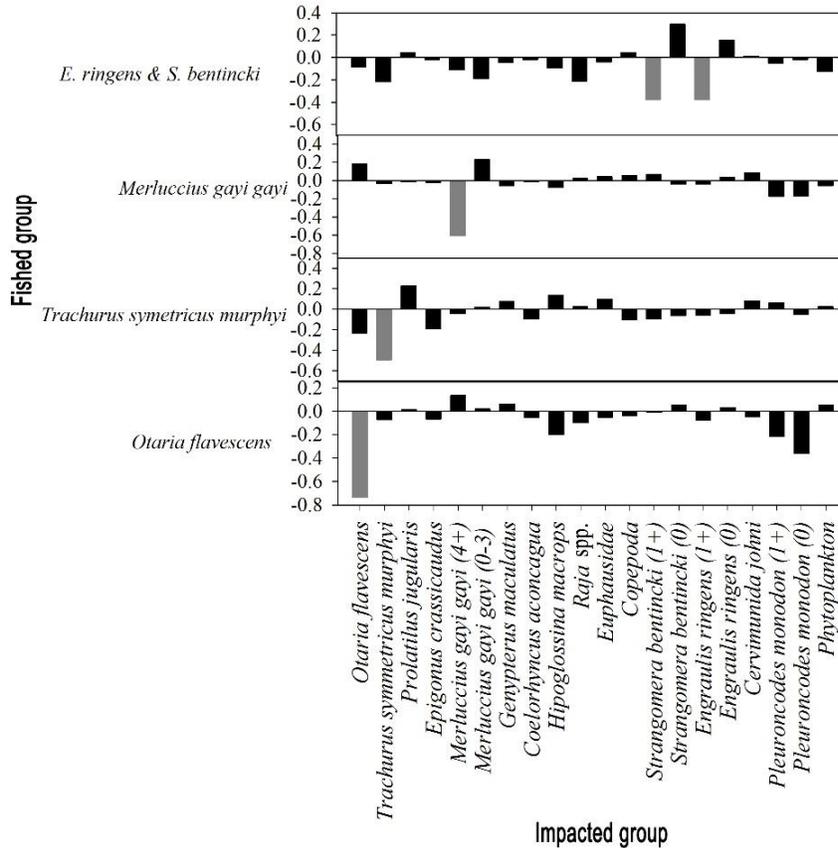


Figure 4. Mixed trophic impacts in the marine zone off Central Chile (33°-39°S). The figure shows the possible impacts caused by the fishing of each of the principal species groups in the system (fished group “Y” axis) across all functional groups (impacted group “X” axis). Positive impacts are above the line, negative impacts are below the line. The grey bar indicates the species that was directly being fished. The initial biomass were from 2009, when 3 out of the 4 principal resources were in a critical state. The possible impacts are relative but comparable between groups. Species are ordered according to trophic level.

scenario are expected to only delay a future collapse of the fisheries, since eventually all commercial species will be replaced by no commercial value species (Parrish, 1995).

The mean trophic level of the catch and the mean trophic level of the entire community exhibited a decreasing trend over 800 time steps, which suggests a process of fishing down the food web (FDFW; Pauly *et al.*, 1998), as has been previously reported for central-south Chile (Arancibia & Neira, 2005). This process is supported by the negative values of the FiB index observed throughout the simulations, which indicates that either discarding is occurring but is not represented in the catch, or that ecosystem function is being impaired by the excessive removal of biomass by fishing (Pauly & Palomares, 2005; Kleisner & Pauly, 2011). FDFW is usually explained by the sequential replacement in the catch of species of high commercial value and high trophic level by species of lower trophic

level, due to a decline in the abundance of the former (Pauly *et al.*, 1998). In our simulations, there is evidence of catch reduction at all trophic levels (Fig. 3); the reduction in the mTL_k is a consequence of a relative increase in the abundance of low trophic level species. In our simulations, the mean trophic level of the entire community behaves similarly to the mTL_k of the catch (results not shown). We therefore conclude that these results are not affected by artifacts of the way fishing data are reported (Branch *et al.*, 2010). Our model is not spatially explicit and does not allow the entry of new species into the system, thus it is not possible to simulate other proposed mechanisms able to change the mean trophic level of the catch, such as the displacement of the fisheries to areas that have not been exploited, or the inclusion of recently added fisheries. The latter is an alternative mechanism proposed by Essington *et al.* (2006) known as fishing through the marine food web (FTFW).

Table 4. Expected response of the different ecological indicators used in this research and actual response during simulations.

| Ecological indicator | Expected effect of fishing | Reference | Simulation outcome |
|--|--|---------------------------------|---|
| Total community stability | Reduction | Worm & Duffy (2003) | Remain stable |
| Number of species suffering extinction | Increase | Brose <i>et al.</i> (2005) | Increase |
| Clustering coefficient | Reduction | Watts & Strogatz (1998) | Remain stable |
| Mean trophic level of the catches | Reduction | Pauly <i>et al.</i> (1998) | Reduction |
| Fishing in balance | Values lower than 0.4 indicate an impaired fishery | Pauly <i>et al.</i> (2000) | Values lower than 0.4 were displayed |
| Normalized biomass size spectra slope | Reduction | Platt & Denman (1977) | Reduction |
| Normalized biomass size spectra coefficient of determination | Reduction | Platt & Denman (1977) | Reduction |
| Total biomass of the community | Reduction | Platt <i>et al.</i> (1984) | Reduction |
| Cumulative relative biomass spectra along the trophic level gradient | Reduction, particularly of populations with larger sized individuals | Sosa-López <i>et al.</i> (2005) | Reduction, particularly of populations with larger sized individuals, but increase of smaller sized individuals |
| Mixed trophic impact | Impact on all the species of the food web | Ulanowicz & Pucia (1990) | Impact on all the species of the food web |

Changes observed in the NBSS slope (more negative values) are also in accordance with the predicted decline of this indicator as fishing pressure increases (Gislason & Rice, 1998; Bianchi *et al.*, 2000; Law *et al.*, 2012). However, the observed increase in the dispersion of NBSS residuals (*i.e.*, lower R^2 , Fig. 7b) and the reduction in the capacity of the NBSS linear model to describe community size structure, reflect the gradual loss of community size structure (Jennings & Kaiser, 1998), which becomes further displaced from equilibrium states (Quiñones, 1994; Rodríguez, 1994). In addition to the increase in residual dispersion, Gómez-Canchong *et al.* (2011) observed, in the case of shrimp trawl fisheries, that discards and the mechanical action of the trawl modified the size structure of the community, rendering a linear model inadequate for describing those communities. In fact, Benoit & Rochet (2004) and Shin & Cury (2004) suggested that the effects of fishing are better captured by the curvature of the size spectrum than by its slope.

A reduction in total community biomass was observed due to fishing, but also due to a redistribution in the allocation of biomass in different size ranges and trophic levels, increasing the proportion of planktonic organisms and reducing the proportion of larger individuals (Figs. 2i, 3). The interpretation of observed changes in the abundance of non-commercial species that are not caught as by-catch is not straightforward, and could be explained by i) indirect trophic impacts due to lower predation mortality as predators are depleted by fishing, ii) fewer competition interactions as competitors are depleted by fishing, or iii) increased competition when competitors are favored as their

predators and competitors are removed by fishing. The reduction in the abundance of commercial species, despite the increase in food supply (abundance of planktonic organisms and detritus), can easily lead to the dominance of smaller-sized species with no commercial value that are not subjected to fishing pressure (Parrish, 1995). This reduction in the abundance of commercial species can allow the entrance of allochthonous species into the ecosystem (something not possible to simulate in our model in its actual state), or the increase in abundance of previously less abundant species. This seems to have been the case in central-south Chile given the observed recent population outbreak of species that were not traditionally targeted by any fishery (*i.e.*, jumbo squid; Payá, 2006; SUBPESCA, 2013) or had no commercial interest (*e.g.*, gelatinous organisms; Neira *et al.*, 2009; Pavez *et al.*, 2010).

The FiB index, Mean Trophic Level of the catch, NBSS slope and estimated total community biomass changed quickly from a non-fishing scenario to a low fishing pressure scenario. However, with higher fishing pressure these indicators reduced their rates of change or even became constant. Suggesting the existence of thresholds that need to be examined further. Those indicators are less informative for fisheries management once the fishery has developed, but those thresholds can provide a useful early warning system for newly established fisheries where the target community has not yet been affected (Mullon *et al.*, 2005; McClanahan *et al.*, 2011; Foley *et al.*, 2015). The lack of responsiveness of these indicators beyond a certain level of fishing impact may suggest that beyond

those ecological thresholds the ecosystem may reach a point of no return, or a shift to an alternative ecosystem phase, *i.e.*, an overexploited state (*sensu* Scheffer & Carpenter, 2003; Knowlton, 2004).

Despite the high levels of recovery observed in various functional groups once the fishery is closed, these model results need to be handled with caution for the following two reasons: firstly, recovery rate is slightly lower than the rate of initial depletion, and consequently the recovery period is slightly longer than that of active fishing; and secondly, in this model we did not consider the other effects of fisheries on communities and ecosystems (*e.g.*, change in genetic structure, Hutchings & Fraser, 2008; increase physical disturbance, Jennings & Kaiser, 1998; change in size structure, Gómez-Canchong *et al.*, 2011), which are expected to slow down or even preclude stock and ecosystem recovery following fishery closure. Lastly, we have to consider that fishing acts on several species at the same time, and therefore individual effects can be amplified.

Anchovy and common sardine exhibited strong biomass fluctuations as a result of simulated fishing scenarios (Fig. 3), the period of the fluctuation component was close to nine months. Considering the mathematical structure of our model, fluctuations in abundance can only be explained by endogenous factors (density-dependent factors), which can be represented by feedback events due to interactions among populations (Turchin & Taylor, 1992).

This kind of fluctuations can appear in consumer-resource models when nutrient enrichment is increased (Rosenzweig, 1971; Gilpin & Rosenzweig, 1972; Lima *et al.*, 2002; Rall *et al.*, 2008), driving population dynamics from equilibrium dynamics (*i.e.*, species biomass remains constant) into limited cycles dynamics (*i.e.*, biomass species oscillations). The lack of environmental factors in our model could explain differences between model outputs and the observed fluctuations in small pelagic fish in empirical data, where the fluctuation component is close to 4 years (Pedraza-García & Cubillos, 2008). The amplitude of the oscillations in the biomass of small pelagic fish in our simulations was amplified when the fishing pressure increased. This is in agreement with Rochet & Benoit (2012), who argued that fishing amplifies temporal oscillations in biomass flow. These authors also proposed that biomass oscillations are hazardous, because unstable dynamics increase the risk of change in the ecosystem state and dynamics, increasing system sensitivity to environmental variability and the probability of collapse (Rochet & Benoit, 2012).

The analysis of fishing effects, shows that the effects on one species (Fig. 4) showed different impacts

on each functional group. Different species were favored in each case, but in all simulations most species showed decreased abundance, and the magnitude of positive effects was always lower than the magnitude of negative effects. Those results highlight the difficulties to predict the effects of fishing on the abundance of interacting species. Those difficulties arise from the indirect effects of fishing, such as the release of predation or competition (Yodzis, 2001). This could explain why the decline of populations perceived as competitors of fisheries may not necessarily have the desired effect, *i.e.*, improved fishery yields. This is particularly relevant due to the increasing concern regarding the interaction of sea lions and fisheries in Chile (Oliva *et al.*, 2008; De la Torre *et al.*, 2010). Simulations showed that harvesting sea lions would negatively affect most species, probably with the exception of Chilean hake, which was found to experience a slight increase in abundance. A sea lion cull would therefore have a negative effect at the population, ecosystem and fishery levels.

Our simulations revealed several important ecological and management considerations. Increasing fishing pressure increments the oscillation amplitude of the catch and biomass, which is not economically and socially desirable. Stabilizing fisheries has been recognized as an important management objective (*e.g.*, Horwood *et al.*, 1990; Morin, 2000; Rochet & Benoit, 2012). The possible change to an alternate ecosystem phase due to high fishing pressure which is suggested by our simulations could cause large losses of ecological and economic resources, and eventually restoring an ecosystem to a desired state may require drastic and expensive intervention (Scheffer *et al.*, 2001). As stated by Rochet & Benoit (2012), limiting both fishing intensity and selectivity (García *et al.*, 2012) could be an appropriate exploitation strategy to avoid unstable food web dynamics with potentially harmful consequences for fisheries. A third consideration is that given the mixed character of aggregations of small pelagic fish, our results (biomass oscillations amplified by fishing) support conservative approaches when establishing fishing quotas in the future. Unfortunately, as stated by Leal *et al.* (2010), the risk of overexploitation for many important stocks in Chile has been aggravated by failures at the decision-making level; the scientifically recommended quotas for those fisheries that generate the highest levels of employment and have the greatest economic value have been regularly disregarded by the Chilean National Fisheries Council (CNFC). Strong criticism regarding the limited capacity of the CNFC to comply with conservation objectives (Leal *et al.*, 2010) recently produced (February 2013) a major change in the

Chilean Fisheries and Aquaculture Law where the responsibility to establish quotas was transfer from the CNFC to the Fisheries Scientific-Technical Committees and to the Undersecretary of Fisheries (LGPA, 2013).

CONCLUSIONS

It is evident that conservation measures should not rely solely on reducing fishing mortality for a given species, as is done in the single-species approach, but should also take into account the status of the other species with which the target species interacts (*e.g.*, prey, predators, and competitors). In fact, when reviewing the causes suggested for the collapse of Chilean fisheries, the food web-mediated mechanisms were not often mentioned. An exception is the analysis of the impact of jumbo squid on demersal fisheries, in particular on Chilean hake (Arancibia *et al.*, 2007). Considering the current state of the main Chilean fishing stocks, there is an urgent need to accelerate an ecosystem approach to fisheries. Our research is in direct concordance with the FAO guidelines (García *et al.*, 2003) and the mandates of the current General Law of Fisheries and Aquaculture (LPGA, 2013) respect to the approach to the conservation and management of fishery resources and the protection of their ecosystems. The approach used in this paper has the potential to advance both our knowledge on the direct and indirect impacts of fishing on the exploited community of the continental shelf off central-south Chile, and the likely responses of the food web under future fishing scenarios. Thus, the size-based food web approach should be part of a toolbox for managing Chilean fisheries under an ecosystem approach. However, in order to translate our results into useful management recommendations for the central-south Chile fishery, it is still necessary to include spatially explicit information and the effect of the environment on the network interactions analyzed in this work.

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