# OVERVIEW OF THE CHILEAN HAKE (*MERLUCCIUS GAYI*) STOCK, A BIOMASS FORECAST, AND THE JUMBO SQUID (*DOSIDICUS GIGAS*) PREDATOR-PREY RELATIONSHIP OFF CENTRAL CHILE (33°S–39°S)

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## ABSTRACT

Total Chilean hake (*Merluccius gayi*) landings from off central Chile (33°–39°S) declined from 120,000 t in 2004 to 40,000 t in 2007. This paper evaluates the impacts of both fishing and *Dosidicus gigas* predation relative to the observed collapse of *M. gayi*. We provide a brief review of the state of *M. gayi* stock using population indicators. In addition, we evaluate the predator-prey interaction between *D. gigas* and fishing to explain changes observed in the *M. gayi* stock in recent years using a dynamic food web model. Estimates of predation mortality suggest that cannibalism in *M. gayi* is more important than predation by *D. gigas*. In addition, a decline in length at catch, in the proportion of mature females, and in the catch per unit of effort in the *M. gayi* fishery has been observed since summer 2000, i.e., three years before the outbreak of *D. gigas* in central Chile. We projected the *M. gayi* biomass using two Ecopath models describing the system in 2000 and 2005 and the software Ecopath with Ecosim. The increase in *D. gigas* biomass resulted in a slow decrease in *M. gayi* biomass from 2000 to 2010. Fishing scenarios resulted in a decrease in *M. gayi* biomass from 2004 (juveniles) and from 2003 (adults).

## INTRODUCTION

Historically, Chilean hake (*Merluccius gayi*) has been the main fishing resource for human consumption in Chile, with production exported mainly as frozen filets. The *M. gayi* fishery is considered fully-exploited[1]; from 1975 to 1986 annual landings were below 40,000 tons, and slowly increased to a maximum of approximately 150,000 t in 2001. Landings declined in 2002 and 2003, decreasing rapidly back to 40,000 tons in 2007 (fig. 1).

Although the National Fishery Council (NFC) in Chile set the total allowable catch (TAC) for the *M. gayi* fishery at 62,000 t for 2007, the advice from Subsecretaría de Pesca (Undersecretary of Fishery, SubPesca) was to catch only 50,000 t (SubPesca 2006). However, statistics from the Servicio Nacional de Pesca (National Fishery Service; www.sernapesca.cl) indicate that only the industrial sector (vessels greater than 1,000 hp) achieved its quota (ca. 37,000 t), while the artisan sector (long-liners with fishing gear not larger than 10,000 hooks) landed only 3,000 t out of a 25,000 t allocation. This was attributed primarily to the reduced availability of *M. gayi* (Lillo et al. 2005) in the coastal waters where the artisan boats operate.

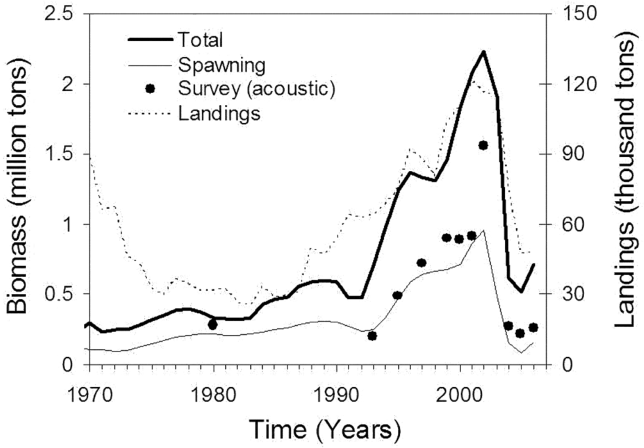

Figure 1. Landings and stock biomass of *Merluccius gayi* off central Chile from 1970 to 2006.

This decline in landings since 2004 has resulted in a loss of about 1,500 direct jobs in fishing companies. As a comparison, each direct job in the industrial sector (e.g., members of crews, workers in frozen fishing companies) supports four indirect jobs (services like transport, food supply, restoration of nets and electronic equipments, among others). In addition, in the artisanal sector approximately 5,000 fishermen left the fishery between 2005 and 2007 (Dresdner pers. comm.[2]) The consequences of these declines have been increasing conflict among stakeholders (e.g., managers and representatives of workers in fishing companies, and artisan fishers) and the Fishing Authority. In interviews and opinion articles in the local press, stakeholders used economic and social reasons to protest against any potential decrease in the annual TAC.

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[1] Based on the Chilean Fishing and Aquaculture Law N° 18,892 and subsequent amendments (www.subpesca.cl).

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The *M. gayi* stock was managed using a statistical stock assessment model (SubPesca 2006) that indicated that the *M. gayi* biomass peaked in 2002 with ca. 2.2 million t (Payá 2006; fig. 1). This assessment was based on an age-structured model calibrated with biomass estimates from acoustic surveys. The *M. gayi* biomass estimated during the acoustic survey in 2002 reached 1.6 million t, 70% greater than the biomass estimated in 2001 (917,000 t). There was no acoustic survey conducted in 2003, and the subsequent survey in 2004 estimated only 272,000 t, a decrease by one order of magnitude with respect to 2002. We considered the unusual nature of the 2002 point estimate in Arancibia and Neira (2003) and Arancibia[3] has presented an unpublished analysis on the subject. However, Payá (2006) and SubPesca (2006) related the drastic drop in the *M. gayi* biomass in 2004 (see fig. 1) to "a catastrophic event of unknown origin, likely predation by jumbo squid (*Dosidicus gigas*)." More recently, Arancibia et al. (2007) reviewed available life-history data for *D. gigas* (age, growth, maturity, reproduction, and mortality, among others) and estimated *D. gigas* consumption of *M. gayi*.

Several factors may be responsible for the significant drop of *M. gayi* biomass off central Chile. The aim of this paper is to evaluate the impacts of both fishing and *D. gigas* predation relative to the observed collapse of *M. gayi*. We provide a brief review of the state of *M. gayi* stock using population indicators. In addition, we evaluate the predator-prey interaction between *D. gigas* and fishing to changes observed in the stock of *M. gayi* in recent years, using a dynamic food web model.

## MATERIALS AND METHODS

The overview of the *M. gayi* stock was conducted with a meta-analysis using a time series of biological indicators that cover the period 1997–2007. The indicators were monthly mean length, inmature/mature ratio, and catch per unit of effort (Alarcón unpubl. data[4]). The aim is to analyze population signals in the *M. gayi* stock before and after 2002–03, which is the period of the *D. gigas* invasion.

The study area corresponds to the upwelling system off central Chile (fig. 2) located in the southern section of the Humboldt Current System, one of the four major eastern boundary ecosystems of the world. The study area supports high levels of primary productivity (19.9 g C/m$^2$/d; Daneri et al. 2000) and globally significant landings (>4.5 million t in 1995). The models represent the marine area that extends from 33°S to 39°S and from the coastline to 30 nm westward, covering a total area of approximately 50,000 km$^2$. This is a relatively independent ecological and geographical unit (Camus 2001) characterized by a narrow continental shelf (<30 nautical miles), strongly seasonal upwelling (September to March), and high levels of primary productivity (Strub et al. 1998; Daneri et al. 2000; Escribano et al. 2003).

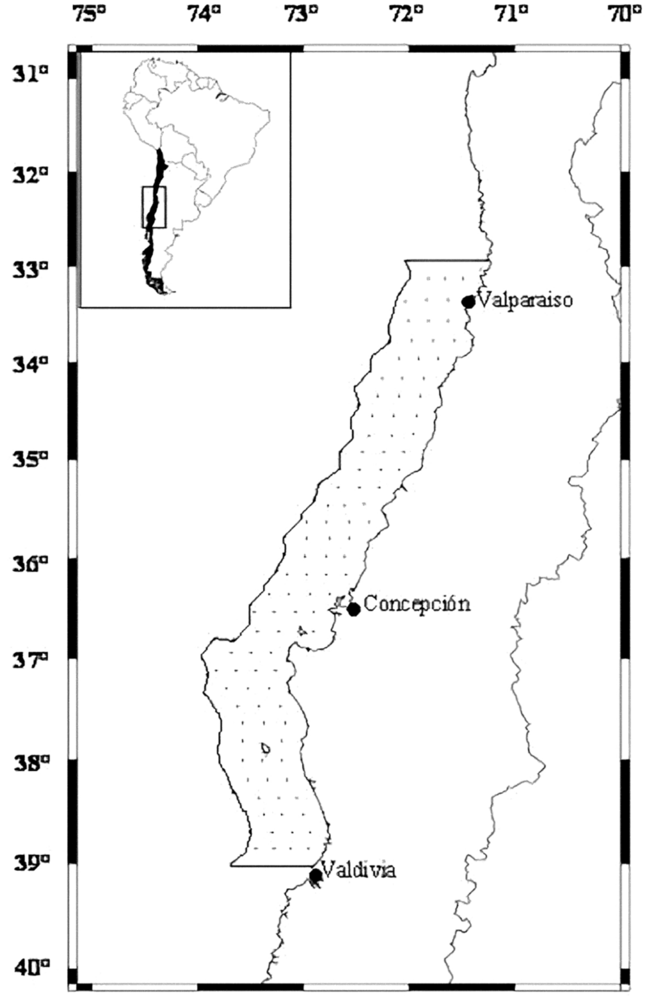

Figure 2. Study area.

In terms of the main biological components, the study area sustains a diverse and productive food web (Neira and Arancibia 2004; 2007; Neira et al. 2004). The phytoplankton group is dominated by large diatoms for most of the year, while the zooplankton group is dominated by herbivorous copepods and euphausiids. Jellyfish also constitute an important group in the plankton domain. Macrocrustaceans are significant benthic components and some species such as red squat lobster (*Pleuroncodes monodon*), yellow squat lobster (*Cervimunida johni*), and pink shrimp (*Heterocarpus reedi*) support important fisheries. The finfish community is dominated by pelagic

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[3] Arancibia, H. Analysis of the interaction between jumbo squid and common hake using an ecotrophic post-modern method: EwE. Talk to the National Fishing Council of Chile (original in Spanish). Valparaíso, September 4th, 2007 (www.subpesca.cl).

[4] Alarcón-Muñoz, R., Instituto de Investigación Pesquera Octava Región S.A., Av. Colón 2780, Talcahuano, Chile. E-mail: ralarco@inpesca.cl.

species; small pelagic fishes such as anchovy (*Engraulis ringens*) and the endemic common sardine (*Strangomera bentincki*), in particular, are present at high biomass levels off central Chile and dominate landings. Horse mackerel (*Trachurus symmetricus*) is another important resource in the study area. This highly migratory species performs large-scale migrations in the Pacific Ocean. The demersal fish community is dominated by Chilean hake (*M. gayi*) both in biomass and landings.

To evaluate the relative influence of fishing and *D. gigas* predation on *M. gayi* dynamics from 2000 to 2010, we used a food-web approach. We used two Ecopath (Christensen and Pauly 1992) models (with 31 functional groups) that represent the upwelling system off central Chile in 2000 (before the *D. gigas* invasion; Neira and Arancibia 2007; Appendices 1 and 2) and 2005 (after the invasion of *D. gigas*; Arancibia and Neira unpubl. data; Appendices 3 and 4). The models include age structure in groups where enough data are available to split adult and juvenile stages. Based on Arancibia (1987), *M. gayi* juveniles are those in age groups 0–3 years old, while adults are 4+ years old. For *S. bentincki*, *E. ringens*, and *P. monodon*, we considered juveniles to be age 0 fish (recruits) and adults to be age 1+.

The data sources used to parameterize the models are described in Arancibia et al. (2007) and Neira and Arancibia (2007). Using the model representing the system in 2000, we performed the following series of simulations using the Ecopath with Ecosim software, EwE (Walters et al. 1997):

(i) *D. gigas* biomass from 2000 to 2005 was increased by one order of magnitude. This was conducted in EwE assuming a biomass accumulation rate (Ba) of 1.66/year for *D. gigas*.

(ii) The observed fishing mortality ($F = Y/B$) of *M. gayi* from 2000 to 2005 was applied based on the stock assessment results.

(iii) Based on Arancibia and Neira (2003), a fishing mortality coefficient was applied to *M. gayi* which was corrected for discards and underreported catch. This corresponds to a 30% increase in *F*.

(iv) Scenario (i) was independently combined with scenarios (ii) and (iii).

Later, we performed two extra sets of simulations using the model representing the system in 2005 where:

(v) Fishing mortality of *M. gayi* was constant (i.e., $F = F_{2005}$) from 2005 to 2010;

(vi) $F = 0$ from 2005 to 2010;

(vii) $F = F_{2005}$ from 2005 to 2007, and $F = 0$ from 2008 to 2010.

We introduced the EwE main equations and hypotheses (for more details on model equations and assumptions see Christensen and Pauly 1992; Walters et al. 1997; and Christensen et al. 2005). EwE is a software that allows mass balance snapshots (Ecopath) and time dynamics (Ecosim) to be constructed using direct and indirect trophic relationships in any food web. Ecopath is based on two equations. The first balances the new production of each group, *i*, into removals by fisheries, predators, unexplained mortality, migration, and biomass trends:

$$P_i = Y_i + B_i \cdot M2_i + BA_i + E_i + P_i \cdot (1 - EE_i), \qquad (1)$$

where $P_i$ is total production, $Y_i$ is total fishery catch, $B_i$ is biomass, $BA_i$ is biomass accumulation, $M2_i$ is total predation rate, $E_i$ is net migration rate (emigration - immigration), and $P_i\ (1 - EE_i)$ is other mortality ($M0_i$), based on the ecotrophic efficiency (*EE*) which represents the total fraction of the production that is either eaten by predators or exported from the system, including in the form of fishery catch.

Following Winberg (1956), the second main equation in EwE expresses the mass balance for each group *i* of the system as:

$$Q_i = P_i + R_i + U_i, \qquad (2)$$

where $Q_i$ is prey consumption both inside and outside the system (imports), $P_i$ must be eaten by predators, exported from the system, or contributed to detritus, $R_i$ is respiration, and $U_i$ is unassimilated food.

In Ecopath, the term describing predation mortality (*M2*) is calculated as follows:

$$M2_i = \sum_{j=1}^{n} Q_j \cdot DC_{ji}, \qquad (3)$$

where the summation is over all *n* predators feeding on the prey *i*, $Q_j$ is the consumption ratio of predator *j*, $DC_{ji}$ is the diet composition of predator *j* (i.e. proportion in weight of prey *i* in the stomach content of predator *j*) which is calculated as follows:

$$Q_j = B_j \cdot (Q/B)_j, \qquad (4)$$

Ecosim 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 Ecosim to simulate the dynamics of fast- and slow-growing groups. The model explicitly incorporates the effects of trophic controls and allows for limited size/age structure (Walters et al. 1997). In Ecosim, the biomass changes for functional groups are functions of biomass, harvest rate, other mortalities, and predator consumption (for more detailed equations see Walters et al. 1997; Pauly et al. 2000; Christensen and Walters 2004; Christensen et al. 2005):

$$\frac{dB_i}{dt} = f(B_i) - M0_i B_i - F_i B_i - \sum_{j=1}^{n} c_{ij} \cdot (B_i, B_j), \qquad (5)$$

where $f(B)$ is a positive function of biomass *B* for each

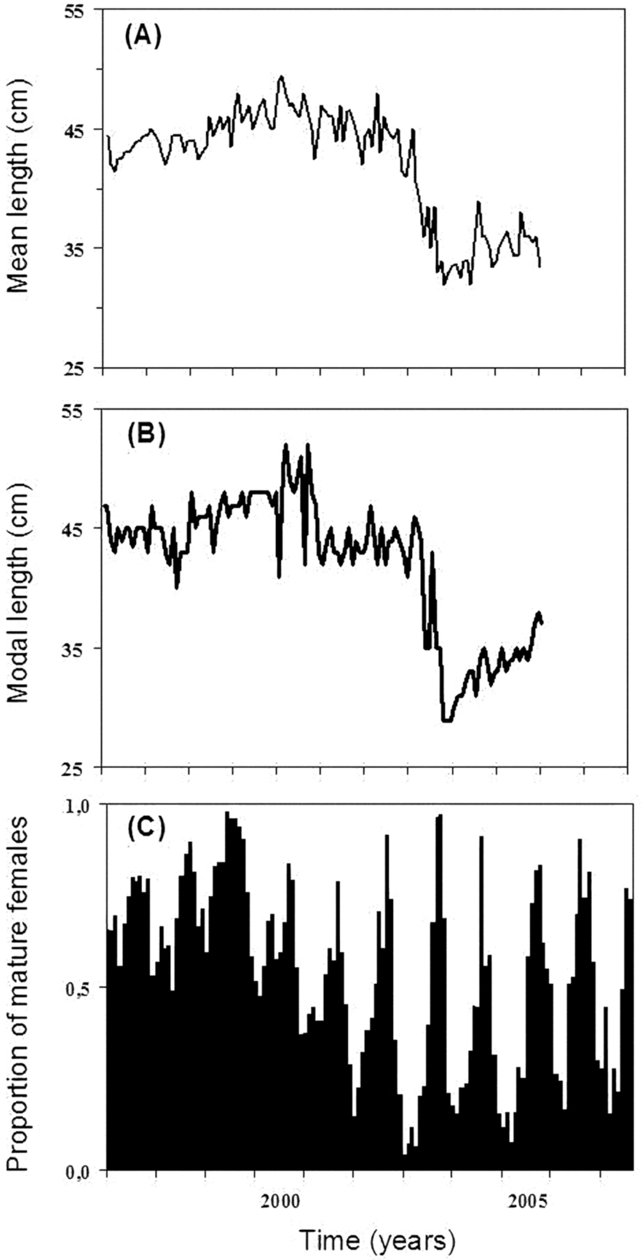

Figure 3. Stock indicators of *Merluccius gayi* (males and females combined) for the years 1997–2007. (A) mean of total length; (B) model of total length; (C) proportion of mature females.

group $i$ in the model, $M0_i$ 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 $j$.

Predator-prey interactions in Ecosim are assumed to be moderated by prey behavior to limit exposure to predation (vulnerability), and overall food web dynamics can show either bottom-up or top-down control (Walters et al. 1997; Christensen et al. 2005). In the absence of further knowledge, we used default values for the vulnerability parameters as well as the maximum $P/B$ ratio, feeding and handling time for all predator-prey interactions.

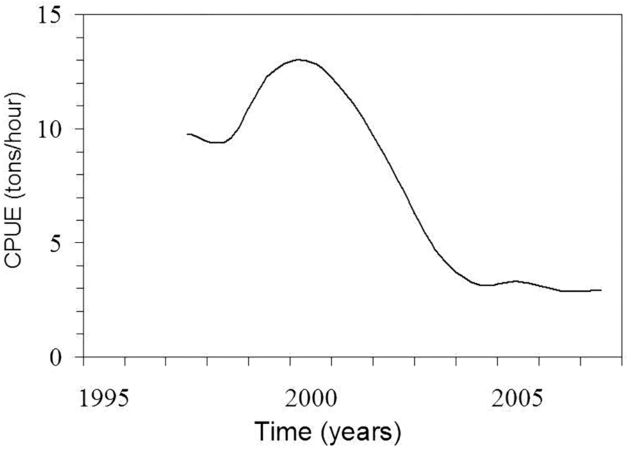

Figure 4. Non-standardized catch per unit of effort (CPUE) of the industrial trawling fleet targeting *Merluccius gayi* off central Chile.

## RESULTS

The monthly average length of *M. gayi* (combined sexes) is shown in Figure 3A. The indicator increased from early 1997 to late 2000, then slightly declined until 2003, and dropped until mid 2005. The modal length in catch follows the same trend as the monthly average length, but the contrast is more apparent (fig. 3B).The proportion of mature females in *M. gayi* shows strong seasonality, with mature females being more abundant in the second half of any year (fig. 3C). However, the proportion of immature individuals increased from 1999 to 2005 (the slight decrease in the percentage of immature females in 2004 may be linked to greater availability of larger females during sampling). The proportion of immature females in catches was high until 2007, but recruitment has been relatively low in more recent years (SubPesca 2006).

The non-standardized CPUE of the industrial trawling fleet targeting *M. gayi* was at a maximum in 2000, quickly dropping from 2001 to 2004 and staying very low until 2007 (fig. 4). Raw CPUEs previous to 1998 have not been estimated.

Results from the mass-balanced models are shown in Figures 5A and B (mortality coefficients) and Figure 5C (removed biomass). In terms of juvenile mortality coefficients, the biggest changes between the two models were observed in predation mortality (strongly decreased) and "other mortalities" (those that increased). In *M. gayi* adults, fishing mortality ($F$) and predation mortality ($M2$) increased, while "other mortalities" ($M0$) decreased from 2000 to 2005.

Figure 5C shows comparisons of *M. gayi* biomass (juveniles and adults combined) removed by *M. gayi* (can-

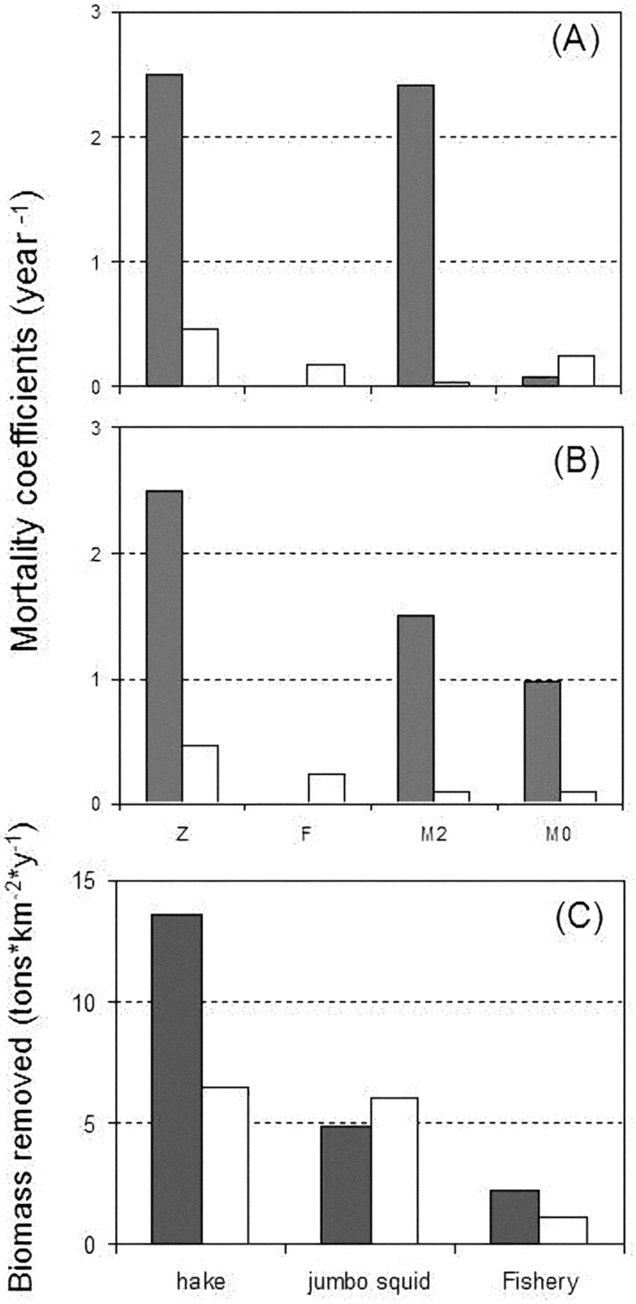

Figure 5. Ecopath-based indicators from two models off central Chile. Mortality coefficients in *M. gayi* calculated for (A) year 2000 and (B) year 2005; grey bars: juveniles (0 to 3 years old); white bars: adults (4+). (C) comparison of *Merluccius gayi* biomass (adults and juveniles) removed by *M. gayi*, *Dosidicus gigas* and the fishery in 2000 (grey bars) and 2005 (white bars).

nibalism), *D. gigas* (predation), and the fishery (catch). In the two analyzed periods, *M. gayi* removed the most *M. gayi* biomass, followed by *D. gigas*, and then the fishery. However, in 2005 *M. gayi* and the fishery removed about 50% of what they removed in 2000, and *D. gigas* removed about 10% more compared to 2000.

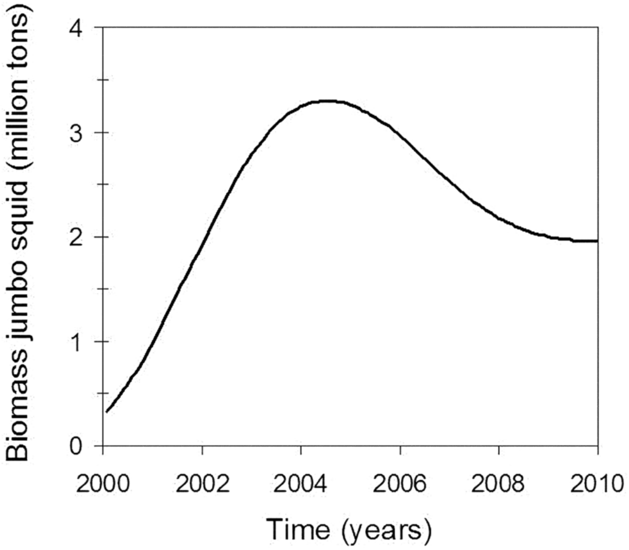

Figure 6. Simulated trend in the biomass of *Dosidicus gigas* from 2000 to 2010.

Results from simulated scenarios using EwE are shown in Figures 6 and 7. In Figure 6 we show the biomass of *D. gigas* simulated by assuming a biomass accumulation rate of 1.66/year using the model representing the system in 2000. The biomass of *D. gigas* increased from 2000 to 2005 (maximum) and then decreased until 2010.

Figures 7A and 7B show the *M. gayi* biomass trend (juveniles and adults) under several fishing and predation scenarios. The simulated increase in *D. gigas* biomass led to a slow decrease in *M. gayi* biomass (adults and juveniles) from 2000 to 2010. Fishing scenarios led to a decrease in *M. gayi* biomass starting in 2004 for juveniles and in 2003 for adults. The strongest effects were found when fishing and *D. gigas* predation were combined, with *M. gayi* biomass decreasing by 30% in juveniles and 40% in adults in 2000.

Trends in the biomass of *M. gayi* under several scenarios of fishing mortality (2005–10) are shown in Figures 7C and D. Applying a constant fishing mortality $F = F_{2005}$ from 2005 to 2010 did not result in observable changes in the *M. gayi* biomass (juveniles and adults). $F = 0$ from 2005 to 2010 would have resulted in a recovery of 20% in juveniles and more than 50% in adults. The simulation of $F = F_{2005}$ from 2005 to 2007 and $F = 0$ from 2007 to 2010 led to a recovery in the biomass of *M. gayi* juveniles (10%) and adults (35%).

## DISCUSSION

The results of our evaluation of the key biological and fishery indicators for the *M. gayi* stock off central Chile (33°–39°S) (fig. 3) suggest that fishing was the primary (driving) factor behind the observed decline in the stock. The decline in CPUE was matched by a decline

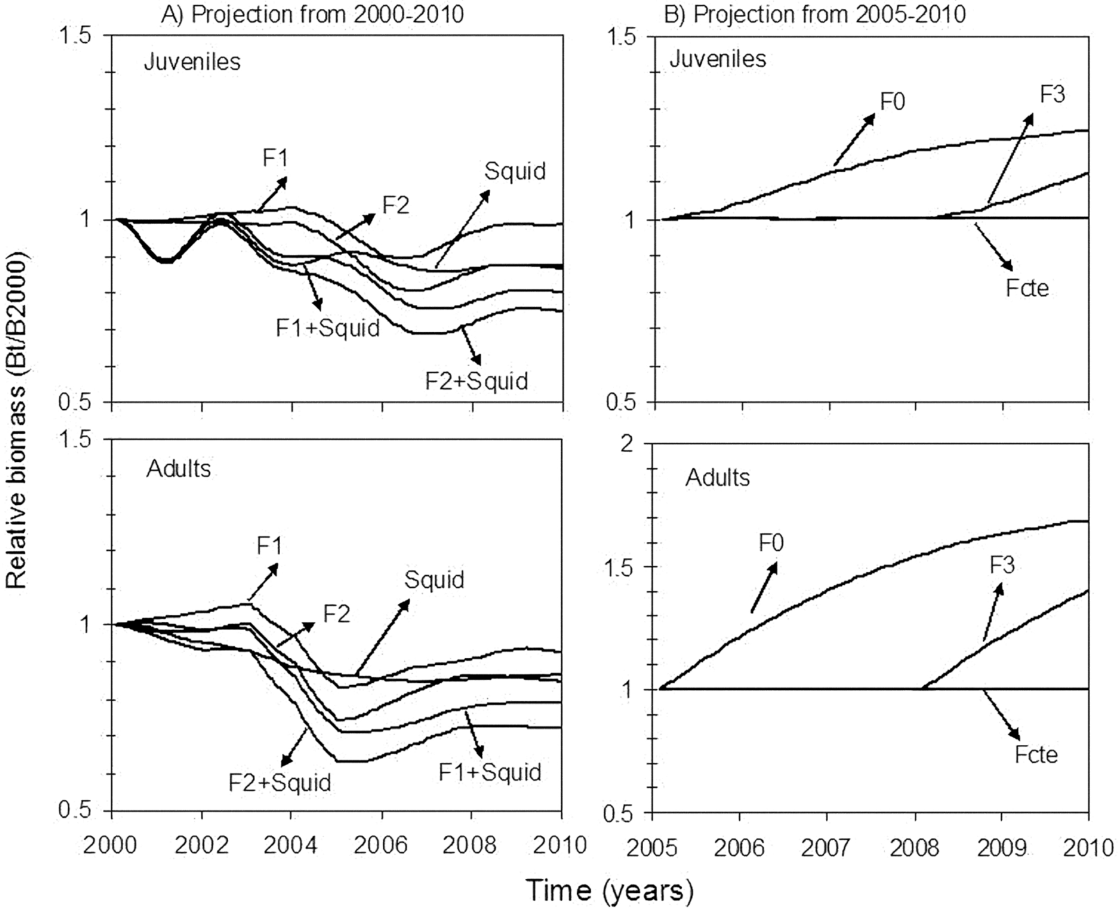

Figure 7. Trends in the *Merluccius gayi* biomass under several scenarios simulated using Ecopath models built in this study. (A) Projection from 2000 to 2010; (B) Projection 2005–10. F = fishing mortality; F1 = official fishing mortality (F = Y/B) 2000-2005; Squid: increase in the *Dosidicus gigas* biomass; F2 = corrected fishing mortality (see text); F1+Squid: combination of official fishing mortality and increase in *D. gigas* biomass; F2+Squid = combination of fishing mortality (corrected) and increase in *D. gigas* biomass; Fcte = $F_{2005}$ constant; F0 = no fishing from 2005 to 2010; F3 = $F_{2005}$ applied from 2005 to 2007 and then no fishing from 2008 to 2010.

in the mean total length of *M. gayi* catch as well as a rapid decline in the percentage of mature females. This indicates a decrease in the reproductive potential of the stock since 2000, two years before the maximum relative abundance (CPUE) of *D. gigas* was observed. This suggests that management control rules failed to protect the stock from overexploitation. The continuous increase in annual landings of *M. gayi* from the mid 1980s to mid 2000s (fig. 1) resulted in stock depletion below target biomass levels. Consequently, we recommend that the basic biological data for the *M. gayi* stock and its fishery be reviewed and evaluated based on the indicators that we have discussed here.

The comparison between ecotrophic models (for 2000 and 2005, see Appendices 1 and 2) indicated that an important decrease in predation mortality in *M. gayi* juveniles occurred between 2000 and 2005 (figs. 5A, B). This change is explained by the decrease in cannibalism, which in turn is explained by the decrease in the adult stock biomass. This is in agreement with Arancibia et al. (1998), who reported that *M. gayi* adults are opportunistic predators that cannibalize juveniles (mainly pre-recruits, i.e., individuals of age-group 0 with total length less than 12 cm). Later, Jurado-Molina et al. (2006) also reported similar results, that *M. gayi* juveniles represent more than 90% of cannibalized individuals.

Model results indicate that in 2000, *D. gigas* removed about one third of what was removed by cannibalism in *M. gayi*. In 2005, removal by *D. gigas* was still lower than that by cannibalism, even when the adult stock of *M. gayi* was decimated (fig. 5C). It does not seem likely that catastrophic *D. gigas* predation on *M. gayi* (sensu Payá 2006; and SubPesca 2006) occurred since predation by *D. gigas* was lower than cannibalism in *M. gayi* in both models for 2000 (previous to the collapse of the fishery operating on *M. gayi*) and 2005 (after the collapse).

During the time periods considered here, the most *M. gayi* biomass was removed by cannibalism, followed by *D. gigas* predation, and then the fishery. However, in 2005, *M. gayi* and the fishery removed about 50% of the biomass that they removed in 2000, while removal by *D. gigas* increased by about 10% compared to 2000 (fig. 5C). Therefore, the most parsimonious explanation for the observed changes in *M. gayi* biomass are changes in cannibalism and fishing, rather than *D. gigas*.

The EwE approach assumes that the vulnerability of individuals to predation within a life-history period is independent of size or age. Under this assumption, cannibalism in *M. gayi* is a bigger source of mortality than *D. gigas* predation. However, there is a hypothetical situation when *D. gigas* could exert strong top-down trophodynamic control on smaller (younger) individuals within a life-history period. Under these conditions, and with the same total consumption rate of juvenile *M. gayi* by *D. gigas*, the age-specific mortality rates of *M. gayi* would be extraordinarily high in the size/age ranges affected both by cannibalism and *D. gigas* predation, and for which cohort biomass was relatively small. There is no evidence of such strong trophic control of *D. gigas* on *M. gayi* off central Chile, and therefore our simulations did not explore the effect of changes in vulnerability of *M. gayi* life-history periods. However, the effects of predation and cannibalism on different *M. gayi* life-history periods could be explored in future studies.

Our simulations indicated that, all else being equal, an increase in *D. gigas* biomass by one order of magnitude would lead to a slow decrease in *M. gayi* biomass (adults and juveniles) from 2000 to 2010. By contrast, fishing scenarios based on assessment estimates of fishing mortality led to a noticeable decrease in *M. gayi* biomass from 2004 (in juveniles) and 2003 (in adults), which is consistent with the observed dynamics of the *M. gayi* stock before 2004 (fig. 1). The greatest declines in hake biomass were observed when the effects of fishing and *D. gigas* predation were combined, with declines of 30% (juveniles) and 40% (adults) relative to the *M. gayi* biomass in 2000. However, the simulated increase in *D. gigas* may be overestimated, as it is based on a biomass increase of one order of magnitude from 2000 to 2005, which, due to the highly uncertain data, may be unlikely (fig. 8).

The simulations may have captured fishing effects (fig. 7) because they included estimates of discards in the industrial trawling and underreported catch reported (Arancibia and Neira 2003). Arancibia and Neira (2003) estimated that underreported catch in the industrial *M. gayi* fishery was 20% of the official landing (www.sernapesca.cl). This value has historically been estimated at 12%, but was raised to 20% after 2000 due to Law N° 19,713, when maximum individual transferable quotas by owner of fishing vessels were implemented.

The last set of simulations (fig. 7) indicate that if the *M. gayi* fishery were to be managed using levels of fishing mortality (*F*) similar to those observed in 2005, the stock would be expected to remain at low biomass levels. These simulations indicate that had the fishery been closed in 2005 ($F = 0$), then recovery of the stock would be expected to take place from 2005 to 2010. In Chile, some stakeholders agree with the idea of a temporary moratorium for the *M. gayi* fishery, however more widespread support for this closure has so far been impracticable due to social impacts (such as job loss). Arancibia and Cubillos (1993) previously evaluated options for protecting the spawning biomass of *M. gayi*, and recommended a threshold of 225,000 t as a management limit. By contrast, the spawning biomass of *M. gayi* in 2006 was as low as 140,000 t (SubPesca 2006).

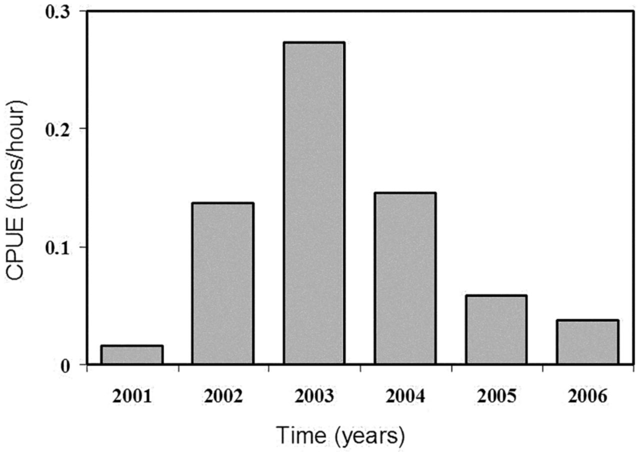

Figure 8. Catch per unit of effort (ton/hour) of *Dosidicus gigas* as by-catch in the trawling fishery of *Merluccius gayi* off central Chile, from 2001–06 (data source: Arancibia et al. 2007).

A question that remains is how the biomass of a demersal species of low growth (von Bertalanfy growth coefficient K = 0.1 – 0.2/y; www. fishbase.org) could increase by 70% in one year (e.g., from 2001 to 2002) in the absence of good recruitment and in the presence of exploitation. The doubling time for this species is about three years and therefore an increase in biomass in 2002 seems unlikely. Consequently, it is possible that the acoustic survey in 2002 was affected by anomalous behavior of *M. gayi* or misidentification of acoustic signals with other co-occurring fish species. There is some indirect evidence to suggest that *M. gayi* could have been erroneously identified during the acoustic survey, as the species dominating the study area during 2002 was hoki (*Macruronus magellanicus*). In fact, the density of hoki increased 15 times from 2001 (1.25 t/km$^2$) to 2002 (19.04 t/km$^2$), decreasing again in 2004 (1.98 t/km$^2$) as measured in an acoustic survey (Lillo, S. pers. commun.[5]).

Our analysis suggests that the *M. gayi* stock has been affected by overfishing since 2000, as indicated by a decline in catch per unit of effort, length of catch, and the

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proportion of mature females in the stock. These are typical effects of fishing and cannot be ascribed to predation since *D. gigas* prey primarily on juvenile *M. gayi* (Arancibia et al. 2007). In addition, any strong predation by *D. gigas* would have been expected to occur primarily since 2003 (when the maximum *D. gigas* abundance was observed), and observed in the adult biomass only three to four years later. We suggest that it is unlikely that *M. gayi* biomass almost doubled in one year, as indicated by the acoustic data and assessment model, and it is consequently very likely that the abundance was never as high as was estimated. If this is true, then catastrophic predation by *D. gigas* is not needed to explain the drop in *M. gayi* biomass. We propose that, although potentially important, predation by *D. gigas* is unlikely to have been the driving factor in *M. gayi* population dynamics since 2000. Therefore, we suggest that the idea of catastrophic predation of *D. gigas* on *M. gayi* lacks biological and ecological support.

Results and conclusions from this study may be affected by unavoidable uncertainties associated with the available data and assumptions in ecosystem models. For example, although abundant data are available for determining diets and consumption rates of *M. gayi* adults and for cannibalism, both in the short and long term (Arancibia 1987; Arancibia et al. 1998; Cubillos et al. 2003), data on diet and other important trophodynamic parameters of predators such as jumbo squid are less available (e.g., Arancibia et al. 2007). Moreover, the starting values for estimating jumbo squid abundance are poorly known, and for this exercise are based on top-down model estimates. Therefore, more ecosystem-based research is strongly needed in order to understand and model strong predator-prey interactions and fishing effects on fishing resources in this very productive food web.

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## APPENDIX 1

**Inputs (bold) and outputs of the balanced model representing the upwelling system off central Chile in 2000.**

| Group/Parameter | B | P/B | Q/B | EE | P/Q | F | M2 | M0 |
|---|---|---|---|---|---|---|---|---|
| cetaceans | **0.01** | **0.60** | **10.00** | 0.17 | 0.06 | 0.00 | 0.10 | 0.50 |
| sea lions | **0.07** | **0.25** | **20.00** | 0.38 | 0.01 | 0.00 | 0.10 | 0.16 |
| marine birds | **0.07** | **0.50** | **20.00** | 0.00 | 0.03 | 0.00 | 0.00 | 0.50 |
| hake (j) | **8.57** | **2.50** | **8.32** | 0.97 | 0.30 | 0.01 | 2.42 | 0.08 |
| hake (a) | **12.19** | **0.46** | **5.16** | 0.46 | 0.09 | 0.18 | 0.03 | 0.25 |
| sardine (j) | **41.36** | **1.45** | 14.53 | 0.36 | **0.10** | 0.21 | 0.32 | 0.93 |
| sardine (a) | **14.60** | **1.88** | 18.75 | 0.37 | **0.10** | 0.32 | 0.38 | 1.18 |
| anchovy (j) | **23.97** | **0.70** | 7.03 | 0.77 | **0.10** | 0.15 | 0.39 | 0.16 |
| anchovy (a) | **14.63** | **2.12** | 21.20 | 0.32 | **0.10** | 0.31 | 0.37 | 1.44 |
| squid | 3.34 | **3.50** | 10.61 | **1.00** | **0.33** | 0.00 | 3.50 | 0.00 |
| jumbo squid | **6.50** | **1.75** | **5.00** | 1.14 | 0.35 | 0.00 | 1.00 | 0.75 |
| mesopelagic fish | 56.05 | **1.20** | **12.00** | **1.00** | 0.10 | 0.00 | 1.20 | 0.00 |
| red s. lobster (j) | 0.22 | **5.90** | **18.00** | **1.00** | 0.33 | 0.00 | 5.89 | 0.01 |
| red s. lobster (a) | 0.48 | **3.57** | **12.50** | **1.00** | 0.29 | 0.17 | 3.40 | 0.00 |
| yellow s. lobster | **0.08** | **3.57** | **11.60** | 0.85 | 0.31 | 0.77 | 2.27 | 0.53 |
| pink shrimp | **0.40** | **2.50** | **12.00** | 0.47 | 0.21 | 0.22 | 0.94 | 1.33 |
| horse mackerel | **23.98** | **0.56** | **14.20** | 0.36 | 0.04 | 0.13 | 0.07 | 0.36 |
| hoki | **21.90** | **0.53** | 5.28 | 0.30 | **0.10** | 0.07 | 0.09 | 0.37 |
| sword fish | 0.64 | **0.50** | 5.00 | **0.75** | **0.10** | 0.38 | 0.00 | 0.13 |
| congers | **0.30** | **0.70** | 3.50 | 0.35 | **0.20** | 0.23 | 0.02 | 0.45 |
| rattail fish | 0.65 | **0.70** | 3.50 | **1.00** | **0.20** | 0.00 | 0.70 | 0.00 |
| flat fishes | 0.47 | **0.70** | 3.50 | **1.00** | **0.20** | 0.00 | 0.70 | 0.00 |
| cardinal fish | **0.78** | **0.70** | 3.50 | 0.29 | **0.20** | 0.15 | 0.06 | 0.50 |
| sand perch | **0.05** | **0.70** | 3.50 | 0.10 | **0.20** | 0.07 | 0.00 | 0.63 |
| skates | **0.25** | **0.36** | 2.41 | 0.13 | **0.15** | 0.05 | 0.00 | 0.32 |
| polychaetes | **1.89** | **2.41** | **15.90** | 0.00 | 0.15 | 0.00 | 0.00 | 2.41 |
| jellies | 7.77 | **0.58** | **1.42** | **0.15** | 0.41 | 0.00 | 0.09 | 0.50 |
| copepods | 84.71 | **45.00** | **154.52** | **1.00** | 0.29 | 0.00 | 44.96 | 0.05 |
| euphausiids | 68.79 | **13.00** | 31.71 | **1.00** | **0.41** | 0.00 | 12.99 | 0.01 |
| phytoplankton | 364.23 | **120.00** | — | **0.30** | — | 0.00 | 36.00 | 84.00 |

# APPENDIX 2

## Diet composition of the predators in the balanced model representing the upwelling system off central Chile in 2000.

| Prey/Predator | cetaceans | sea lions | marine birds | hake (j) | hake (a) | sardine (j) | sardine (a) | anchovy (j) | anchovy (a) | squid | jumbo squid | mesopelagic fish | red s. lobster (j) | red s. lobster (a) | yellow s. lobster | pink shrimp | horse mackerel | hoki | sword fish | congers | rattail fish | flat fishes | cardinal fish | sand perch | skates | polychaetes | jellies | copepods | euphausiids |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| cetaceans | 0.010 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| sea lions | 0.098 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| marine birds | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| hake (j) | 0.060 | 0.250 | 0.100 | 0.040 | 0.170 | | | | | 0.050 | 0.150 | | | | | | | | | 0.013 | | | | 0.065 | | | | | |
| hake (a) | 0.070 | 0.200 | 0.050 | | | | | | | | | | | | | | | | | 0.036 | | | | | | | | | |
| sardine (j) | 0.098 | 0.180 | 0.284 | 0.118 | | | | | | 0.050 | 0.073 | | | | | | | | | | | | | | | | | | |
| sardine (a) | 0.034 | 0.065 | 0.100 | 0.042 | | | | | | | 0.072 | | | | | | | | | | | | | | | | | | |
| anchovy (j) | 0.056 | 0.110 | 0.165 | 0.070 | | | | | | 0.050 | 0.066 | | | | | | | | | | | | | | | | | | |
| anchovy (a) | 0.036 | 0.062 | 0.101 | 0.042 | | | | | | | 0.069 | | | | | | | | | | | | | | | | | | |
| squid | 0.150 | | 0.040 | | 0.002 | | | | | 0.210 | | | | | | | | 0.035 | 0.010 | | | | | | | | | | |
| jumbo squid | 0.150 | | 0.040 | | 0.002 | | | | | | 0.070 | | | | | | | 0.035 | 0.010 | | | | | | | | | | |
| mesopelagic fish | 0.098 | | 0.120 | | 0.300 | | | | | 0.100 | 0.470 | | | | | | 0.025 | 0.180 | | | | | | | | | | | |
| red s. lobster (j) | | | | 0.015 | 0.002 | | | | | | | | | | | | | | | 0.004 | 0.030 | 0.020 | | | 0.002 | | | | |
| red s. lobster (a) | | | | 0.008 | 0.001 | | | | | | | | | | | | | | | 0.107 | 0.110 | 0.300 | | | 0.210 | | | | |
| yellow s. lobster | | | | | 0.002 | | | | | | | | | | | | | | | 0.002 | | 0.020 | | | 0.023 | | | | |
| pink shrimp | | | | | 0.006 | | | | | | | | | | | | | | | | | | | | | | | | |
| horse mackerel | 0.100 | 0.100 | | | | | | | | | | | | | | | | | 0.480 | | | | | | | | | | |
| hoki | | | | | | | | | | | 0.010 | | | | | | | | 0.500 | | | | | | | | | | |
| sword fish | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| congers | | 0.004 | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| rattail fish | | | | | 0.002 | | | | | | 0.010 | | | | | | | | | | | | | | | | | | |
| flat fishes | | | | | | | | | | | 0.010 | | | | | | | | | | | | | | | | | | |
| cardinal fish | | 0.030 | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| sand perch | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| skates | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| polychaetes | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| jellies | | | | | | | | | | | | | | | | | 0.002 | | | | | | | | | | | | |
| copepods | | | | | | 0.020 | 0.020 | 0.020 | 0.020 | 0.440 | | 0.400 | | | | | 0.002 | | | | | | | | | | 0.500 | 0.200 | 0.400 |
| euphausiids | | | | 0.500 | 0.506 | | | | | 0.100 | | 0.600 | | | | | 0.971 | 0.750 | | | | | 0.500 | 0.679 | | | | | |
| phytoplankton | | | | | | 0.980 | 0.980 | 0.980 | 0.980 | | | | | | | | | | | | | | | | | | 0.500 | 0.800 | 0.600 |
| detritus | | | | | | | | | | | | | 1.000 | 1.000 | 1.000 | 1.000 | | | | | | | | | | 1.000 | | | |
| Import | 0.040 | | | 0.165 | 0.008 | | | | | | | | | | | | | | | 0.838 | 0.860 | 0.660 | 0.500 | 0.256 | 0.765 | | | | |
| Sum | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |

## APPENDIX 3

**Inputs (bold) and outputs of the balanced model representing the upwelling system off central Chile in 2005.**

| Group/Parameter B | P/B | Q/B | EE | P/Q | F | M2 | M0 | |
|---|---|---|---|---|---|---|---|---|
| cetaceans | **0.01** | **0.60** | **10.0** | 0.167 | 0.06 | 0.00 | 0.10 | 0.50 |
| sea lions | **0.07** | **0.25** | **20.0** | 0.381 | 0.01 | 0.00 | 0.10 | 0.16 |
| marine birds | **0.07** | **0.50** | **20.0** | 0.000 | 0.03 | 0.00 | 0.00 | 0.50 |
| hake (j) | **9.40** | **2.50** | **8.3** | 0.609 | 0.30 | 0.02 | 1.51 | 0.98 |
| hake (a) | **3.80** | **0.46** | **5.2** | 0.777 | 0.09 | 0.25 | 0.10 | 0.10 |
| sardine (j) | **16.67** | **1.45** | 14.5 | 0.726 | **0.10** | 0.22 | 0.84 | 0.40 |
| sardine (a) | **16.37** | **1.88** | 18.8 | 0.322 | **0.10** | 0.21 | 0.39 | 1.27 |
| anchovy (j) | **18.80** | **0.70** | 7.0 | **0.999** | **0.10** | 0.19 | 0.52 | 0.00 |
| anchovy (a) | **16.03** | **2.12** | 21.2 | 0.293 | **0.10** | 0.23 | 0.39 | 1.50 |
| squid | 2.27 | **3.50** | 10.6 | **0.999** | **0.33** | 0.00 | 3.50 | 0.00 |
| jumbo squid | **7.99** | **1.75** | **5.0** | 0.718 | 0.35 | 0.55 | 0.71 | 0.49 |
| mesopelagic fish | 35.13 | **1.20** | **12.0** | **0.999** | 0.10 | 0.00 | 1.20 | 0.00 |
| red s. lobster (j) | 0.22 | **5.90** | **18.0** | **0.999** | 0.33 | 0.00 | 5.89 | 0.01 |
| red s. lobster (a) | 0.40 | **3.57** | **12.5** | **0.999** | 0.29 | 0.00 | 3.57 | 0.00 |
| yellow s. lobster | **0.52** | **3.57** | **11.6** | 0.041 | 0.31 | 0.00 | 0.15 | 3.42 |
| pink shrimp | **0.39** | **2.50** | **12.0** | 0.172 | 0.21 | 0.13 | 0.30 | 2.07 |
| horse mackerel | 1.57 | **0.56** | **14.2** | **0.999** | 0.04 | 0.45 | 0.11 | 0.00 |
| hoki | **15.07** | **0.53** | 5.3 | 0.118 | 0.10 | 0.03 | 0.03 | 0.47 |
| sword fish | **0.01** | **0.50** | 5.0 | 0.000 | **0.10** | 0.00 | 0.00 | 0.50 |
| congers | **0.30** | **0.70** | 3.5 | 0.027 | **0.20** | 0.00 | 0.02 | 0.68 |
| rattail fish | 0.63 | **0.70** | 3.5 | **0.999** | **0.20** | 0.00 | 0.70 | 0.00 |
| flat fishes | 0.29 | **0.70** | 3.5 | **0.999** | **0.20** | 0.00 | 0.70 | 0.00 |
| cardinal fish | 0.06 | **0.70** | 3.5 | **0.999** | **0.20** | 0.00 | 0.70 | 0.00 |
| sand perch | **0.05** | **0.70** | 3.5 | 0.000 | **0.20** | 0.00 | 0.00 | 0.70 |
| skates | **0.25** | **0.36** | 2.4 | 0.000 | **0.15** | 0.00 | 0.00 | 0.36 |
| polychaetes | **1.89** | **2.41** | **15.9** | 0.000 | 0.15 | 0.00 | 0.00 | 2.41 |
| jellies | 0.51 | **0.58** | **1.4** | **0.150** | 0.41 | 0.00 | 0.09 | 0.50 |
| copepods | 41.06 | **45.00** | **154.5** | **0.999** | 0.29 | 0.00 | 44.96 | 0.05 |
| euphausiids | 29.72 | **13.00** | 31.7 | **0.999** | **0.41** | 0.00 | 12.99 | 0.01 |
| phytoplankton | 184.49 | **120.00** | — | **0.300** | — | 0.00 | 36.00 | 84.00 |

# APPENDIX 4

**Diet composition of the predators in the balanced model representing the upwelling system off central Chile in 2005.**

| Prey/Predator | cetaceans | sea lions | marine birds | hake (j) | hake (a) | sardine (j) | sardine (a) | anchovy (j) | anchovy (a) | squid | jumbo squid | mesopelagic fish | red s. lobster (j) | red s. lobster (a) | yellow s. lobster | pink shrimp | horse mackerel | hoki | sword fish | congers | rattail fish | flat fishes | cardinal fish | sand perch | skates | polychaetes | jellies | copepods | euphausiids |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| cetaceans | 0.010 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| sea lions | 0.098 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| marine birds | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| hake (j) | 0.060 | 0.250 | 0.100 | 0.040 | 0.170 | | | | | 0.050 | 0.150 | | | | | | | | | 0.013 | | | | 0.065 | | | | | |
| hake (a) | 0.070 | 0.200 | 0.050 | | | | | | | | | | | | | | | | | 0.036 | | | | | | | | | |
| sardine (j) | 0.098 | 0.180 | 0.284 | 0.118 | | | | | | 0.050 | 0.073 | | | | | | | | | | | | | | | | | | |
| sardine (a) | 0.034 | 0.065 | 0.100 | 0.042 | | | | | | | 0.072 | | | | | | | | | | | | | | | | | | |
| anchovy (j) | 0.056 | 0.110 | 0.165 | 0.070 | | | | | | 0.050 | 0.066 | | | | | | | | | | | | | | | | | | |
| anchovy (a) | 0.036 | 0.062 | 0.101 | 0.042 | | | | | | | 0.069 | | | | | | | | | | | | | | | | | | |
| squid | 0.150 | | 0.040 | | 0.002 | | | | | 0.210 | | | | | | | | 0.035 | 0.010 | | | | | | | | | | |
| jumbo squid | 0.150 | | 0.040 | | 0.002 | | | | | | 0.070 | | | | | | | 0.035 | 0.010 | | | | | | | | | | |
| mesopelagic fish | 0.098 | | 0.120 | | 0.300 | | | | | 0.100 | 0.470 | | | | | | 0.025 | 0.180 | | | | | | | | | | | |
| red s lobster (j) | | | | 0.015 | 0.002 | | | | | | | | | | | | | | | 0.004 | 0.030 | 0.020 | | | 0.002 | | | | |
| red s. lobster (a) | | | | 0.008 | 0.001 | | | | | | | | | | | | | | | 0.107 | 0.110 | 0.300 | | | 0.210 | | | | |
| yellow s. lobster | | | | | 0.002 | | | | | | | | | | | | | | | 0.002 | | 0.020 | | | 0.023 | | | | |
| pink shrimp | | | | | 0.006 | | | | | | | | | | | | | | | | | | | | | | | | |
| horse mackerel | 0.100 | 0.100 | | | | | | | | | | | | | | | | | 0.480 | | | | | | | | | | |
| hoki | | | | | | | | | | | 0.010 | | | | | | | | 0.500 | | | | | | | | | | |
| sword fish | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| congers | | 0.004 | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| rattail fish | | | | | 0.002 | | | | | | 0.010 | | | | | | | | | | | | | | | | | | |
| flat fishes | | | | | | | | | | | 0.005 | | | | | | | | | | | | | | | | | | |
| cardinal fish | | 0.030 | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| sand perch | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| skates | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| polychaetes | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| jellies | | | | | | | | | | | | | | | | | 0.002 | | | | | | | | | | | | |
| copepods | | | | | | 0.020 | 0.020 | 0.020 | 0.020 | 0.440 | | 0.400 | | | | | 0.002 | | | | | | | | | | 0.500 | 0.200 | 0.400 |
| euphausiids | | | | 0.500 | 0.506 | | | | | 0.100 | | 0.600 | | | | | 0.971 | 0.750 | | | | | 0.500 | 0.679 | | | | | |
| phytoplankton | | | | | | 0.980 | 0.980 | 0.980 | 0.980 | | | | | | | | | | | | | | | | | | 0.500 | 0.800 | 0.600 |
| detritus | | | | | | | | | | | | | 1.000 | 1.000 | 1.000 | 1.000 | | | | | | | | | | 1.000 | | | |
| Import | 0.040 | | | 0.165 | 0.008 | | | | | | 0.005 | | | | | | | | | 0.838 | 0.860 | 0.660 | 0.500 | 0.256 | 0.765 | | | | |
| Sum | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |