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ARTICLE

A Multispecies Virtual Population Analysis for the Southern Chilean Demersal Fishery

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Abstract

A multispecies virtual population analysis (MSVPA) model for the southern Chilean demersal fishery was developed. Species included the Southern Hake *Merluccius australis*, Pink Cusk-eel *Genypterus blacodes* (hereafter, "Kingklip"), Southern Blue Whiting (SBW) *Micromesistius australis*, and Patagonian Grenadier (also known as Argentine Straptail) *Macruronus magellanicus* (hereafter, "Hoki"). Due to a lack of stomach content data, we constructed suitability coefficients based on predator–prey size ratios. Terminal fishing mortality (F_{term}) was estimated by fitting a cohort analysis model to estimates of abundance from single-species models developed by the Chilean Instituto de Fomento Pesquero (IFOP; Institute for Fishing Development). Values of F_{term} were used as input data in the MSVPA, driving the dynamics of the species and producing adult abundance estimates that were similar to IFOP estimates. Comparison of MSVPA and IFOP estimates suggested consistency in adult abundance and total abundance estimates for SBW. Differences were identified for adult Hoki abundance estimates. Differences in recruitment estimates were small for SBW, whereas greater differences

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were found for Hoki. The MSVPA revealed high estimates of predation mortality for Hoki, while predation played a minor role in SBW population dynamics. Cannibalism and predation by Southern Hake were the main components of predation mortality for age-0 Hoki; Southern Hake were the most important source of predation for age-1 Hoki. Sensitivity analysis suggested that Hoki response variables were sensitive to 10% perturbations in suitability coefficients, while SBW response variables were not. This study is a first step toward building a multispecies framework that could provide complementary information for the sustainable management of fishing resources in southern Chile.

In recent decades, the global agreement that marine populations are not isolated entities in their ecosystems but instead are part of complex webs of interactions with other species and the environment (Hollowed et al. 2000; Livingston and Jurado-Molina 2000; Kempf et al. 2006) has increased the interest in developing an ecosystem approach to fisheries management.

The search for tools that can be incorporated into ecosystem-based fishery management has resulted in the development of several modeling approaches (Plagányi 2007), such as multispecies models with technological interactions (Siegel et al. 1979), static and dynamic food web models, (Walters et al. 2000; Christensen and Walters 2004), dynamic models that include oceanographic forcing (e.g., SEAPODYM; Lehodey et al. 2008; Senina et al. 2008), and individual-based models (Ginot et al. 2006). In particular, multispecies virtual population analysis (MSVPA) and multispecies forecasting (MSFOR) analysis are two age-structured modeling approaches that include biological interactions (i.e., predation) and were developed by the International Council for the Exploration of the Sea (ICES) Multispecies Assessment Working Group. These two types of model have been used to provide complementary information in stock assessment and management of important fisheries from the North Sea (ICES 1989; Sparre 1991), the Baltic Sea (Sparholt 1991), Georges Bank (Tsou and Collie 2001), and the Bering Sea (Livingston and Jurado-Molina 2000; Jurado-Molina and Livingston 2002a, 2002b). Multispecies virtual population analysis and MSFOR models have provided complementary information for the management of fisheries resources; for example, they have been useful in assessing the indirect effects of fishing (Jurado-Molina and Livingston 2002a), food consumption by predators and the associated implications for prey species recruitment (Livingston and Jurado-Molina 2000), and the relative importance of predation and climate in affecting species dynamics (Jurado-Molina and Livingston 2002b). Multispecies models that employ statistical estimation of parameters have been used for the Bering Sea (Jurado-Molina et al. 2005); the Aleutian Shelf, Alaska (Kinzey and Punt 2009); and other regions. In Chile, multispecies management advice has not yet been used to support the management of any fishery; only isolated efforts have been focused on estimating cannibalism of Chilean Hake *Merluccius gayi* (Jurado-Molina et al. 2006) and analyzing the food web that sustains the most important fishery resources in central Chile (Neira and Arancibia 2004).

The southern Chilean demersal fishery (SCDF; 41°28–57°00′S) for the Patagonian Grenadier (also known as Argentine Straptail) *Macruronus magellanicus* (hereafter, "Hoki"), Southern Hake *Merluccius australis*, Southern Blue Whiting (SBW) *Micromesistius australis*, and Pink Cusk-eel *Genypterus blacodes* (hereafter, "Kingklip") represents an important fishery. In this complex multispecies system, the Hoki is considered a key species due to (1) its role as the main prey for Southern Hake and Kingklip and (2) the presence of substantial cannibalism on the juvenile fraction (Pool et al. 1997).

The SCDF is characterized by the operation of several fishing fleets, including an artisanal longline fleet that targets Southern Hake; an industrial longline fleet that also targets Southern Hake; a purse-seine fleet that targets Hoki; a factory trawler fleet that targets Hoki and SBW; and a surimi fleet that targets SBW and skates (Céspedes et al. 2006, 2007; Roa et al. 2009). Management of the SCDF is based on information that is produced by single-species statistical catch-at-age models developed by the Chilean Instituto de Fomento Pesquero (IFOP; Institute for Fishing Development), one of the institutions that is responsible for the scientific advice underlying the management of Chilean fisheries resources. Single-species models developed by IFOP use catch-at-age data and are fitted to catch rates and acoustic biomass estimates by using a maximum likelihood estimation approach (Canales et al. 2008; Feltrim et al. 2008; Quiroz et al. 2009a, 2009b). For simplicity, we use the term "single-species models" to refer to the statistical single-species models produced by IFOP scientists.

Fishery characteristics suggest the need for moving toward a more holistic approach to improve our understanding of the SCDF and to provide complementary scientific advice that will improve the management of this multispecies fishery system. We developed an MSVPA model as a first step in building a multispecies approach to the management of these fisheries resources. We attempted to identify difficulties, lack of data, advantages, and needs for future research to support the establishment of an ecosystem approach to fisheries management, as was mandated by the recently amended Chilean Fisheries and Aquaculture Law (www.subpesca.cl/normativa/605/w3-propertyvalue-50857.html).

METHODS

The SCDF operates in an area located between 41°S and 57°S. The analysis covered the period 1990–2007. We defined a system in which Southern Hake and Kingklip were the main predators, while Hoki and SBW were the prey species (Figure 1). Cannibalism on the juvenile fraction of Hoki is strong (Pool et al. 1997). Here, we briefly describe the MSVPA model and its data inputs.

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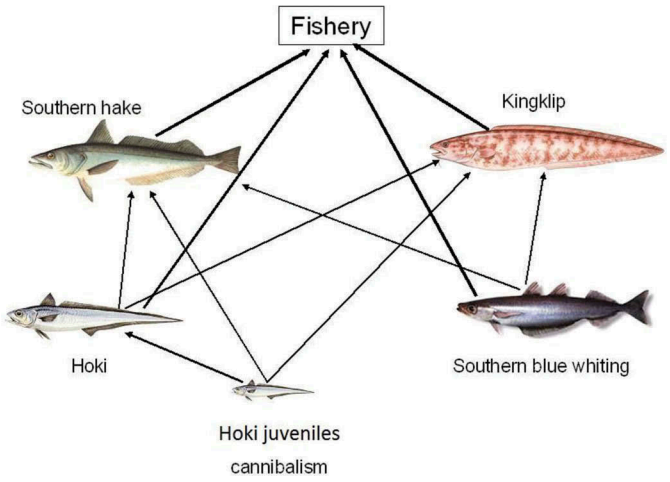


FIGURE 1. Predation interactions for the species system used in the multispecies virtual population analysis model defined for the southern Chilean demersal fishery.

Multispecies virtual population analysis is an extension of single-species virtual population analysis (SSVPA) and estimates fishing mortality, recruitment, stock abundance, and predation mortality based on catch-at-age data and stomach content data. Therefore, MSVPA uses the same equations and backward algorithm as SSVPA (Gulland 1965). Abundance for the plus group and the final year of the assessment is calculated from Baranov's catch equation,

$$N^{+}_{a,t} = \frac{C_{a,t} Z_{a,t}}{F_{term,a,t}\left(1 - e^{-Z_{a,t}}\right)}, \quad (1)$$

where $C_{a,t}$ represents the annual catch at age; $Z_{a,t}$ represents the total mortality at age ($Z_{a,t} = F_{term,a,t} + M_{a,t}$); $F_{term,a,t}$ represents the terminal fishing mortality at age; $M_{a,t}$ represents natural mortality (described in detail below); and $N^{+}_{a,t}$ represents the abundance of the plus group or the abundance of age-class a in the final year of the assessment (2007). The abundance of the remaining age-classes is backward calculated as

$$N_{a-1,t-1} = N_{a,t} e^{Z_{a,t}}. \quad (2)$$

Equation (2) is also used directly to estimate recruitment ($N_{0,t}$). Fishing mortality at age is also calculated iteratively from equation (1).

The MSVPA differs from SSVPA primarily by separating natural mortality (M) into two components: residual mortality (M_1) and predation mortality (M_2). Residual mortality encompasses several causes of mortality, such as aging, starvation, diseases, and predation by other species not included in the model; M_1 is assumed to be constant for each age-class within each species. This separation hypothesis allows predation mortality to be estimated for each age-class through time. Predation mortality is calculated with the following equation (Sparre 1991),

$$M_{2,p,a} = \sum_i \sum_j \frac{\bar{N}_{i,j} R_{i,j} S_{p,a,i,j}}{B_{of} S_{i,of} + \sum_p \sum_a \bar{N}_{p,a} \bar{W}_{p,a} S_{p,a,i,j}}, \quad (3)$$

where $M_{2,p,a}$ is the predation mortality of prey p at age a; $\bar{N}_{i,j}$ is the average abundance of predator i at age j $\left(\bar{N}_{i,j} = \frac{N_{i,j,t+1} - N_{i,j,t}}{Z_{i,j,t}}\right)$; R_{ij} is the annual ration (total annual food consumption, kg) for the predator species; $S_{p,a,i,j}$ is the suitability coefficient for each predator–prey combination; B_{of} is the biomass of other prey ("other food") available to the predator; $S_{i,of}$ is the suitability coefficient for the predator–other prey combination; $\bar{N}_{p,a}$ is the average abundance of prey p at age a; and $\bar{W}_{p,a}$ is the average weight of the prey. For simplicity, the index t for time has been omitted from equation (3).

Suitability coefficients reflect the predator's diet composition relative to the available food (Sparre 1991). Estimation of suitability is based on stomach content data according to the following operational definition:

$$S_{p,a,i,j} = \frac{U_{p,a,i,j} / \bar{N}_{p,a} W_{p,a}}{\sum_p \sum_a U_{p,a,i,j} / \bar{N}_{p,a} W_{p,a}}, \quad (4)$$

where $U_{p,a,i,j}$ is the observed food composition in the predator's stomach contents; a is the age of prey p; and j is the age of predator i. Predator/prey suitability values have also been defined as a weighting factor determining the availability of prey p as food for predator i (Gislason and Sparre 1987). Solution of the previous equations (1–4) requires the use of three nested iterative algorithms (Sparre 1991). More details on MSVPA assumptions, equations, and algorithms are provided by Sparre (1991) and Magnusson (1995).

Due to its complexity, MSVPA requires several types of input data, including stomach content data, annual predator ration, M_1, catch at age, and F_{term}, all of which are described below.

The food composition or stomach content data are probably the most important data for estimating predation mortality M_2 in the MSVPA. However, diet composition information is scarce for SCDF species; therefore, we considered a different approach for these fisheries based on the work of Ursin (1973). The approach uses parameters from the predator–prey size ratios to arrive at a theoretical estimate of Ursin's prey selectivity index.

Using a simplification from Bogstad et al. (2003), the suitability coefficients were calculated with the following equation:

$$S_{p,a,i,j} = e^{\left[-\frac{\left(\ln\left(W_{i,j}/W_{p,a}\right) - \eta\right)^2}{2\sigma^2}\right]}, \quad (5)$$

where $W_{i,j}$ is the weight of predator i at age j; and $W_{p,a}$ is the weight of prey p at age a. The constant η represents the mean log ratio between the predator weight and prey weight,

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TABLE 1. Parameters from the von Bertalanffy growth model (length) for Southern Hake, Hoki, Southern Blue Whiting (SBW), and Kingklip (L_∞ = asymptotic length [cm]; K = Brody growth coefficient [year^{-1}]; t_0 = hypothetical age [years] at which length is zero; α, β = constants from the length–weight relationship).

Species	Source	L_∞	K	t_0	α	β
Southern Hake	Ojeda and Aguayo 1986	121.0	0.080	–1.457	0.002	3.313
Hoki	Chong et al. 2007	101.3	0.176	–0.812	0.003	2.961
SBW	Ojeda et al. 1998	53.3	0.255	–1.558	0.001	3.416
Kingklip	Wiff et al. 2007	117.4	0.167	–1.345	0.002	–

$$\eta = \frac{\sum_{i=1}^{N} \log_e\left(W_{i,j}/W_{p,a}\right)}{N},$$

and is the corresponding SD. The predator and prey weights, η, σ, and the suitability coefficients were calculated by using the corresponding von Bertalanffy growth parameters reported in the literature (Table 1).

Another important input parameter is the predator's annual ration, which requires accounting for the observed weight and the age-dependent gross food conversion efficiency (GCE). According to Brett and Groves (1979), the proportion of consumed food that is converted into somatic tissue fluctuates at around 0.3 in juveniles and 0.1 in adults. The GCE in juveniles and adults declines linearly (Brett and Groves 1979) as

$$\mathrm{GCE}_i = \frac{(0.1 - 0.3)}{b}(i - 0.5) + 0.3, \quad (6)$$

where b is the mean age at maturity; and i is predator age. The predator's annual ration or consumption (R_i) is determined as

$$R_i = \frac{W_i - W_{i-1}}{\mathrm{GCE}_i}, \quad (7)$$

where $W_i - W_{i-1}$ is the annual weight increment.

The estimation of M_1 for Hoki and SBW involved an iterative process starting with an initial MSVPA run, assuming $M_1 = M$ (i.e., natural mortality from the single-species model). As a result, we obtained an initial set of average M_2 at age; these values were subtracted from M_1 to obtain a new set of values for M_1 at age. A new MSVPA run was then performed with these new M_1 values. The same procedure was repeated until the following criterion of convergence was reached:

$$\left|M_{1,previous} - M_{1,current}\right| \leq 0.0001. \quad (8)$$

As a result of this procedure, the M of older age-classes was similar to the M value used in the single-species models; however, M for younger ages changed significantly due to the addition of predation. For Southern Hake and Kingklip, we used the M assigned in the single-species models. Catch-at-age data (1990–2007) for each species included in the system were acquired from IFOP databases.

The F_{term} values used as MSVPA input were estimated by fitting a cohort analysis model to abundance estimates from the single-species models. The cohort analysis model uses the same backward algorithm as the SSVPA model, allowing for the estimation of F_{term}. The M used in the cohort analysis model was 0.21 per year for Southern Hake and SBW (Feltrim et al. 2008; Quiroz et al. 2009b), 0.26 per year for Kingklip (Quiroz et al. 2009a), and 0.35 per year for Hoki (Roa et al. 2009).

The main cohort analysis equations were

$$N_{a,t} = N_{a+1,t+1}e^{-\left(M+F_{a,t}\right)} \text{ when } 1 \leq a < m \text{ and } 1 \leq t < n; \quad (9)$$

$$N_{a,t} = \frac{C_{a,t}}{\left[1 - e^{-(F_{ter}+M)}\right]}\left(\frac{F_{term} + M}{F_{term}}\right) \text{ when } a = m \text{ and } t = n, \quad (10)$$

where $N_{a,t}$ is the abundance at age a and at time t; n is the total number of years; m is the total number of age-classes; C is the catch; M is the corresponding natural mortality for each species; F is the fishing mortality; and F_{term} is the terminal fishing mortality (MSVPA input) corresponding to the older age-class and the final year of the assessment.

Cohort analysis models that were used to estimate F_{term} were fitted to abundance estimates from the statistical single-species models used in SCDF management by assuming log-normally distributed observation error. Therefore, for a given year t, the individual negative log-likelihood (LL) was given by (Hilborn and Mangel 1997)

$$\mathrm{LL} = \log_e(\sigma_*) + \frac{\left[\log_e\left(N^{3+}_{IFOP,t}\right) - \log_e\left(N^{3+}_{CA,t}\right)\right]^2}{2\sigma_*}, \quad (11)$$

where $N^{3+}_{IFOP,t}$ is the adult abundance estimate from the IFOP model; $N^{3+}_{CA,t}$ is the estimate from cohort analysis; and σ_* is the standard error. The total negative LL is the sum of the n components. The estimation of parameters F_{term} and σ_* was carried out using the Microsoft Excel Premium Solver Platform (Frontline Systems, Inc.).

The MSVPA model was set up to run annually from 1990 to 2007. We included ages 0 to 24 for Southern Hake (Quiroz et al. 2009a, 2009b), ages 0 to 18 for SBW (Feltrim et al. 2008), ages

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0 to 14 for Hoki (Canales et al. 2008), and ages 0 to 12 for Kingklip (Quiroz et al. 2009a).

Comparisons between estimates of abundance and recruitment from the MSVPA model and the single-species model were carried out by using the relative error,

$$\mathrm{RE} = \frac{x_i - x_0}{x_0} \times 100, \tag{12}$$

where x_0 is the estimate from the single-species model; and x_i is the estimate from MSVPA. We used the mean relative error (MRE) for assessing the bias and the median absolute relative error (MDARE) for measuring the variance, (Oscar 1999) given by

$$\mathrm{MDARE} = \mathrm{median}|\mathrm{RE}| \tag{13}$$

Finally, due to potential uncertainty in the suitability coefficients, we carried out a sensitivity analysis to assess the effects on the MSVPA response variables produced by perturbations of these parameters. We used a 10% perturbation (positive or negative) and followed the methodology from ICES (1991), wherein a response variable was considered insensitive if the effect produced by a 10% perturbation was smaller than 3%. The response variables chosen for this sensitivity analysis were adult abundances (N^{3+}), total abundances, and average (1990–2007) M_2 at age for SBW and Hoki. The first two response variables were chosen due to the potential role of predation on SBW and Hoki population dynamics.

We used the same methodology (equations 12 and 13) to analyze the results of the sensitivity analysis; in this case, x_0 was the value of the response variable without perturbation and x_i corresponded to the perturbed response variable.

RESULTS

Our results included estimates of total population abundance (age 0 to the maximum age), adult abundance N^{3+} (age 3 to the maximum age), and recruitment (age 0). For Hoki and SBW, we also evaluated the temporal trend in M_2 at age and the average M_2 at age.

Estimates of Southern Hake adult abundance from the MSVPA model and the single-species model were similar and exhibited the same temporal trend, with an MRE of 8.8%. Similar scenarios were observed for total abundance (MRE = 7.9%) and recruitment (MRE = 5.2%) of Southern Hake. Likewise, for Kingklip, the MREs comparing estimates from the MSVPA model and the single-species model were 5.6% for adult abundance, 3.2% for total abundance, and 2.7% for recruitment.

The temporal trends in Hoki adult abundance and total abundance estimates from the single-species and MSVPA models are shown in Figure 2. In general, temporal trends from the two models were consistent, showing a period of high adult abundance followed by a period in which abundance seemed to stabilize at a lower level (Figure 2a). The MRE for adult abundance estimates was 4.4%, and the MDARE was 26.16%. In contrast, estimates of Hoki total abundance (ages 0–14) differed between the two models. The MSVPA estimates were larger than the single-species model estimates (Figure 2b) during the period of time evaluated by the stock assessment, and the MRE was 384.5%.

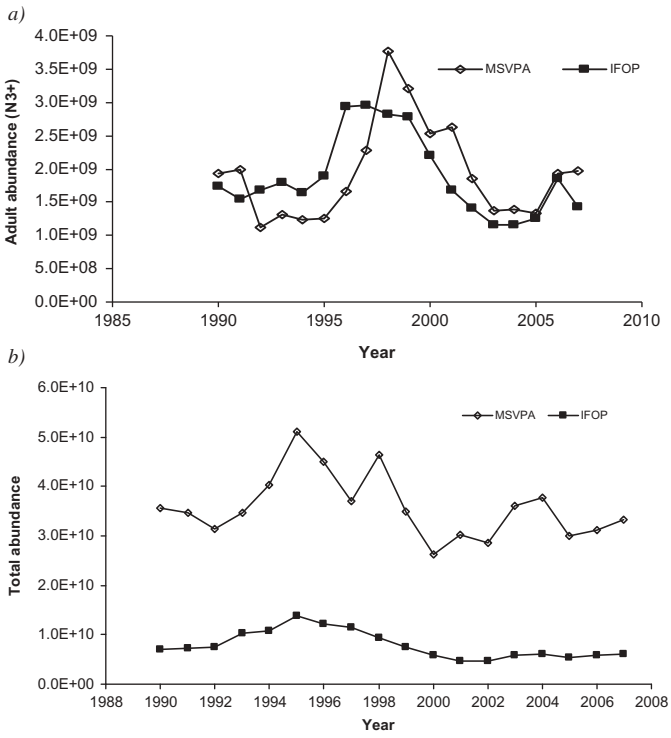


FIGURE 2. Comparison of estimates from the multispecies virtual population analysis (MSVPA) model and the Chilean Instituto de Fomento Pesquero (IFOP; i.e., single-species) model for the southern Chilean demersal fishery: **(a)** Hoki adult abundance and **(b)** Hoki total abundance.

For SBW, adult abundance estimates were consistent between the MSVPA and single-species models and exhibited a noticeable decreasing temporal trend (Figure 3a). The MSVPA estimates of SBW adult abundance were smaller than the single-species model estimates most of the time; the MRE was –10.6%, and the MDARE was 11.5%. The total abundance estimates (ages 1–18) for SBW presented a similar scenario, with a decreasing trend; the MSVPA estimates varied from 1.5×10^8 individuals (in 2007) to 3.6×10^9 individuals (in 1990). The IFOP estimates of total abundance followed the same temporal trend, with a minimum occurring in 2007 (2.0×10^8 individuals) and a maximum observed in 1990 (4.6×10^9 individuals).

For comparisons of recruitment, we defined recruitment in both models as the strength of age-class 0 (Figures 4, 5). In the case of Hoki, recruitment estimates from the MSVPA and single-species models were consistent in showing similar temporal trends; however, the difference between the two estimates was around one order of magnitude (Figure 4). The average recruitment of Hoki from the MSVPA model was 2.16×10^{10}

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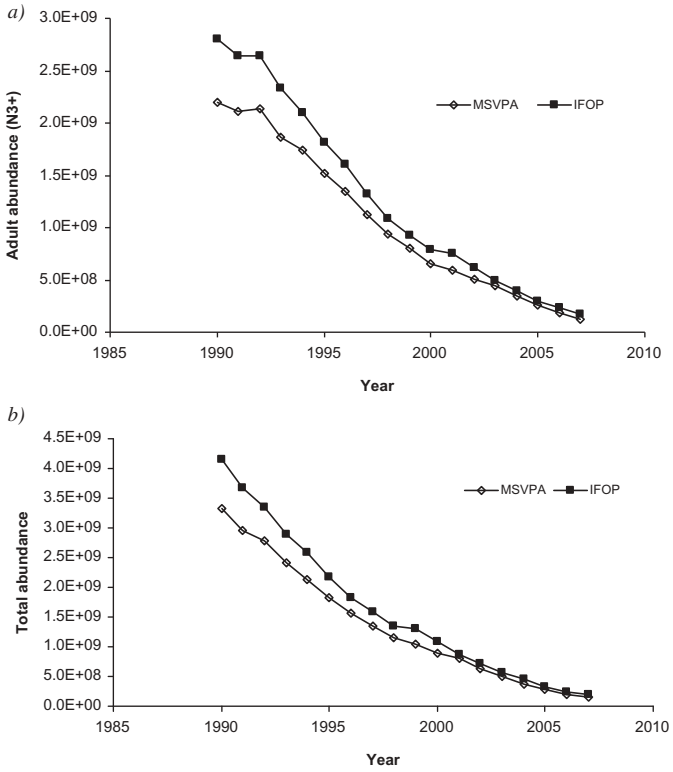


FIGURE 3. Comparison of estimates from the multispecies virtual population analysis (MSVPA) model and the Chilean Instituto de Fomento Pesquero (IFOP; i.e., single-species) model for the southern Chilean demersal fishery: **(a)** Southern Blue Whiting adult abundance and **(b)** Southern Blue Whiting total abundance.

individuals, whereas the average recruitment from the IFOP single-species model was 2.7×10^9. The MSVPA and IFOP estimates did not show a clear decreasing pattern.

The recruitment scenario was very different for SBW (Figure 5), demonstrating a clear decreasing trend and high variability in recruitment. Contrary to the Hoki case, the SBW recruitment estimates were similar for the two models (i.e., on the same order of magnitude). Average SBW recruitment was 1.4×10^8

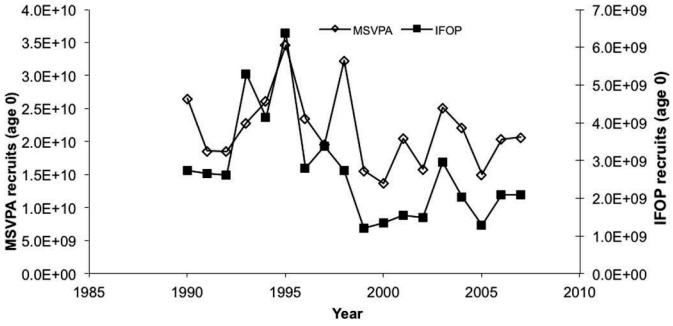


FIGURE 4. Temporal trend in Hoki recruitment (age-0) estimates from the multispecies virtual population analysis (MSVPA) model and the Chilean Instituto de Fomento Pesquero (IFOP; i.e., single-species) model for the southern Chilean demersal fishery.

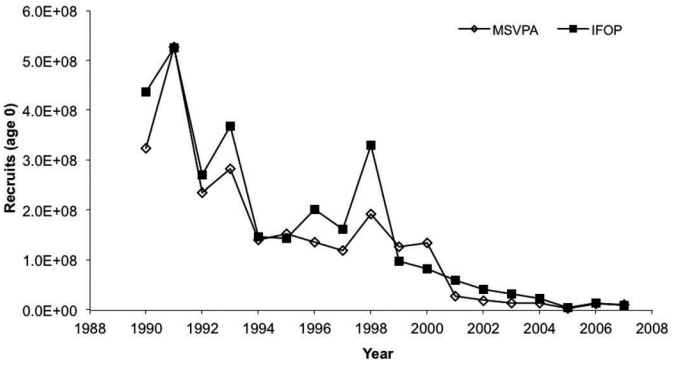


FIGURE 5. Temporal trend in Southern Blue Whiting recruitment (age-0) estimates from the multispecies virtual population analysis (MSVPA) model and the Chilean Instituto de Fomento Pesquero (IFOP; i.e., single-species) model for the southern Chilean demersal fishery.

individuals (coefficient of variation [CV] = 1.02) from the MSVPA and 1.6×10^8 individuals (CV = 0.98) from the single-species model.

The temporal trend in annual average mortality rates is depicted in Figure 6. Predation mortality (M_2) estimates for Hoki remained relatively stable during 1990–2007 (Figure 6a); the average M_2 was 0.22 per year (CV = 0.15). Fishing mortality for Hoki showed a similar pattern: it was stable and on the same order of magnitude as M_2, presenting two peaks (F = 0.45 per year in 2000; 0.481 per year in 2007). Average F of Hoki was 0.23 per year (CV = 0.41).

In the case of SBW (Figure 6b), mortality exhibited complex patterns. Predation mortality values were lower, with an average of 6.0×10^{-3} per year (CV = 0.25). Predation mortality estimates for SBW were one order of magnitude lower than F, which reached a minimum in 1991 (2.5×10^{-3} per year) and a maximum in 2007 (2.1×10^{-1} per year). There was a notable increase in F (two orders of magnitude) for SBW during the period of analysis. The average F was 5.9×10^{-2} per year (CV = 0.99).

For Hoki and SBW, the average M_2 at age was higher for younger age-classes. On the other hand, the average F at age was higher for older age-classes (Figure 7). Hoki exhibited their highest average M_2 at age 1 (1.53 per year), with older age-classes showing negligible predation mortality (Figure 7a). In contrast, younger age-classes of Hoki received no fishing pressure, while age-classes older than 7 years were subject to high fishing pressure. Predation mortality was also negligible for older age-classes of SBW. The highest M_2 values for SBW were observed at age 2 (M_2 = 0.027 per year) and age 1 (M_2 = 0.025 per year). Younger age-classes of SBW suffered negligible fishing pressure. For SBW, the highest average F at age was observed at age 7 (F = 0.08 per year), whereas older ages (ages 17 and 18) presented lower levels of F.

It is important to point out that the MSVPA provided complementary information—for example, the temporal trends in age-0 and age-1 Hoki that were consumed by

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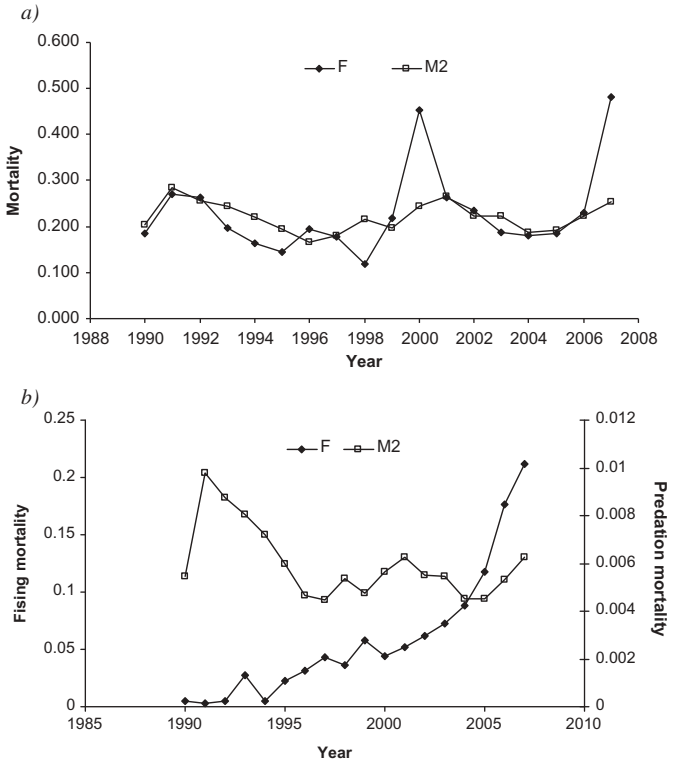


FIGURE 6. Temporal trends in average annual fishing mortality (F) and predation mortality ($M2$) for **(a)** Hoki and **(b)** Southern Blue Whiting in the southern Chilean demersal fishery.

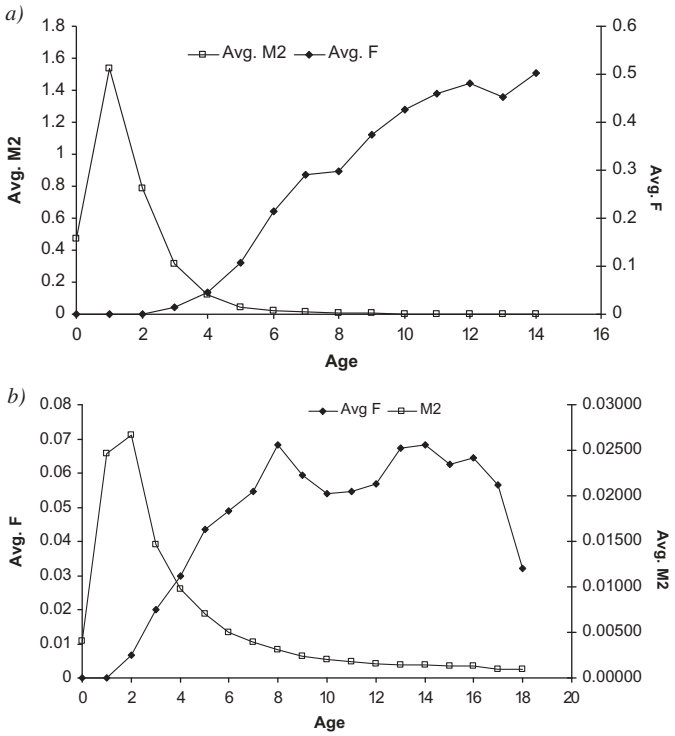


FIGURE 7. Average (1990–2007) predation mortality ($M2$) at age and average (1990–2007) fishing mortality (F) at age for **(a)** Hoki and **(b)** Southern Blue Whiting in the southern Chilean demersal fishery.

predators. The most important predator for age-0 Hoki was the Southern Hake (Figure 8a); the maximum consumption of Hoki by Southern Hake occurred in 1995, with 5.2×10^9 individuals (52% of the total predatory consumption of Hoki in that year). The average consumption of Hoki by Southern Hake was 3.5×10^9 individuals, representing 57% of the total consumption of Hoki. For age-0 Hoki, there was also a strong cannibalism effect; average cannibalism was 2.7×10^9 individuals (42% of the total predatory consumption of Hoki). In contrast, the average consumption of age-0 Hoki by Kingklip was 3.4×10^7 (1% of the total predatory consumption of Hoki), an amount that was almost negligible in comparison with consumption by the other predators.

Southern Hake were also the main predators of age-1 Hoki (Figure 8a). The largest number of age-1 Hoki consumed by Southern Hake was observed in 1999: 8.5×10^9 individuals were consumed, representing 82% of Hoki consumption in that year. The average number of age-1 Hoki consumed by Southern Hake was 6.0×10^9 individuals (86% of the total predatory consumption of Hoki). The maximum number of age-1 Hoki that were cannibalized was 1.9×10^9 individuals in 1999 (representing 18% of the total number of Hoki consumed during that year); average cannibalism was 9.5×10^8 individuals. The average consumption of age-1 Hoki by Kingklip was 1.6×10^7 individuals, which was almost negligible in comparison with the Southern Hake's consumption of Hoki.

The sensitivity analysis showed that four response variables—Hoki average M_2, SBW M_2, Hoki adult abundance, and Hoki total abundance—were sensitive to a negative 10% perturbation in suitability coefficients (Table 2). Two response variables, SBW adult abundance and SBW total abundance, were not sensitive to perturbations in the suitability coefficients (Table 2). Positive 10% perturbations in suitability coefficients made the MSVPA unstable.

DISCUSSION

We have explored a new approach that might be useful for fisheries in several regions of the world for which stomach content data are lacking. Our approach involves approximating the suitability coefficients from the MSVPA model by using the parameters from the von Bertalanffy growth equation. This paper is also a first effort toward developing a predator–prey analysis for the SCDF in accordance with studies of other important fisheries around the world (Sparre 1991; Tsou and Collie 2001; Jurado-Molina and Livingston 2002a; Jurado-Molina et al. 2005; Kinzey and Punt 2009). In this regard, the MSVPA model we constructed for the SCDF is the first quantitative approach of this kind to ever be applied to a Chilean fishery. In this first step, we sought to examine the

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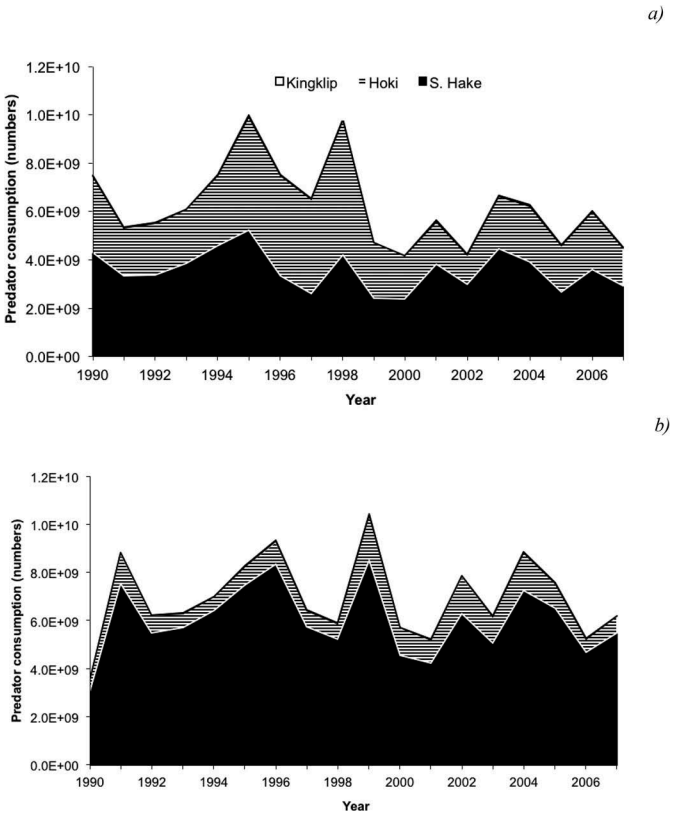


FIGURE 8. Temporal trends in predator consumption of **(a)** age-0 Hoki and **(b)** age-1 Hoki in the southern Chilean demersal fishery. Predators included conspecifics, Southern Hake (S. Hake), and Kingklip.

potential and problems in using the modified suitability coefficients within the MSVPA model for the SCDF.

Our results suggest that trophic interactions in the study area are mainly driven by the Southern Hake's predation on its main prey species: the Hoki and SBW. Predation by Kingklip on the two prey species is minor. Our results also suggest that cannibalism plays an important role in the Hoki's population dynamics: the number of age-0 Hoki that were cannibalized was similar to the number consumed by Southern Hake. Hoki population dynamics are complex due to the magnitude of the various drivers, including cannibalism, predation, and fishing pressure.

TABLE 2. Results of the sensitivity analysis used to evaluate the multispecies virtual population analysis model defined for the southern Chilean demersal fishery. In all cases, the perturbation was a 10% decrease in suitability coefficients (SBW = Southern Blue Whiting; MRE = mean relative error; MDARE = median absolute relative error).

Response variable	MRE (%)	MDARE (%)
Hoki average predation mortality	–59.00	66.78
SBW average predation mortality	–70.00	72.78
Hoki adult abundance	–13.00	11.91
SBW adult abundance	–1.13	0.66
Hoki total abundance	–76.50	75.90
SBW total abundance	–1.93	1.78

For hake species caught in the Chilean fishery, predation and cannibalism processes are characteristic features that are shared with hake species around the world, such as the Pacific Hake *Merluccius productus* (Livingston and Bailey 1985; Livingston et al. 1986) in the USA and the Cape Hake *Merluccius capensis* and Deepwater Hake *Merluccius paradoxus* in South Africa (Macpherson and Roel 1987; Punt et al. 1992). Our modeling results suggested that predation mortality had an important influence on Hoki dynamics and played a secondary role in SBW dynamics. For both prey species, M_2 is variable among years and among age-classes, depending on the abundances of predator and prey (Sparre 1991).

The IFOP and MSVPA adult population estimates for Hoki showed some discrepancies, but in general there was good agreement, as supported by the low MRE. On the other hand, the total abundance of Hoki demonstrated the classical pattern observed in the Bering Sea; the MSVPA estimates were higher than the IFOP estimates due to the addition of individuals that were preyed upon.

The comparison of SBW population indicators obtained from the single-species IFOP model and the MSVPA model revealed good agreement in adult abundance and total abundance estimates. The single-species estimates were larger than the MSVPA estimates, even for the total abundance of SBW; this finding is opposite to those reported for species from the eastern Bering Sea (Livingston and Jurado-Molina 2000; Jurado-Molina and Livingston 2002a). The discrepancy might be caused by the selection of M_1, which is estimated by an iterative process. The M_1 and M_2 estimates in the MSVPA were lower than the M used in the single-species model, thus causing lower abundance estimates. To solve this problem, a better approach might be to estimate M_1 in a statistical framework, as was suggested by Jurado-Molina et al. (2005).

Regarding recruitment, results were consistent with previous analyses (Livingston and Jurado-Molina 2000); the MSVPA model estimates for Hoki were higher than the single-species model estimates, which can be explained by the higher predation on the juvenile fractions in the MSVPA model. The differences in recruitment estimates for the juvenile fractions have important effects, as they indicate strong year-classes in specific years resulting from high predation on those year-classes. The IFOP models do not capture this aspect of population dynamics. In the case of SBW, recruitment estimates from the two approaches were similar, possibly due to the low values of M_2 estimated for SBW in the MSVPA model. Our results suggest that the use of suitability coefficients based on equation (5) produced recruitment estimates that agreed with the general trend observed in the single-species models.

As was observed with MSVPA models for the eastern Bering Sea, our results indicated that the importance of

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predation mortality decreases with age while the importance of fishing mortality increases. For the SCDF, predation mortality and cannibalism were identified as playing important roles in the population dynamics of Hoki; for age-0 Hoki, cannibalism and predation by Southern Hake were comparable. The importance of cannibalism decreased with age; for age-1 and age-2 Hoki, predation by Southern Hake was the most important source of predation mortality overall. For older age-classes, fishing mortality became the most important factor driving Hoki dynamics. The MSVPA provided complementary information that will be useful for fisheries managers, such as the importance of Hoki as prey in the system and the need for maintaining a meaningful abundance of this resource as a food source for predators.

Results for the SBW revealed an interesting pattern in dynamics. Specifically, M_2 was almost negligible, suggesting that the observed declines in adult and total abundances of SBW are due not to the influence of predation mortality but rather to a fishing mortality increase, which could be responsible for the decreases in SBW abundance and recruitment. Our results indicated that changes in F for the predators of SBW might not significantly impact SBW population dynamics due to the indirect effects of fishing. However, this hypothesis must be confirmed in an MSFOR framework.

Some MSVPA model estimates for the Bering Sea were sensitive to perturbations in the M_1 values of some predators, the abundance of predators, and the annual consumption by the predators (ICES 1991; Jurado-Molina et al. 2004). In our present approach, results from the sensitivity analysis suggested that some outputs, including Hoki and SBW average M_2 at age, Hoki adult abundance, and Hoki total abundance, were sensitive to perturbations in the suitability coefficients. These findings could indicate strong indirect effects of fishing that should be analyzed in an MSFOR framework. Importantly, the adult abundance and total abundance of SBW were not sensitive to a 10% perturbation in the suitability coefficients, in agreement with the small influence of predation mortality on SBW population dynamics. Furthermore, the sensitivity analysis included only negative 10% perturbations (90% of the base values) in suitability coefficients because positive perturbations made the model unstable.

Sensitivity analysis is useful for determining how response variables are affected by perturbations in a set of parameters over a specific region of interest (Box et al. 1978; Schnute and McKinnell 1984). Such analyses allow for identification of the relative importance of the changes produced and provide feedback for potential improvement of the model, identifying those parameters with potential problems. In the approach taken here, results from the sensitivity analysis suggested that only some outputs were sensitive to perturbations in the suitability coefficients. The importance of cannibalism and predation in affecting the population dynamics of the analyzed prey species was indicated. Our findings also suggest that the MSVPA model can be considered robust, in agreement with the main results from previous MSVPA models (Finn et al. 1986; ICES 1986, 1991; Jurado-Molina et al. 2004) that were parameterized for the North Sea and Bering Sea.

As mentioned, due to the lack of stomach content data, we took a different approach to estimating the suitability coefficients. Although we did not conduct formal tests, our results are consistent with results from other MSVPA studies, such as from the eastern Bering Sea, where high M_2 values corresponded to younger ages. However, some aspects must be analyzed with more detail. In particular, for the eastern Bering Sea, there is a large stomach content database, which could allow indicators from a normal MSVPA run to be compared with indicators from the approach taken here, thereby validating the use of suitability coefficients based on predator–prey length relationships in MSVPA. This approach would allow extending the use of MSVPA and MSFOR to fisheries in other regions of the world where funds and programs for conducting a formal stomach sampling program are lacking.

Consumption estimates together with M_2 are complementary data that cannot be captured by traditional single-species modeling approaches. Therefore, they constitute new and relevant information that is useful for the management of these exploited species. We did not set up an MSFOR model, which would have provided a useful ability to simulate the indirect effects of fishing on nontarget species. Nevertheless, the basic work for developing the MSFOR model is already done, and the development of this tool is one of our future objectives.

A relevant aspect of models that include biological interactions is their higher information demand in comparison with single-species models. In addition, they require detailed knowledge on the population dynamics of the target species, including information from a wide range of disciplines, such as fish biology, trophic ecology, and fishing technology. In this sense, the lack of stomach sampling programs and trophic analysis is a factor that limits the potential for conducting a more complete multispecies analysis for southern Chile. Therefore, more research funding should be directed to better study this important multispecies system and perhaps extend its results to other Chilean fisheries, such as the fishery for Chilean Hake in central Chile (Jurado-Molina et al. 2006). This is particularly important considering that the current Chilean Fisheries and Aquaculture Law mandates the full inclusion of the ecosystem approach to fisheries in order to reach sustainability in the management of these fisheries.

In addition to research actions, the complexity of the interactions involved in a multispecies system requires new and more complex data analysis and modeling platforms in order to carry out parameter estimation in a multispecies model. In

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this work, we used Microsoft Excel for building the MSVPA model because it made the implementation of predation equations and error debugging easier. Our primary task was to test the feasibility of using suitability coefficients based on the predator–prey length ratio. Future work will require a better platform for the MSVPA, such as AD Model Builder, which has been used to apply the multispecies statistical model in the Bering Sea (Jurado-Molina et al. 2005) and allows the use of the maximum likelihood estimation and Bayesian approaches for parameter and uncertainty estimation.

The MSVPA model for the SCDF does not consider the uncertainty associated with the parameter estimation process and performance indicators. This could be improved by implementing a multispecies statistical catch-at-age model (Jurado-Molina et al. 2005). Such an approach would help to obtain an estimate of M_1 and would employ state-of-the-art methods, such as Bayesian parameter estimation and decision analysis. However, that approach is a rather difficult challenge that requires additional efforts beyond the scope of this paper and should be explored in future applications.

Worldwide, single-species approaches are the main tools that are used to assess the effects of different exploitation levels on the population dynamics of target species and to set up quotas and reference points. However, wider considerations of the effects of fishery management actions on other target or nontarget species and on the whole ecosystem are also of growing interest. In this context, the results of our analysis are consistent with previous work in the Bering Sea and the North Sea and help to disseminate the use of this type of quantitative multispecies tool outside of developed countries. Our results also suggest the feasibility of applying a multispecies approach to the SCDF and point to areas of model improvement to ensure the gathering of auxiliary information that could help fisheries managers enhance the decision making process, thus facilitating the sustainable exploitation of fishery resources in this area of the world.

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