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Multispecies modelling of some components of the marine community of northern and central Patagonia, Argentina¹

Mariano Koen-Alonso and Peter Yodzis

Abstract: Using a bioenergetic and allometric approach, we developed multispecies trophodynamic models of the marine community of northern and central Patagonia in the southwestern South Atlantic Ocean that included hake (*Merluccius hubbsi*), squid (*Illex argentinus*), anchovy (*Engraulis anchoita*), and South American sea lions (*Otaria flavescens*). We used these to explore the effects of model structure and parameter uncertainty on predictions of the effects of different management regimes using continuation and bifurcation analysis. We considered five different functional responses and used the Akaike Information Criterion for model selection. The best models involved laissez-faire Holling Type III-shaped functional responses and the worst one corresponded to the Ecosim form. These models showed many similar behaviours but also showed marked differences in some exploitation scenarios. This suggests that using a single model structure as the basis for managing these stocks could lead to misleading, and potentially dangerous, conclusions.

Résumé : Une approche bioénergétique et allométrique nous sert à mettre au point des modèles trophodynamiques multispécifiques de la communauté marine du nord et du centre de la Patagonie dans le sud-ouest de l'Atlantique Sud qui regroupe le merlu argentin (*Merluccius hubbsi*), l'encornet rouge argentin (*Illex argentinus*), l'anchois (*Engraulis anchoita*) et le lion de mer austral (*Otaria flavescens*). Les modèles nous permettent d'étudier, à l'aide d'une analyse de continuation-bifurcation, les effets de la structure du modèle et de l'incertitude des paramètres sur les prédictions des effets de différents régimes de gestion. Nous examinons cinq différents types de réponses fonctionnelles et utilisons le critère d'information d'Akaike pour le choix du modèle. Le meilleur modèle contient des réponses fonctionnelles de type « laissez-aller » de forme III de Holling et le pire correspond à la forme Ecosim. Ces modèles possèdent plusieurs comportements similaires, mais ils présentent des différences marquées pour certains scénarios d'exploitation. Cette observation montre que l'utilisation d'une seule structure de modèle comme base de la gestion de ces stocks pourrait mener à des conclusions trompeuses et potentiellement dangereuses.

[Traduit par la Rédaction]

Introduction

The notion that fisheries affect much more than just the species being fished is undoubtedly widespread and accepted worldwide. Ecosystem and multispecies models are being used increasingly often to account for these effects (Hollowed et al. 2000; Whipple et al. 2000; Fulton et al. 2003). However, the popularity of the concept that we are exploiting systems rather than specific species/resources (e.g., the Symposium on Ecosystem Effects of Fishing held by the International Council for the Exploration of the Sea's Scien-

tific Committee on Oceanic Research; Hollingworth 2000), the efforts to define and frame ecosystem-based management (Link 2002a, 2002b), and the advocacy of holistic approaches to fishery management (Agardy 2003) do not mean that we understand how exploited ecosystems really work. Actually, our understanding of ecosystem functioning is far from accurate or complete. In the last 30 years we have progressed a lot, from both theoretical (e.g., Polis and Winemiller 1996) and applied perspectives (e.g., Sinclair and Valdimarsson 2003), but there is still a long way to go (Link 2002b; Fulton et al. 2003; Stefansson 2003). Today, in many

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ways, we are still discussing which is the best way of grabbing this bull and where the horns are located.

Another facet of the problem is that in today's marine ecosystems, fisheries are becoming just one of the activities that take place in them and (or) use their resources (Rosenberg 2003), and not necessarily the most important one. Oil and gas exploration and exploitation, transport of goods, aquaculture, and tourism/leisure are some of the activities that also use marine resources and (or) habitats, and hence, the management of marine systems expands from a traditional, typically fishery-oriented one to a more complex and broader one (e.g., Crespo and Hall 2002; Sainsbury and Sumaila 2003). Many of the current management and conservation questions are framed within the context of ecosystems and communities, and only by looking at and addressing them at these levels will we have some hope of success.

Furthermore, while the distribution of many of these problems is global (e.g., Myers and Worm 2003), it is unlikely that the solutions will be. Each exploited system (i.e., ecosystem + human activities) has its own idiosyncratic features that make it unique. Effective solutions will likely need to be locally tailored. However, if there are truly general ecological mechanisms, and we believe that this is so, the ecological processes involved in the regulation and dynamics of these exploited systems are likely to be common to all of them. In each case, taxonomical identities, food-web structures, environmental/climatic forcing, and relative regulatory importance may vary, but the ecological processes involved should remain the same. Therefore, modelling and comparing these exploited ecosystems with mechanistically oriented approaches should help us to understand how they are regulated and how the different processes are integrated. From this perspective, the present study tries to provide some insight into one specific case, with the hope that it can also contribute to elucidating some of the common issues.

The biological community involved in this analysis is the marine community of northern and central Patagonia on the Argentine continental shelf in the southwestern South Atlantic Ocean, coarsely bounded by 41 and 48°S. The core species in this community are the Argentine hake (*Merluccius hubbsi*), the Argentine anchoita or anchovy (*Engraulis anchoita*), and the squid *Illex argentinus* (Angelescu and Prenske 1987). The rest of the food web is built around the tritrophic system constituted by them (Angelescu and Prenske 1987) (Fig. 1). Hake, squid, and anchovy are also the main common prey of a large suite of top predators, including the sea lion *Otaria flavescens* (Koen-Alonso et al. 2000a), dolphins (e.g., *Lagenorhynchus obscurus* and *Cephalorhynchus commersonnii*) (Koen-Alonso et al. 1998; Dans et al. 2003), dogfish and sharks (e.g., *Squalus acanthias* and *Galeorhinus galeus*, respectively) (Koen-Alonso et al. 2002; Dans et al. 2003), and the beaked skate (*Dipturus chilensis*) (Koen-Alonso et al. 2001). The hake supports the most traditional commercial fishery in the region since the 1970s, with reported landings around 500 000 t per year in the 1990s. Also in that decade, the hake stock virtually collapsed (Aubone et al. 1999). The squid fishery developed in the 1980s and was as important as the hake fishery in terms of landings during the late 1990s (Brunetti et al. 1999a, 1999b). The Patagonian anchovy stock is also fished,

but with catches of less than 10 000 t per year, which is below the total allowable catch for this stock (Hansen 1999). Another important fishery in this region is the shrimp (*Pleoticus muelleri*) fishery, but its socioeconomic importance is associated with the higher revenues it generates and not with its catch levels (ranging between roughly 10 000 and 30 000 t·year⁻¹ during the past decade) (Bertuche et al. 1999).

Among the top predators, the sea lion is the most conspicuous for our purpose here. This species was drastically reduced between 1930 and 1960, and is believed to have dropped from approximately 200 000 individuals to fewer than 18 000 between 1938 and 1946 in northern Patagonia (Crespo and Pedraza 1991; Dans et al. 2004), where the most intense harvesting took place (Reyes et al. 1999; Dans et al. 2004). Even though the central-Patagonia stock suffered a much smaller harvest, it also dropped dramatically, which strongly suggests that the two nominal stocks have a common population identity (Reyes et al. 1999). Signs of population recovery were not detected until 1990 (Crespo and Pedraza 1991), but it is believed that the population has been recovering since the end of the harvest (Reyes et al. 1999; Dans et al. 2004). Although recent estimates of abundance indicate that this population is still below the pre-harvest level (Dans et al. 2004), the sea lion is today the most abundant marine mammal in the region that actually forages on the continental shelf, and hake and squid are among its main prey items (Koen-Alonso et al. 2000a). Sea lions are also one of the wildlife attractions that sustain the growing tourism activity in Patagonia (Tagliorete and Losano 1996).

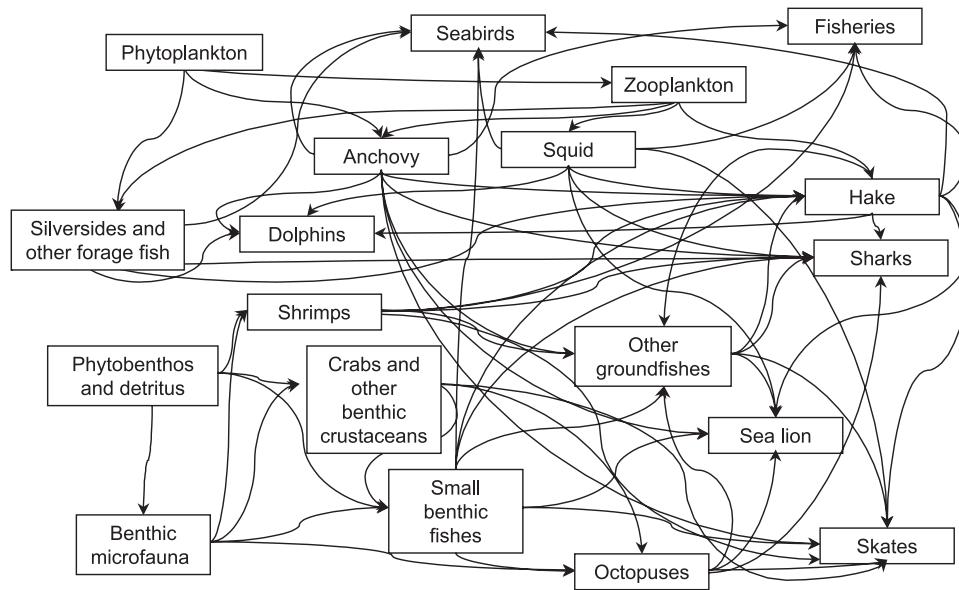
Our purpose here is to develop simple trophodynamic models that integrate the dynamics of squid, anchovy, hake, and sea lion and the corresponding harvesting impacts on these populations, and to evaluate how these models behave under different exploitation scenarios. We do not aim here to develop management models (i.e., accurate enough to support management decisions); rather, we are trying to explore how these species might be interacting, and also how our choice of model structures, together with parameter uncertainty, may influence our conclusions.

Methods

The system modelled

We have a fairly good understanding of the marine food web of northern and central Patagonia (Fig. 1). However, from a time-series perspective, we have very few data to incorporate into that picture. This is the main reason for focusing our modelling attempt on the core species of this community, for which, fortunately, we have a reasonable amount of data (see the next section).

We know that, among the key species, hake feed primarily on anchovy, squid, and zooplankton, although other prey and cannibalism are, to a lesser extent, also part of the picture (Prenske and Angelescu 1993). The anchovy is the most important forage fish in this community and, like the squid, feeds mainly, but not exclusively, on zooplankton (Angelescu 1982; Ivanovic and Brunetti 1994). The sea lion is a generalist and opportunistic predator, but hake and squid are important components of its diet (Koen-Alonso et al.

Fig. 1. Simplified food web for the marine community of northern and central Patagonia.

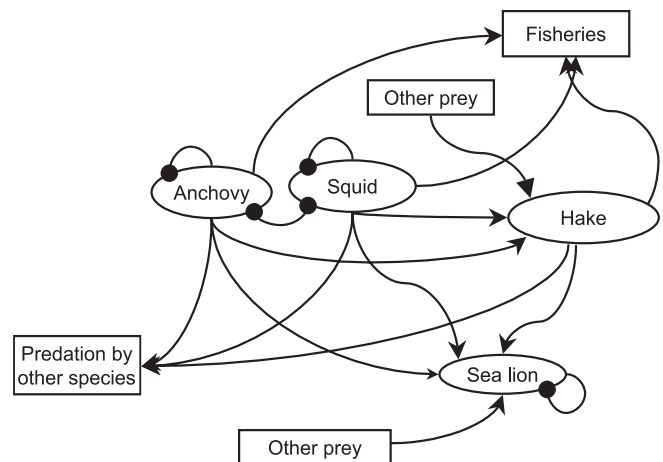
2000a). The resulting food web of core species is not a closed system, but incorporates the expected inputs and outputs from and to the rest of the food web as well as outputs to the fisheries (Fig. 2). Because we have no zooplankton abundance data, anchovy and squid are shown without prey. Instead, they are assigned carrying capacities and — to express their dietary overlap — competition coefficients.

In terms of stock identities, the system consists of the summer and south-Patagonian spawning stocks of squid (Brunetti et al. 1999a), the Patagonian stocks of anchovy and hake (Aubone et al. 1999; Hansen 1999), and the north- and central-Patagonian population of sea lions (Crespo and Pedraza 1991; Reyes et al. 1999; Dans et al. 2004). There are other stocks of hake, anchovy, and squid on the Argentine continental shelf (Aubone et al. 1999; Brunetti et al. 1999a; Hansen 1999), but they are mainly associated with the Bonaerensis region (north of 41°S), and belong to a different species assemblage (Angelescu and Prenski 1987).

The data

The type, quality, and amount of data are always the main constraint in the development of multispecies models. In our case, we had available a heterogeneous database from many different sources that included primary literature, technical reports, theses, and unpublished information. We sorted, organized, and standardized this information to build a single and coherent database that contains estimates of stock biomasses and fishery catches over time periods ranging from 10 to 30 years. For example, sometimes we needed to build the biomass estimates from censuses of individuals and individual mean weights (e.g., sea lion biomass), reconstruct total catches from national and foreign/international catch databases (e.g., for hake and squid), estimate annual catches from previous models (e.g., for sea lions), make decisions about contradictory information (e.g., differences in reported catches among sources), etc. Therefore, each time series represents our best effort to build a coherent overall database with as many data as possible. In this way, even if our data

Fig. 2. General structure of the Patagonian models. The ovals correspond to the dynamic equations for squid (*Illex argentinus*), anchovy (*Engraulis anchoita*), hake (*Merluccius hubbsi*), and sea lion (*Otaria flavescens*) (the first two with basal equations and the other two with consumer equations); the boxes correspond to constant rates (predation by other species) or components (“other prey” is a constant food biomass in the functional responses). The negative self-loop for the sea lion indicates density-dependent mortality, while the negative self-loops for anchovy and squid correspond to the self-limitation imposed by their carrying capacities. The double negative link between anchovy and squid indicates Lotka–Volterra competition.



are not perfect, they represent in a reasonable way the abundances and catches for the populations considered.

The sources consulted were Otero and Simonnazzi (1980), Angelescu (1982), Otero et al. (1982), Angelescu and Prenski (1987), Crespo (1988), Otero and Verazay (1988), Cousseau et al. (1981), Ciechomski and Sánchez (1988), Brunetti and Pérez Comas (1989), Crespo and Pedraza (1991), Programa de Modernización de los Servicios Agropecuarios, Secretaría de Agricultura Ganadería y Pesca and Instituto Inter-

americano de Cooperación para la Agricultura (1992, 1993, 1994, 1995), Prenski and Angelescu (1993), Bezzi et al. (1994), Santos (1994), Bezzi and Dato (1995), Guía Pesquera Argentina (1995), Bambill et al. (1996), Dans et al. (1996), Hansen and Madirolas (1996), Anonymous (1997), Dato (1997), Pájaro et al. (1997), Brunetti et al. (1998, 1999a, 1999b), Aubone et al. (1999) Hansen (1999), Reyes et al. (1999), Aubone (2000), Dato et al. (2000), Pérez (2000), and unpublished information from N. Brunetti, National Institute of Fisheries Research and Development of Argentina (INIDEP), Casilla de Correo 175, 7600 Mar del Plata, Buenos Aires, Argentina, E.A. Crespo, Patagonian National Centre (CENPAT; a research centre of the National Research Council of Argentina), Boulevard Brown 3600, 9120 Puerto Madryn, Chubut, Argentina, S. Dans (CENPAT), S. García de la Rosa (INIDEP), M. Lasta (INIDEP), M. Pérez (INIDEP), B. Prenski (formerly of INIDEP), F. Sánchez (INIDEP), and R. Sánchez (INIDEP).

The database (Appendix A) contains biomass estimates for squid ($N_s = 10$ for the period 1982–1999), anchovy ($N_a = 14$ for the period 1970–1999), hake ($N_h = 30$ for the period 1970–1999), and sea lion ($N_l = 16$ for the period 1972–1998), together with catch estimates for these species. The catch time series for squid, anchovy, and hake covers the period 1970–1999, while the sea lion catches cover the period 1929–1960. Outside these periods we assumed no catches for the modelled stocks. This assumption is not fully realistic but is still reasonable. For example, even though there was a hake fishery before 1970, catches were comparatively small and came mainly from the Bonaerensis region (i.e., they affected a stock not modelled here).

The modelling approach

The models are based on a bioenergetic and allometric framework (Yodzis and Innes 1992; Yodzis 1998). We need to specify two different types of equations: basal and consumer. A basal equation describes the dynamic of a species that does not prey upon others also included in the model. Conversely, a consumer equation represents a species that does prey on others included in the model.

A general expression for the basal equation is

$$(1) \quad \frac{dB_j}{dt} = \left[r_j \frac{B_j}{K_j} \left(K_j - B_j - \sum_c \alpha_{jc} B_c \right) \right] - \sum_i B_i F_{ji} - m_j B_j - H_j$$

where B_j is the biomass of species j , r_j is its intrinsic production/biomass ratio, K_j is its carrying capacity, α_{jc} is the competition coefficient between species j and a competitor species, c , B_c is the biomass of this competitor (the summation over c indicates a summation over all competitors of species j), F_{ji} is the functional response of predator i when preying on species j , B_i is the biomass of this predator (the summation over i indicates a summation over all predators of species j), m_j is the “other mortality” rate of j and represents losses due to predation by species not included in the model, and H_j is the harvest rate of species j .

Following the bioenergetic and allometric approach (Yodzis and Innes 1992; Yodzis 1998), r_j was modelled as

$$(2) \quad r_j = f_{r_j} a_{r_j} w_j^{-0.25}$$

where f_{r_j} represents the fraction ($0 < f_{r_j} \leq 1$) of the maximum physiological capacity for production actually realized by species j , a_{r_j} is an allometric coefficient that depends on the metabolic type of species j (endotherm, vertebrate ectotherm, invertebrate, or phytoplankton), and w_j is the mean individual biomass of species j (Yodzis and Innes 1992).

A general expression for the consumer equation is

$$(3) \quad \frac{dB_j}{dt} = B_j \left(-T_j + \sum_k e_{kj} F_{kj} \right) - \sum_i B_i F_{ji} - m_j B_j - \mu_j B_j^{v_j} - H_j$$

where T_j is the mass-specific respiration rate of species j , e_{kj} is the assimilation efficiency of predator j when eating prey k , F_{kj} is the functional response of species j preying on species k (the summation over k indicates a summation over all prey of species j), and the term $\mu_j B_j^{v_j}$ represents density-dependent mortality, μ_j being a constant coefficient and v_j the exponent specifying the density-dependence. The other parameters were already described in the basal equation (for a complete list of the symbols used in this paper see Appendix B).

In similar way to r_j , T_j was modelled as

$$(4) \quad T_j = a_{T_j} w_j^{-0.25}$$

where a_{T_j} is another allometric coefficient that also depends on the organism's metabolic type (Yodzis and Innes 1992).

The functional response

The functional response is a core structural feature of a trophodynamic model (Yodzis 1994). Its precise mathematical form represents the researcher's view of the biological details of that particular predation process and profoundly affects model behaviour. In most cases, however, so little is known of these biological details that there is only weak evidence, if any, that points towards a given specific mathematical formulation. Under these circumstances, it is essential to avoid the temptation to assume some particular form for the functional response and proceed on that basis to get answers that are reassuringly, but meaninglessly, definitive. Rather, one needs to explore the range of behaviours that are consistent with what we do know about the system.

We therefore fitted the same general model using five different functional responses: multispecies Holling Type II with predator interference (T2), multispecies generalized Holling (GH), frequency-dependent predation (FD), Evans (EV), and Ecosim (EC). Four of these functional responses (T2, GH, FD, and EV) can easily be derived from a more general expression for handling-time/satiation-limited functional responses (i.e., the predator's consumption rate reaches an asymptotic maximum when prey density increases). The fifth one, the Ecosim functional response, was included because of its wide use as part of the Ecopath with Ecosim software package (Walters et al. 1997; Walters and Kitchell 2001).

If we derive the functional response from time budgeting and simple foraging theory we can write a fairly general

form for many functional responses (eq. 3 in Yodzis 1994), which, expanded to a multispecies framework, becomes

$$(5) \quad F_{ij} = \frac{C_{ij}}{1 + \sum_i h_{ij} C_{ij}}$$

where F_{ij} is the functional response (amount of prey i consumed by predator j per unit of time), C_{ij} is the capture rate (attack rate sensu Yodzis 1994) (the amount of prey i captured and consumed by predator j per unit of searching time), h_{ij} is the handling time per unit of prey i , and the summation in the denominator is over all prey of predator j . By using eq. 5 with different forms for C_{ij} we can build many different functional responses.

The handling time, h_{ij} , represents the amount of time that predator j spends off the search for prey because of the capture of a unit of prey i . When prey i tends towards infinity, the inverse of h_{ij} is the asymptotic maximum consumption rate (i.e., the functional response has multiple asymptotic values, one per prey species). The literal interpretation of h_{ij} as “handling” time only is too narrow; there are many other factors that can keep a predator off the search for prey because of a capture. One of the most noticeable of these is related to the physiology of the digestion process (Rindorf 2002), which allows for so-called digestive pauses (Jeschke et al. 2002). In this context, if for the sake of simplicity and to reduce the number of parameters that need to be estimated, we assume a prey-independent digestive pause (i.e., a common handling time per unit of prey for all prey of a given predator), eq. 5 can be written as

$$(6) \quad F_{ij} = \frac{1}{h_{ij}} \left(\frac{C_{ij}}{\frac{1}{h_{ij}} + \sum_i C_{ij}} \right) = \frac{J_j C_{ij}}{J_j + \sum_i C_{ij}}$$

where J_j is now a unique asymptotic maximum of the functional response of predator j . Within the bioenergetic and allometric framework (Yodzis and Innes 1992; Yodzis 1998), we estimate

$$(7) \quad J_j = f_{J_j} a_{J_j} w_j^{-0.25}$$

where f_{J_j} is the realized fraction of the physiological maximum capacity to metabolize food and $a_{J_j} w_j^{-0.25}$ represents this physiological maximum, a_{J_j} being another allometric coefficient that depends on the predator's metabolic type (Yodzis and Innes 1992; Yodzis 1998).

The precise mathematical formulations for the functional responses considered here are as follows.

The T2 functional response is derived considering

$$C_{ij} = \frac{\xi_{ij} B_i}{(Q_j + B_j)^{q_j}}$$

and is

$$(8) \quad F_{ij} = J_j \frac{\xi_{ij} B_i}{J_j (Q_j + B_j)^{q_j} + \sum_i \xi_{ij} B_i}$$

where J_j is the realized maximum capacity to metabolize food by predator j (eq. 7), B_i is the biomass of prey i , B_j is the biomass of predator j , Q_j and q_j are positive constants that define the predator-interference effect in the functional response (e.g., $q_j = 0$ corresponds to no predator interference and $Q_j = 0$ and $q_j = 1$ correspond to ratio-dependence), and ξ_{ij} is a positive constant.

The GH functional response is derived considering $C_{ij} = \gamma_{ij} B_i^{b_j}$, and is

$$(9) \quad F_{ij} = \frac{J_j \gamma_{ij} B_i^{b_j}}{J_j + \sum_i \gamma_{ij} B_i^{b_j}}$$

where γ_{ij} is a positive constant and b_j is a shape parameter ($b_j = 1$ is a Type II functional response and $b_j > 1$ is a Type III functional response).

The FD functional response is derived considering

$$C_{ij} = \frac{p_{ij} B_i^{\beta_j}}{\sum_i p_{ij} B_i^{\beta_j}} \rho_{ij} B_i$$

and is

$$(10) \quad F_{ij} = \frac{J_j p_{ij} \rho_{ij} B_i^{1+\beta_j}}{J_j \sum_i p_{ij} B_i^{\beta_j} + \sum_i p_{ij} \rho_{ij} B_i^{1+\beta_j}}$$

where p_{ij} represents the preference for prey i by predator j when all prey biomasses are equal ($\sum_i p_{ij} = 1$), ρ_{ij} is a positive

constant, and β_j is a shape parameter; $\beta_j = 0$ reduces this functional response to a multispecies Holling Type II, while $\beta_j > 0$ corresponds to a Type III functional response. Also, in the absence of alternative prey, this functional response reduces to a Type II independently of β_j , showing that any Type III-ness is caused by frequency-dependent prey preferences. This functional response has not, to the best of our knowledge, appeared elsewhere in the literature, and is under active investigation by us.

The EV functional response (Evans and Garc n 1997) can be derived considering $C_{ij} = \tau_{ij} B_i (1 + \delta_j B_i)$ and is

$$(11) \quad F_{ij} = \frac{J_j \tau_{ij} B_i (1 + \delta_j B_i)}{J_j + \sum_i \tau_{ij} B_i (1 + \delta_j B_i)}$$

where τ_{ij} is a positive constant and δ_j is a shape parameter. This functional response allows both linear and nonlinear (with a fixed exponent of 2) components in the capture rate; δ_j determines the relative weight of these components and can reduce this functional response to a multispecies Holling Type II. While most standard forms for Type III, including GH, have zero slope at the origin, this one has a finite slope there. We think of GH and EV as expressing prey refuges: “strong refuges” in the case of GH, “weak refuges” for EV. Nevertheless, this functional response was originally devised considering a “search-image” concept (G.T. Evans, Northwest Atlantic Fisheries Centre, Department of Fisheries and

Oceans, P.O. Box 5667, St. John's, NL A1C 5X1, Canada, personal communication).

The EC functional response (Walters et al. 1997; Walters and Kitchell 2001) is

$$(12) \quad F_{ij} = \frac{a_{ij} v_{ij} B_i}{v'_{ij} + v_{ij} + a_{ij} B_j}$$

where B_i is the biomass of prey i , B_j is the biomass of predator j , and a_{ij} , v_{ij} , and v'_{ij} are positive constants. Unlike the other three functional responses, this one is not truly multispecies (i.e., the rate of predation on a given prey, i , is not affected by changes in the abundance of alternative prey). In the original Ecosim derivation (Walters et al. 1997) it was assumed that $v_{ij} = v'_{ij}$ (which is why it is common to see $2v_{ij}$ in the denominator), but in later publications (Walters and Kitchell 2001) this assumption was not kept. Considering this, and the fact that eq. 12 also provides more freedom to the functional response (i.e., more chances to obtain a good fit), we used it as presented here.

However, independently of their original derivations, the same mathematical forms can be achieved using different frameworks (Yodzis 1994), and different forms can be derived from the same ecological concept. For example, EC was motivated by the foraging-arena idea (Walters et al. 1997), but most functional-response theorists would view it as a single-species Type 0 functional response (i.e., linear and without saturation) with predator interference. In the same way, since one possible interpretation of the S-shape of Type III functional responses is the existence of prey refuges (Murdoch 1973), GH (with $b_j > 1$) can also be interpreted as another possible representation of the foraging-arena concept. Therefore, comparison of a common general model with different functional responses will provide insight into how the structure of the model affects the output and which functional forms may produce better representations of the data, but will provide no real support for any particular interpretation of the predation mechanisms involved.

The general model

The modelled system (Fig. 2) was represented by a system of four ordinary differential equations, basal equations for squid and anchovy (eqs. 13 and 14) and consumer equations for hake and sea lion (eqs. 15 and 16). Terms that represent competition (α_{ij}) were included in the squid and anchovy equations, "other mortality" terms ($-m_j B_j$) were included in the squid, anchovy, and hake equations to simulate consumption by other predators not explicitly included in the model. In the cases of hake and sea lion, which both have consumer equations, the effects of other prey sources were included by adding "other prey" terms in their functional responses, where the biomasses of these other prey were represented by positive constants. Finally, a density-dependent term ($-\mu_k B_k^{v_1}$) was included in the sea lion equation to represent the anticipated crowding-related effects during the reproductive season, which are expected to vary strongly nonlinearly with density.

$$(13) \quad \frac{dB_s}{dt} = \left[r_s \frac{B_s}{K_s} (K_s - B_s - \alpha_{sa} B_a) \right] - \sum_{i=h,l} B_i F_{is} - m_s B_s - H_s$$

$$(14) \quad \frac{dB_a}{dt} = \left[r_a \frac{B_a}{K_a} (K_a - B_a - \alpha_{as} B_s) \right] - \sum_{i=h,l} B_i F_{ia} - m_a B_a - H_a$$

$$(15) \quad \frac{dB_h}{dt} = B_h \left[-T_h + \sum_{k=s,a,o} e_{hk} F_{hk} \right] - B_l F_{lh} - m_h B_h - H_h$$

$$(16) \quad \frac{dB_l}{dt} = B_l \left[-T_l + \sum_{k=s,a,h,o} e_{lk} F_{lk} \right] - \mu_l B_l^{v_1} - H_l$$

where s, a, h, and l correspond to squid, anchovy, hake, and sea lion, respectively, and o represents the other prey species. This general model was fitted with the five described functional responses.

Parameterization and model evaluation

The allometry-derived parameters (a_{r_j} , a_{T_j} , a_{J_j}) were parameterized following Yodzis and Innes (1992). The remaining parameters and initial conditions were numerically fitted by minimizing the minus loglikelihood ($-\ln[\ell(\theta)]$) between the observed and predicted biomasses. A multiplicative lognormal error structure was assumed, with the variance for each species estimated from the corresponding residuals. The $-\ln[\ell(\theta)]$ function that was minimized for each model was

$$(17) \quad -\ln[\ell(\theta)] = \sum_{i=s,a,h,l} \left\{ N_i \left[\ln(S_i) + \frac{1}{2} \ln(2\pi) \right] + \sum_{N_i} \frac{[\ln(B_{it}) - \ln(\hat{B}_{it})]^2}{2S_i^2} \right\}$$

where N_i is the sample size for species i , S_i^2 is the lognormal variance for species i estimated from the residuals, B_{it} is the observed biomass in year t , and \hat{B}_{it} is the predicted biomass in the year t for any given species, i .

The differential equation system was solved using Gear's backward differentiation formulas (also known as Gear's stiff method (Visual Numerics 1997)), and minimization was performed using a global minimization algorithm developed by the authors (Fortran 77 subroutine, available upon request), which is based on simulated annealing ideas. During the parameter-estimation process, harvest rates (H_j) were updated annually using the corresponding annual catches. All models were written in Fortran 77.

The Akaike Information Criterion corrected for sample size (AIC_c) (Burnham and Anderson 2002) was used to rank and select the models that deserved a more thorough exploration. AIC_c was calculated as

$$(18) \quad AIC_c = 2\{-\ln[\ell(\theta)]\} + 2n_p \left(\frac{N}{N - n_p - 1} \right)$$

where $-\ln[\ell(\theta)]$ is the minus loglikelihood, n_p is the number of estimated parameters in the model, and N is the total sample size.

Following Burnham and Anderson (2002) we calculated the difference between the AIC_c of each model and the lowest AIC_c (i.e., the AIC_c of the best ranked model) and used this difference (ΔAIC_c) to determine which models should be explored further. This was done by considering that all models with ΔAIC_c less than 10 deserved such exploration, while those with ΔAIC_c larger than 10 could be dismissed (Burnham and Anderson 2002).

We explored the behaviour of the selected models under different exploitation scenarios with continuation and bifurcation analysis (Doedel et al. 1991a, 1991b; Strogatz 1994), employing the AUTO 97 package (Doedel et al. 1998). This analysis allows tracking of the genesis, position, and type of equilibria, cycles, and other singular behaviours of the system, such as quasiperiodicity and chaos, while one or more parameters (the bifurcation parameters) are varied. For these analyses we expressed the harvest rate, H_j , as

$$(19) \quad H_j = h_j B_j$$

where h_j is harvesting mortality (= fishing mortality). Only equilibria and cycles were seen in our models.

We used h_j as the bifurcation parameter, and we performed four independent one-parameter bifurcation analyses for each model (one per included species). Each analysis started with the system at equilibrium and no harvest (all $h_j = 0$). From there, the h_j value of the target species was increased until its extinction or until it reached an extremely high value, while the other species were kept unexploited (i.e., $h_j = 0$ for nontarget species). In this way we were able to explore how the exploitation of any given species in the model affects the biomasses of all modelled species.

Consideration of parameter uncertainty

The use of different functional responses allows evaluation of part of the structural uncertainty. However, the behaviour of a model depends on both structure and parameters, and subtle changes in parameter values can produce significant changes in model behaviour. Therefore, to produce a more comprehensive picture we also need to address parameter uncertainty. We did this by implementing the sample-importance-resample algorithm (Punt and Hilborn 1997; McAllister and Kirkwood 1998; Gelman et al. 2000). This procedure essentially consists of creating an initial sample from an importance distribution $\tilde{\eta}(\theta)$ close to the posterior distribution $\eta(\theta)$, taking a resample from it with probabilities proportional to the importance weights $w(\theta) = \ell(\theta)\psi(\theta)/\tilde{\eta}(\theta)$, where $\ell(\theta)$ is the likelihood and $\psi(\theta)$ is the prior distribution, and using this resample $\hat{\eta}(\theta)$ as an estimate of the posterior distribution $\eta(\theta)$. The distribution $\hat{\eta}(\theta)$ is used for making inferences, calculating confidence intervals (e.g., percentile method), and so forth. A common practice is to use the prior distribution $\psi(\theta)$ as $\tilde{\eta}(\theta)$, which reduces the importance weight to $\ell(\theta)$ (Punt and Hilborn 1997).

We followed this approach using the prior distributions as $\tilde{\eta}(\theta)$ and assuming them to be uniform within the ranges defined by $\theta_{MLE} \pm 0.5 \theta_{MLE}$, where θ_{MLE} indicates the parameter value corresponding to the maximum-likelihood estimator (MLE). This approach cannot be considered strictly Bayesian because we chose the range of the priors after fitting the mod-

els, but allows exploration of the joint likelihood for all parameters in the neighbourhood of its maximum.

For each model we generated an initial sample of 10 000 parameter sets and a resample of 1000. Given the number of estimated parameters, these figures only allow a coarse representation of the posterior, but this was a trade-off between the quality of the posterior representation and the limitations of computer storage and time. Considering this, and to avoid distortions in the estimation of the posterior, we used a resampling without replacement scheme to create $\hat{\eta}(\theta)$ (Gelman et al. 2000).

Using $\hat{\eta}(\theta)$, the 95th-percentile range for each parameter was obtained, and the correlations among parameters were evaluated using Spearman's rank correlation coefficient (R_s). Since multiple tests of significance for R_s were made for each model, and to keep a global level of significance $\alpha_g = 0.05$, the level of significance for each individual R_s test (α_c) was estimated as $\alpha_c = \alpha_g/n_R$, where n_R is the total number of correlation tests performed for a given model.

The effect of this parameter uncertainty on model behaviour was assessed in the following way. For each model, we selected from $\hat{\eta}(\theta)$ four parameter sets with the lowest likelihoods (i.e., the worst parameter sets) that still fell within the 95th-percentile range in parameter space. We called them extreme parameter sets, and we performed with each of them the continuation and bifurcation analyses. In this way we expected to capture some of the most extreme model behaviours that still could be considered plausible given the estimated uncertainty.

Results

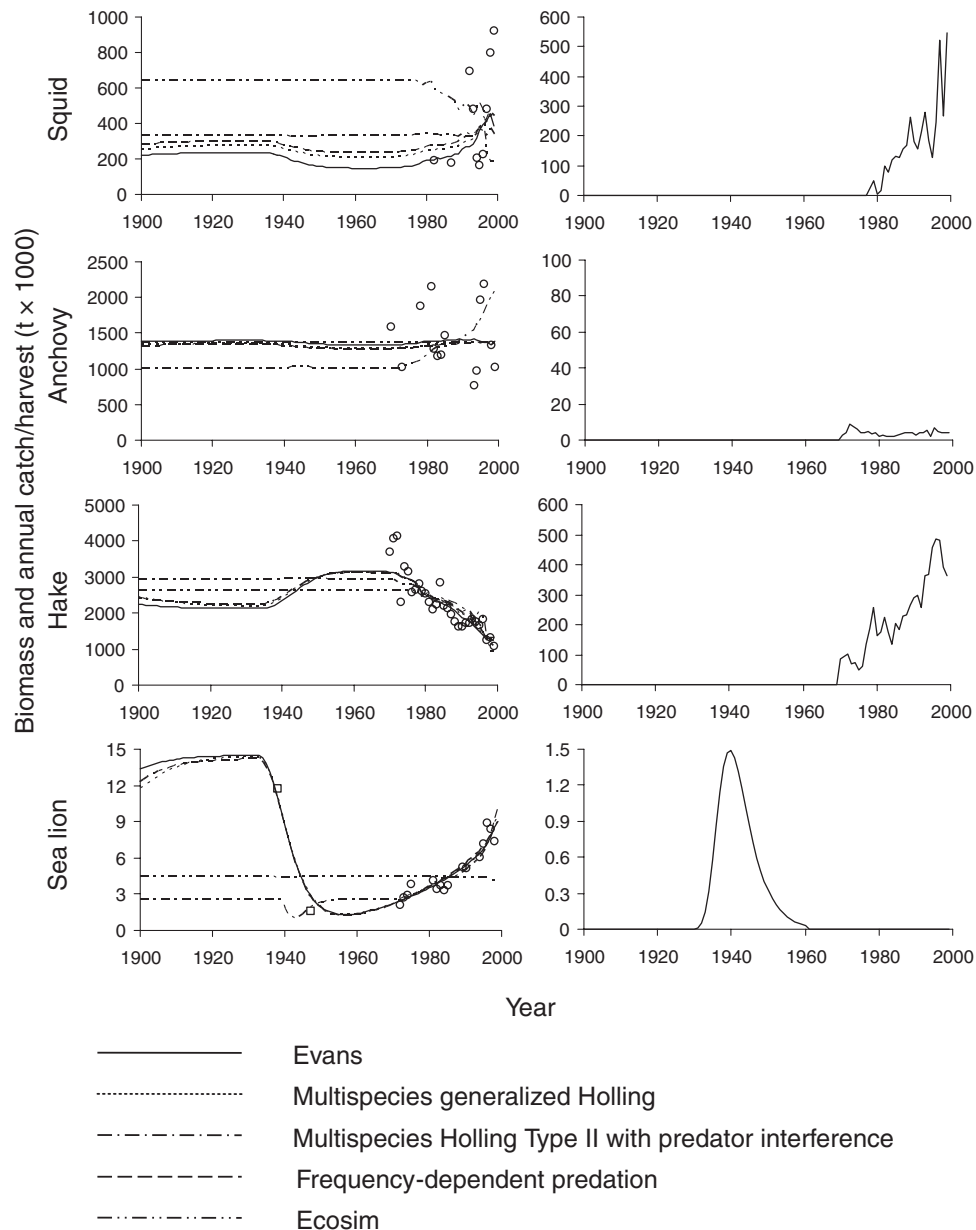
Model fits

Overall, most models were able to describe reasonably well the time series for hake and sea lion, but did a poorer job with squid and anchovy (Fig. 3). In all cases, the best fits produced systems characterized by a single stable equilibrium point in the absence of harvest. The equilibrium biomasses were very similar among the EV, GH, and FD models, while those in the T2 and EC models differed, mostly that for the sea lion, which was predicted to be much lower than in the first three models (Table 1).

The squid data were, in general, poorly described, but the EV, GH, and FD models were able to capture part of the increasing trend observed in the late 1990s, while the T2 model predicted no changes and the EC model predicted a decline (Fig. 3). For anchovy, all models but T2 predicted a fairly constant population level through time; T2 predicted an increasing trend since 1980 (Fig. 3). The declining trend of the hake stock was well captured by all models, but EV, GH, and FD also predicted an increase in hake biomass associated with the harvest of sea lion in the mid-twentieth century (Fig. 3).

The sea lion trajectory was fully captured only by the EV, GH, and FD models. These models predicted a large population reduction as a consequence of the harvest, and a recovery since 1960 (Fig. 3). The T2 model was only able to predict the observed increase in sea lion abundance (Fig. 3). The EC model predicted an essentially constant sea lion biomass through time (i.e., the effects of exploitation on sea

Fig. 3. Best fits of the Patagonian models. The time-series data and the best fits for the five models considered are at the left, while the annual catches for each species are at the right, showing the data used to fit the models (○). For the sea lion, two data points are indicated (□) (around 1940–1950) that correspond to earlier abundance estimates which, because of methodological differences (annual average of the censuses for a given rookery versus censuses done at the peak of the reproductive season), cannot be strictly compared with the rest of the sea lion time series. These two points were not used to fit the models, but still give an approximate idea of the sea lion population trend at that time. It is noteworthy that the Evans (EV), multispecies generalized Holling (GH), and frequency-dependent predation (FD) models were capable of capturing this sharp decline of the sea lion population, predicting values surprisingly close to these earlier abundance values. On a technical note, because the available literature on sea lion harvest reports the total number of leathers produced in 5-year periods, annual catches were estimated as the difference between consecutive years of a Gompertz function fitted to the cumulative catches (unpublished data); this is the reason for the smooth shape of the sea lion annual harvest.



lion dynamics were so slight that at the scale of Fig. 3 its dynamics appear flat-lined).

When the AIC_c values are considered, the EV model was the best and the EC model the worst (Table 1). However, ΔAIC_c indicated that only the EV and GH models were comparatively reasonable descriptions of the data (Table 1). The

FD model had similar goodness of fit to the EV and GH models (Fig. 3), but because of its larger number of fitted parameters its AIC_c was substantially higher (Table 1). The T2 and EC models had clearly worse fits (Fig. 3).

Based on ΔAIC_c (i.e., <10), the EV and GH models were the only ones selected and considered worthy of further anal-

Table 1. Comparison of the best fits among the Evans (EV), multispecies generalized Holling (GH), multispecies Holling Type II with predator interference (T2), frequency-dependent predation (FD), and Ecosim (EC) models.

	EV	GH	T2	FD	EC
n_p	40	40	42	47	50
AIC _c	1963.6	1965.7	2011.7	2073.1	2205.9
Δ AIC	0.000	2.033	48.076	109.461	242.214
Equilibrium biomasses (t) in the absence of harvest					
Squid (<i>Illex argentinus</i>)	236 228	277 135	327 827	297 302	639 411
Anchovy (<i>Engraulis anchoita</i>)	1 395 850	1 347 070	1 002 852	1 333 863	1 374 979
Hake (<i>Merluccius hubbsi</i>)	2 126 308	2 181 730	2 936 672	2 236 017	2 626 688
Sea lion (<i>Otaria flavescens</i>)	14 521	14 454	2 582	14 191	4 482

Note: n_p , number of fitted parameters.

ysis. The combination of the low Δ AIC_c (Table 1) and the similarity of the fits (Fig. 3) did not allow one model to be considered truly better than the other.

Parameter uncertainty and model behaviour

When parameter uncertainty was considered, the EV and GH models exhibited significant variability within the 95th percentile range parameter space (Tables 2 and 3). In spite of the large number of parameters being estimated, the significant correlations among them were few. For both models, when the calculated α_c level is considered, fewer than 3% of the correlations were statistically significant, and if we consider $\alpha_c = 0.05$, this figure rises to less than 11% (Tables 2 and 3).

The continuation and bifurcation analyses indicated large variability in the responses to exploitation. The range of behaviours included changes in the equilibria from point to periodic attractors (Figs. 4 and 5), and hysteresis with two basins of attractions (Fig. 4). Furthermore, even though the EV and GH models had very similar fits, they behaved quite differently in some of these exploitation scenarios.

When the EV model with the MLE parameters is considered, the harvesting of squid produced an unexpected increase and a later decrease of squid and sea lion equilibrium biomasses, hysteresis, and a region with a periodic attractor before squid extinction (Fig. 4). But the GH model had a clear negative effect on squid and sea lion from the very start of the exploitation, and a less marked effect on hake equilibrium biomass (Fig. 5). Another interesting difference between these models is observed when harvesting anchovy. This harvest has a highly negative effect on sea lion equilibrium biomass in the EV model, where sea lion even becomes extinct before anchovy (Fig. 4), while it has a positive effect in the GH model (Fig. 5).

However, there were also many similarities between these models. In a more general view, and also considering the behaviours of the extreme sets, harvesting of squid had neutral to positive effects on anchovy equilibrium biomass and neutral or slightly positive to clearly negative effects on hake equilibrium biomass, including extinction in some cases (Figs. 4 and 5). The effects on sea lion equilibrium biomass ranged from neutral to clearly negative and extinction (Figs. 4 and 5), although they also included the positive effect at intermediate h_s values and the hysteresis behaviour described above for the best fit (MLE parameters) of the EV model (Fig. 4).

Exploitation of anchovy had neutral to clearly positive effects on squid equilibrium biomass and neutral to clearly negative effects on hake equilibrium biomass (Figs. 4 and 5). In the case of the sea lion, the anchovy harvest produced virtually all possible effects, including clearly positive, neutral, clearly negative, and extinction ((Figs. 4 and 5).

The harvesting of hake led in many cases to exploited systems with limit-cycle behaviour at intermediate levels of exploitation. This limit-cycle behaviour was absent in the EV-model best fit (Fig. 4) but present in the GH-model best fit. In both models the hake harvest had a clearly positive effect on squid, while the characteristic effect on anchovy equilibrium biomass was clearly negative at high levels of exploitation, but sometimes neutral or positive at low and (or) intermediate levels of exploitation (Figs. 4 and 5). Sea lion presented an interesting result when harvesting hake. The best fits for both models showed a clear positive effect on sea lion equilibrium biomass, but all extreme sets showed clearly negative effects, including extinction (Figs. 4 and 5).

The harvesting of sea lion had neutral to negative effects on squid equilibrium biomass, virtually neutral effects on anchovy, and neutral to positive effects on hake (Figs. 4 and 5).

Discussion

Our results indicate large variability with respect to both model structure (i.e., different functional responses) and parameter uncertainty. Even the behaviour of the selected models (EV and GH), which also had very similar best fits, differed substantially in some exploitation scenarios. This indicates that model uncertainty is a factor that cannot be dismissed if we want to use simple models to gain insight into the dynamics of much more complex systems such as actual marine communities. The observed variability largely agrees with previous results obtained from local dynamic models of higher complexity (Yodzis 1998, 2000), and suggests that achieving management-quality multispecies models can be even harder than is generally thought. Fortunately, in spite of this variability, it was still possible to reach some coarse-grain conclusions. Given the extent of model uncertainty explored in these analyses, we expect these emerging patterns to be robust to a fairly wide range of structure and parameter uncertainty. The sample and resample sizes used for the implementation of the sample-importance-resample algorithm were small for models of these sizes (e.g., see Givens et al. 1993), but this was imposed by hardware limi-

Table 2. Maximum-likelihood estimators (MLE) and 95th-percentile ranges (A) and correlations among parameters (B) for the EV functional response model.

(A) MLEs and 95th-percentile ranges.					
Parameter	MLE (best fit)	95th-percentile range	Parameter	MLE (best fit)	95th-percentile range
f_{rs}	0.93260	0.53091 to 0.99353	τ_{sl}	0.08178	0.04214 to 0.09826
f_{ra}	0.92857	0.47808 to 0.98425	τ_{al}	0.00167	0.00087 to 0.00245
K_s	2 853 523	1 563 293 to 4 226 968	τ_{hl}	0.08572	0.04429 to 0.09875
K_a	2 145 852	1 343 419 to 3 177 336	τ_{ol}	0.03120	0.01634 to 0.04597
α_{sa}	2.97×10^{-10}	1.54×10^{-10} to 4.34×10^{-10}	e_{sh}	0.54976	0.54021 to 0.82099
α_{as}	0.88012	0.45847 to 1.28900	e_{ah}	0.60702	0.50689 to 0.89731
m_s	0.44936	0.23514 to 0.66297	e_{oh}	0.35681	0.18901 to 0.50492
m_a	2.26988	1.17435 to 3.31945	e_{sl}	0.77471	0.50913 to 0.94185
m_h	0.87788	0.45736 to 1.28366	e_{al}	0.91288	0.50871 to 0.93609
μ_l	1.95×10^{-14}	1.01×10^{-14} to 2.87×10^{-14}	e_{hl}	0.72435	0.67855 to 0.94442
v_l	3.969	2.773 to 5.458	e_{ol}	0.37713	0.20046 to 0.55769
f_{jh}	0.85387	0.52065 to 0.97779	B_{oh}	879 142	501 497 to 1 299 200
f_{jl}	0.85275	0.70718 to 0.99681	B_{ol}	316 166	166 923 to 463 967
δ_h	2.53348	1.32795 to 3.73444	t_0	1849.74	1848.03 to 1849.84
δ_l	1.90571	1.04749 to 2.81641	B_{s0}	527 754	273 690 to 781 512
τ_{sh}	0.13283	0.06806 to 0.19547	B_{a0}	1 235 718	927647 to 1 821 393
τ_{ah}	0.00342	0.00179 to 0.00508	B_{h0}	1 767 966	1 526 734 to 2 608 530
τ_{oh}	0.04768	0.02605 to 0.07058	B_{l0}	2350	1 224 to 3 480
(B) Correlations among parameters.					
	No.	Percentage	Detailed correlations with $p < \alpha_c$		
			Parameters	R_S	p
R_S with $p < 0.05$	63	10.0	$f_{rs} K_s$	-0.134	2.22×10^{-5}
R_S with $p < \alpha_c$	14	2.2	$f_{rs} \tau_{oh}$	-0.156	7.18×10^{-7}
n_R	630		$f_{rs} \tau_{sh}$	0.182	6.48×10^{-9}
α_c	7.94×10^{-5}		$f_{rs} B_{oh}$	-0.131	3.09×10^{-5}
			$K_a e_{oh}$	-0.140	8.35×10^{-6}
			$e_{oh} f_{jh}$	-0.449	0.00
			$\tau_{oh} B_{oh}$	-0.162	2.41×10^{-7}
			$e_{sh} f_{jh}$	-0.263	3.00×10^{-17}
			$\tau_{sh} B_{oh}$	0.138	1.27×10^{-5}
			$m_h f_{jh}$	0.248	1.66×10^{-15}
			$e_{sl} v_l$	0.125	7.29×10^{-5}
			$e_{hl} v_l$	0.167	1.01×10^{-7}
			$e_{hl} f_{jl}$	-0.378	2.88×10^{-35}
			$v_l f_{jl}$	0.295	1.68×10^{-21}

tations (essentially not enough hard drive to handle initial samples 100–1000 times larger than the ones used here). Therefore, our parameter-uncertainty assessment is an approximation; we do not claim that we have fully estimated the posterior distributions. However, this approximation produces a broader $\hat{\eta}(\theta)$, which leads to larger 95th-percentile ranges. Therefore, in terms of any conclusions drawn from these results, an improved assessment of parameter uncertainty should only narrow the range of uncertainty and, hence, make such conclusions more precise.

Regarding the best fits, one interesting point is the dynamic between hake and sea lion and the prediction that hake was above its equilibrium biomass when its fishery started. Even though this feature is not common to all models, its presence in the two selected ones suggests that it

might have been an actual event in the history of the Patagonian marine system. Therefore, the assumption that hake was at equilibrium when the fishery started, which is a classic and common one in many single-species models (e.g., carrying capacity, virgin biomass, etc), is not supported by our results. Furthermore, this also suggests that using the early-1970s biomass estimates for establishing recovery targets or estimating reference points may be misleading and potentially dangerous. Such an assumption implies that the virgin system could have supported a higher biomass of hake than it actually did, at least according to our results.

The squid and anchovy data were poorly described by the models. However, the lack of ability to accurately describe the dynamics of these species is not a surprise. The squid has an annual life cycle (Brunetti et al. 1999a), and the an-

Table 3. MLEs and 95th-percentile ranges (A) and correlations among parameters (B) for the GH functional response model.

(A) MLEs and 95th-percentile ranges.					
Parameter	MLE (best fit)	95th-percentile range	Parameter	MLE (best fit)	95th-percentile range
f_{rs}	0.86801	0.47524 to 0.99484	γ_{sl}	0.08815	0.04558 to 0.09837
f_{ra}	0.91720	0.47417 to 0.98718	γ_{al}	0.00223	0.00117 to 0.00329
K_s	3 321 734	1 792 058 to 4 911 329	γ_{hl}	0.09125	0.04690 to 0.09808
K_a	2 115 283	1 327 527 to 3 152 055	γ_{ol}	0.02900	0.01523 to 0.04268
α_{sa}	2.94×10^{-10}	1.55×10^{-10} to 4.30×10^{-10}	e_{sh}	0.55677	0.52123 to 0.83124
α_{as}	0.97352	0.50919 to 1.41657	e_{ah}	0.59805	0.51342 to 0.88708
m_s	0.55805	0.29021 to 0.82107	e_{oh}	0.35553	0.19197 to 0.50765
m_a	1.76599	0.92432 to 2.60231	e_{sl}	0.82626	0.51004 to 0.94046
m_h	0.84649	0.44126 to 1.24463	e_{al}	0.80062	0.51289 to 0.94019
μ_l	8.36×10^{-15}	4.36×10^{-15} to 1.24×10^{-14}	e_{hl}	0.72923	0.67965 to 0.94534
v_l	4.057	2.878 to 5.491	e_{ol}	0.21560	0.11356 to 0.31836
f_{jh}	0.84003	0.50647 to 0.98389	B_{oh}	865 321	470 852 to 1 278 300
f_{jl}	0.84781	0.70789 to 0.99600	B_{ol}	315 445	167 619 to 465 319
b_h	2.53443	1.74561 to 3.75372	t_0	1 849.84	1848.05 to 1849.86
b_l	1.96523	1.03098 to 2.90281	B_{s0}	523 108	271 218 to 765 839
γ_{sh}	0.14702	0.07662 to 0.21588	B_{a0}	1 144 109	920 713 to 1 692 595
γ_{ah}	0.00238	0.00125 to 0.00351	B_{h0}	1 856 502	1 549 210 to 2 756 074
γ_{oh}	0.03735	0.01955 to 0.05516	B_{l0}	1 358	1028 to 2007
(B) Correlations among parameters.					
			Detailed correlations with $p < \alpha_c$		
	No.	Percentage	Parameters	R_S	p
R_S with $p < 0.05$	68	10.8	f_{rs} e_{oh}	-0.129	4.17×10^{-5}
R_S with $p < \alpha_c$	12	1.9	f_{rs} b_h	-0.154	1.02×10^{-6}
n_R	630		K_a f_{jh}	-0.141	7.15×10^{-6}
α_c	7.94×10^{-5}		e_{oh} m_h	0.127	5.70×10^{-5}
			e_{oh} f_{jh}	-0.513	0.00
			e_{sh} f_{jh}	-0.297	7.18×10^{-22}
			γ_{sh} b_h	0.153	1.15×10^{-6}
			b_h B_{oh}	-0.227	3.93×10^{-13}
			m_h f_{jh}	0.227	3.75×10^{-13}
			e_{hl} v_l	0.172	4.47×10^{-8}
			e_{hl} f_{jl}	-0.344	3.09×10^{-29}

chovy, like many other forage fish, is known to have large fluctuations in abundance (Ciechomski and Sánchez 1988; Hansen and Madirolas 1996; Hansen 1999). Both species are considered highly susceptible to environmental factors (Ciechomski and Sánchez 1988; Brunetti et al. 1999a; Hansen 1999), and no environmental effects were included in these models. Regarded in this light, our fits do not appear to be that bad. Furthermore, the selected models were still capable of capturing some of the observed increase in squid in the late 1990s. This suggests that the increase, or at least part of it, could be related to the interplay between trophodynamics and exploitation.

In approaches like the one implemented here, the scarcity of data usually leaves very little room for model validation, since all available data are typically used for fitting purposes. Our case is no exception: we used the whole database for fitting the models. However, we did not use any quantitative diet or consumption data; the model predicts this information for any given functional response and parameter set.

We can compare consumption by hake and sea lion estimated in this way with any available consumption information. In our case, this cannot constitute formal model validation, but it allows the comparison of some model predictions with fairly independent estimates of the same variables. Furthermore, using $\hat{\eta}(\theta)$ we can build distributions for these variables and obtain their 95th-percentile ranges.

Total trophic consumption by hake was estimated for the period 1970–1986 (Prenski and Angelescu 1993). Because this estimate included both the Bonaerensis and the Patagonian hake stocks (Prenski and Angelescu 1993), we cannot compare consumption estimates directly. However, considering that the Patagonian stock represents more than 80% of the combined biomass, the comparison is still a useful guideline. Like their fits, the consumption estimates from both models were very similar (Table 4). The models estimated more squid and less anchovy consumption by hake than in the previous study, although the 95th-percentile ranges overlapped and included the previous estimate (Table 4).

Fig. 4. Bifurcation analyses for the EV model. Each quadrant corresponds to the bifurcation analysis that considers the harvesting of one species at a time, where the analysis starts with the system at equilibrium and no harvest and ends when the harvested species goes extinct. In each quadrant, the graphs at the left correspond to the maximum-likelihood estimators (MLE) of the parameters (best fit) and those at the right to the extreme parameter sets. The solid lines indicate stable equilibrium points, while the dotted lines indicate unstable ones. In the MLE diagrams, periodic attractors (cycles) are represented by two lines (pitchfork shape), which indicate the amplitude of the cycle for the corresponding harvesting mortality. In the graphs representing the extreme parameter sets, the periodic attractors are indicated with very close solid circles (thick lines), without an indication of the amplitude of the cycles. For visualization purposes, some extreme-set graphs have a secondary y axis; arrows indicate the graphs that should be read on these secondary axes.

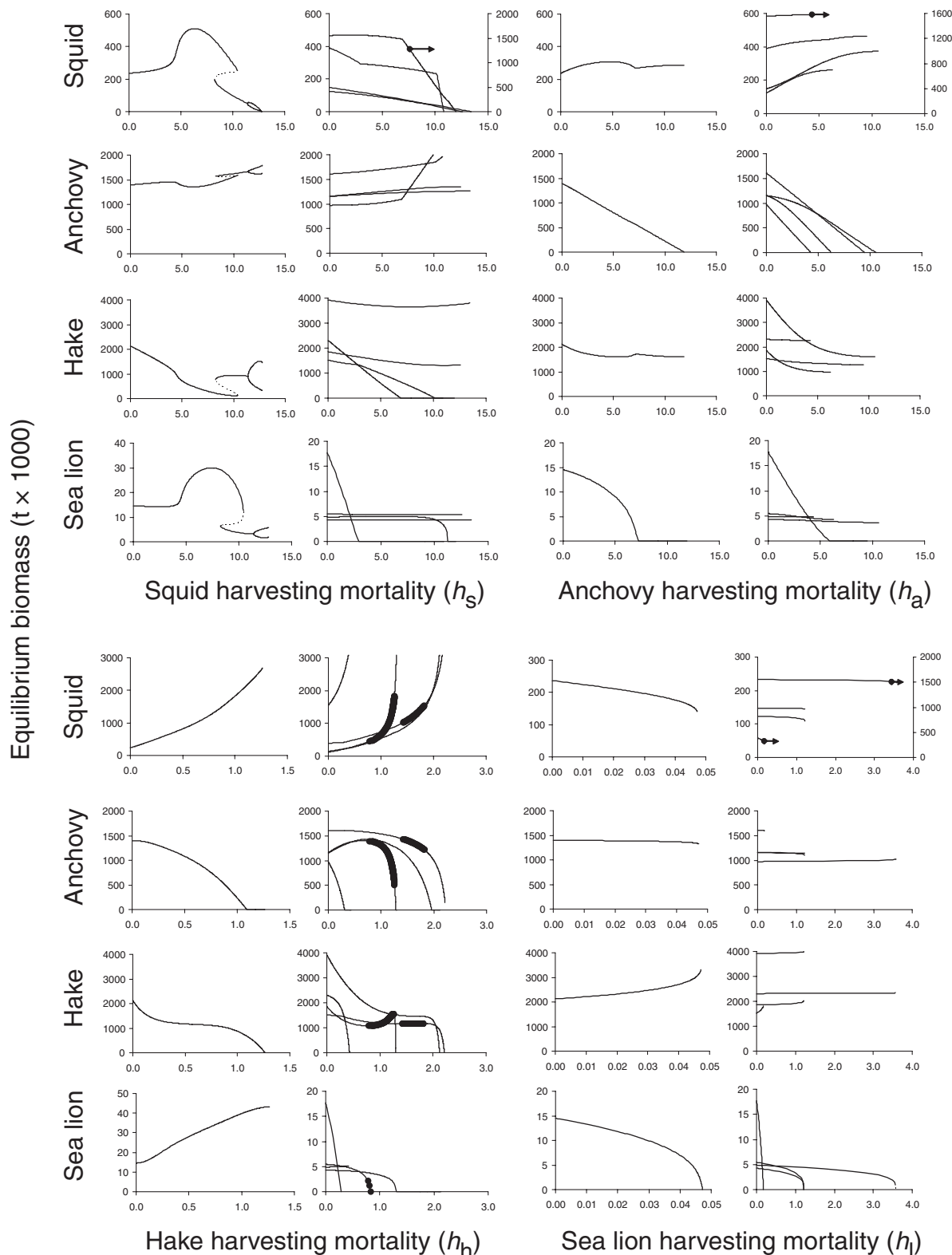
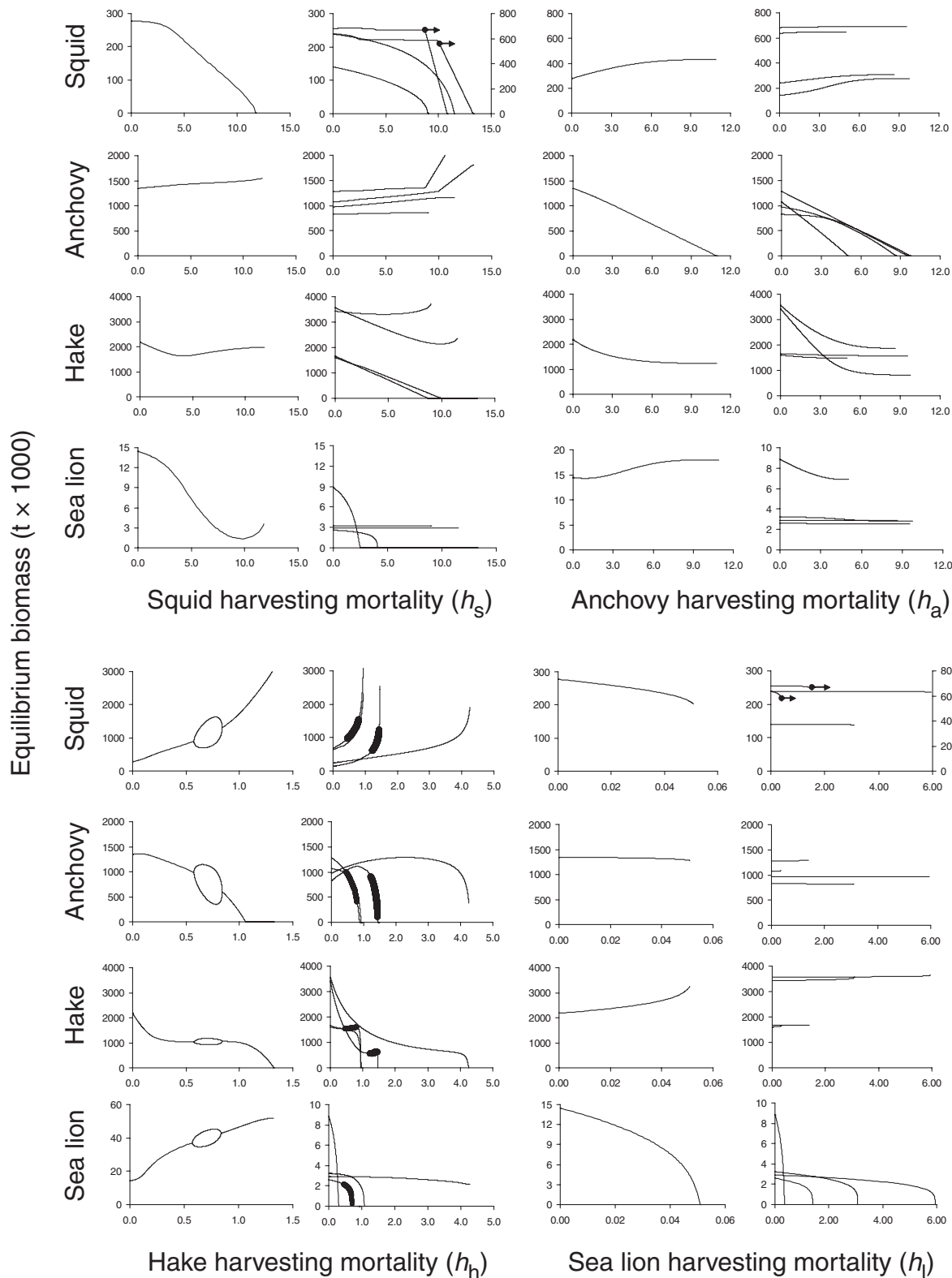


Fig. 5. Bifurcation analyses for the GH model. Each quadrant corresponds to the bifurcation analysis that considers the harvesting of one species at a time, where the analysis starts with the system at equilibrium and no harvest and ends when the harvested species goes extinct. In each quadrant, the graphs at the left correspond to the MLEs of the parameters (best fit), and those at the right to the extreme parameter sets. The solid lines indicate stable equilibrium points. In the MLE graphs, periodic attractors (cycles) are represented by two lines (i.e., defining a bubble-shaped structure in the graph), which indicate the amplitude of the cycle for the corresponding harvesting mortality. In the extreme-set graphs, the periodic attractors are indicated with very close solid circles (thick lines), without an indication of the amplitude of the cycles. For visualization purposes, some extreme-set graphs have a secondary y axis; arrows indicate the graphs that should be read on these secondary axes.



Similarly, when estimates of total hake consumption were compared, those from the models were also higher, but again the 95th-percentile ranges overlapped and included the previous value (Table 4).

In the case of sea lion, the other consumer in these models, the only available estimate of consumption by the population corresponds to the population estimated for 1996, but the diet information used in this analysis was collected during the 1990s (Koen-Alonso et al. 1999). This estimate was based on individual consumption rates (Innes et al. 1987) and diet composition from stomach-content analysis (Koen-Alonso et al. 2000a), and included a bootstrap procedure to incorporate the variability in diet composition (Koen-Alonso et al. 1999). We compared this information with the average annual consumption rates for the period 1990–1999 obtained from the models. Here, as in the case of hake, we also found extremely wide 95th-percentile ranges, which overlapped between models and previous estimates (Table 4). The squid and anchovy consumption rates from the models were very close to previous estimates, but hake consumption from both models was more than double the previous estimate (Table 4). Total prey-consumption rates were also very similar, but this is not completely unexpected, since the individual consumption rate in the earlier study (Koen-Alonso et al. 1999) and the maximum consumption rates in our models had allometrically derived elements (Innes et al. 1987; Yodzis and Innes 1992).

However, at the level of individual prey the consistency between previous consumption estimates and the models' predictions is truly remarkable (all of them are of the same order of magnitude and within a factor of less than 3 of each other). In our models, the consumption predictions are by-products of the modelling approach; estimation of consumption is not the main goal. Still, comparisons like these are very valuable for model validation. More precisely, they are useful for cross-checking models, since consumption estimates are always the result of different kinds of modelling exercises. In our case, the observed high level of consistency improves the odds of capturing some reality in these modelling attempts, but the best models still picture the sea lion as a much more severe hake predator than the few available quantitative diet data suggest (Koen-Alonso et al. 2000a). However, given the typically large uncertainty in estimates of pinniped diet composition and consumption (e.g., Shelton et al. 1997), this difference really indicates that we still have a poor understanding of sea lions' food habits.

Although these models were not intended as management tools, the patterns in the predicted equilibrium biomasses under different exploitation scenarios are still of some use for fishery management. These patterns refer to the equilibrium biomasses of the system, not to the transient behaviour that will bring the system to these equilibrium states (Strogatz 1994). In most applied cases the transient behaviours are likely to be as important as the equilibria themselves because it may take the system a very long time to reach equilibrium (Hastings 1996). Nevertheless, we can still regard these patterns as a road map for the system's response to the exploitation of its individual components.

Within this context, for example, we can say that fishing anchovy will have a negative impact on hake. Since from a single-species perspective the anchovy is considered under-

exploited (Hansen 1999), after the hake stocks collapsed, interest in developing an anchovy fishery as a palliative measure increased (Crespo et al. 2000). Since 2002 there has been an ongoing project within the agency in charge of fishery management in Chubut Province (one of the Patagonian provinces in Argentina) to explore and develop this alternative fishery. Based on our results, such a fishery would likely reduce the chances of hake recovery. In this context, one unexpected prediction arises from considering the effect of the hake fishery on anchovy. Our analysis indicates that high fishing mortalities for hake have a strong negative impact on the equilibrium biomass of anchovy. Despite the poor fits that we obtained for anchovy, it is noteworthy that Hansen and Madirolas (1996) had already discussed their own perceptions that anchovy was showing signs of a decline in abundance. At that time they were not sure if the available evidence was showing a negative trend or just low values within the natural limits of variation, but in view of the hypothesis of a decline, they were wondering how such an observation could be consistent with the decline in hake, its most important predator (Hansen and Madirolas 1996). With all their limitations, it is still very interesting that our models predict this counterintuitive behaviour and provide some insights into the possible causes of such a trend (e.g., competition with squid).

Regarding ways for promoting hake recovery, the culling of sea lions may at first glance seem a possibility. This option has never been seriously considered; sea lions are currently protected by federal law in Argentina and they also constitute one of the core attractions for tourism, which is a growing industry in Patagonia (Tagliorete and Losano 1996). Within our models, culling sea lions can have a positive effect on hake, but in the same cases it has an equally important negative effect on squid. This means that a management strategy of culling sea lions for the sake of the hake fishery would hinder the squid fishery at the same time.

Our results also indicate that the hake fishery might have had a boosting effect on squid, while the squid fishery may reduce the chances of hake recovery. Putting all of this together, even though this is just an exploratory modelling exercise, if we think in terms of a large squid fishery and a potential anchovy fishery, our results clearly suggest that these activities may hinder and (or) delay the rebuilding of the hake stock.

From the point of view of tourism, our results also suggest that the hake fishery does not necessarily have a strong negative effect on sea lions. In both models, the bifurcation analyses considering the maximum-likelihood parameters (i.e., the most likely response) indicated that the hake fishery actually boosts the sea lion equilibrium biomass, but the extreme sets also showed the opposite result, including sea lion extinction. Obviously, there is no robust prediction here, and further research is needed to clarify this issue, but the fact that despite the collapse of the hake stocks, the sea lion population is still recovering (Dans et al. 2004), together with the most likely behaviours derived from our models, suggests as a working hypothesis that the odds in favour of a strong negative impact of the hake fishery on sea lions are low. Nevertheless, this conclusion is based only on the trophodynamic relationships included in the models and does not consider the effects of by-catch.

Table 4. Average annual food consumption (t·year⁻¹) by hake and sea lion during the periods 1970–1986 and 1990–1999, estimated by the EV and GH models and from other available studies.

	EV model	GH model	Other sources ^a
1970–1986			
Squid consumed by hake	2 076 561 (753 042 – 8 520 710)	2 499 038 (1 020 219 – 8 203 621)	1 921 720
Anchovy consumed by hake	3 240 981 (180 906 – 6 280 130)	3 293 086 (165 552 – 6 712 025)	4 050 223
Total consumption by hake	24 066 767 (9 426 029 – 29 481 974)	23 705 215 (10 389 546 – 29 242 748)	14 706 268
Squid consumed by sea lion	367 (65 – 42 662)	653 (67 – 46 667)	
Anchovy consumed by sea lion	402 (126 – 6787)	472 (121 – 6 424)	
Hake consumed by sea lion	72 026 (37 039 – 341 867)	71 894 (39 465 – 298 953)	
Total consumption by sea lion	73 191 (39 520 – 402 496)	73 384 (43 175 – 327 160)	
1990–1999			
Squid consumed by hake	3 487 760 (775 192 – 8 684 187)	3 413 595 (993 785 – 8 621 463)	
Anchovy consumed by hake	1 598 598 (104 302 – 5 552 358)	1 748 327 (100 781 – 6 470 734)	
Total consumption by hake	13 937 979 (8 157 653 – 22 448 813)	13 853 080 (8 739 301 – 24 034 533)	
Squid consumed by sea lion	8 191 (154 – 48 598)	9 522 (175 – 45 217)	13 900 (3709 – 30 829)
Anchovy consumed by sea lion	2 331 (175 – 7 609)	2 873 (226 – 7 499)	2 410 (52 – 8 778)
Hake consumed by sea lion	139 540 (30 543 – 250 614)	138 270 (34 440 – 227 214)	51 260 (30 074 – 76 786)
Total consumption by sea lion	152 345 (36 545 – 268 714)	152 785 (40 984 – 252 430)	148 325

Note: The values provided for the models correspond to the best fit. Values in parentheses show the 95th-percentile range from $\hat{\eta}(\theta)$.

^aThe information on hake consumption for the period 1970–1986 was estimated for the two hake stocks in Argentine waters, the Bonaerensis and the Patagonian stocks (Prenski and Angelescu 1993). The models developed in this paper only deal with the Patagonian stock. However, the Patagonian stock is the largest one, representing 80% or more of the joint biomass. For the period 1990–1999, the information on sea lion consumption was obtained from Koen-Alonso et al. (1999). These estimates were obtained from mean individual consumption rates (Innes et al. 1987) and diet information. In this case, the values in parentheses are the 95% confidence intervals obtained by a bootstrap procedure. This bootstrap analysis only considered the variability in stomach-content composition (Koen-Alonso et al. 1999).

Table 5. Comparison of the effects of harvesting on equilibrium biomasses between predictions based on biological common sense and from the bifurcation analyses of the EV and GH models.

Effect on:	Harvesting of:			
	Squid	Anchovy	Hake	Sea lion
(A) Predicted effects based on biological common sense				
Squid (<i>Illex argentinus</i>)	–	+	+	+
Anchovy (<i>Engraulis anchoita</i>)	+	–	+	+
Hake (<i>Merluccius hubbsi</i>)	–	–	–	+
Sea lion (<i>Otaria flavescens</i>)	–	–	Unknown	–
(B) Synthetic view of the results from the EV and GH models^a				
Squid				
EV	[~] (–)	[~] (+)	[+] (+)	[–] (–)
GH	[–] (–)	[+] (+)	[+] (+)	[–] (0/–)
Anchovy				
EV	[~] (+)	[–] (–)	[–] (–/~)	[–] (0/+)
GH	[+] (+)	[–] (–)	[–] (–/~)	[–] (0/+)
Hake				
EV	[~] (–/~)	[~] (–)	[–] (–/~)	[+] (+)
GH	[~] (–/~)	[–] (–)	[–] (–/~)	[+] (+/0)
Sea lion				
EV	[~] (–/0)	[–] (–)	[+] (–)	[–] (–)
GH	[~] (–/0)	[+] (–)	[+] (–)	[–] (–)
(C) Agreement between biological common sense predictions and models results^b				
Squid	PA	PA	A	D
Anchovy	PA	A	PD	PD
Hake	PD	PA	PA	A
Sea lion	PA	PA	na	A

^aSymbols in brackets correspond to the results from the best fits (i.e., the most likely effects), while symbols in parentheses indicate the results from the “extreme” sets: +, positive effect; –, negative effect; ~, non-monotonic effect (i.e., the sign of the effect depends on the value of the harvesting mortality); 0, neutral effect. For the extreme sets, the slash (/) indicates that more than one type of effect was observed, and the order of the symbols roughly indicates their order of importance.

^bA, agreement; D, disagreement; PA, partial agreement; PD, partial disagreement; na, not applicable.

These general conclusions largely agree with the results of a previous attempt at modelling this system (Koen-Alonso et al. 2000b; Dans et al. 2003). This earlier model was rudimentary and based on a completely different theoretical framework (Berryman et al. 1995), but its results also indicated that the fishing of squid hindered the recovery of hake, and sea lion showed an increasing trend in spite of the increase in fishing catches (Koen-Alonso et al. 2000b; Dans et al. 2003), thus adding to the robustness of those predictions.

The simplest model possible is the conceptual one that we build using biological common sense. Such common sense typically considers only the most direct links between components in a system and dismisses the effect of longer pathways in the food web (e.g., harvesting a predator has a positive effect on its prey; harvesting one competitor has a positive effect on the other). Therefore, we can compare these conceptual models based on biological common sense with the results obtained from our models to determine if biological intuition can be a reasonable “minimum-realistic” model of these simple food-web models.

In our study, such an analysis shows that in some cases there is full agreement, but it also reveals one case of complete disagreement between our biological intuition and the models (Table 5). However, the most remarkable result is that in most cases the agreement or disagreement is only

partial (Table 5), and many of them involve non-monotonic responses to exploitation (Table 5). This result, given also the extremely simplified trophic structure of our models, clearly undermines our self-confidence about our own ability to integrate and incorporate multispecies effects without explicit modelling of such relationships.

It is well known that long-term effects of exploitation are largely structurally undetermined (i.e., whether species' responses to exploitation are positive or negative is not governed by food-web topology alone), and we need to know the precise values of the parameters (and their variability) in order to predict the responses (Yodzis 1988). However, non-monotonic responses are somehow less present in our thoughts, even though they have been already pointed out as a possible theoretical output (Yodzis 1996). The meaning of this type of response is that the effect of exploitation on a given species not only will vary in magnitude with the exploitation rate, but also can change in sign. Depending on the harvest rate, the response can be positive or negative even for the very species being harvested (e.g., fishing squid in the EV model).

From a modelling perspective, several points are noteworthy. The two models that performed best, EV and GH, shared a laissez-faire (i.e., predator-independent) Type III-shaped functional response. This is interesting because there is ap-

parent consensus among many ecologists that the most common functional responses are Type II (e.g., Jeschke et al. 2002). However, many of these observations come from laboratory experiments where, typically, one predator is faced with one prey (e.g., Murdoch 1969). When more than one prey is present, is not unusual to observe Type III functional responses (e.g., Holling 1959). Early on it was clear that very simple biological processes such as prey switching, the presence of prey refuges, or predator learning had the potential to transform an initial Type II functional response into a Type III (Murdoch 1973), and Type III shapes have been observed in switching experiments (e.g., Murdoch 1969; Murdoch et al. 1975). Furthermore, Type III functional responses are frequently used to implicitly model prey switching (Chesson 1983; van Baalen et al. 2001), and have the property of stabilizing predator–prey systems (Oaten and Murdoch 1975). This form is also the phenomenological result of explicitly modelling prey switching with underlying Type II functional responses (Post et al. 2000; our FD model), and is also the expected emergent shape from weak-link interactions (McCann 2000).

The functional response that performed the worst was the Ecosim formulation. The EC model also produced different results from the two best performing functional responses in a bifurcation analysis like the ones presented here. This is disturbing in view of the widespread and uncritical use of the Ecopath with Ecosim package. Fishery modellers are accustomed to carefully scrutinizing parameter estimates. As we move into the new realm of multispecies modelling, we need to recognize that the nonlinear mathematical structures of these models (encapsulated here in the functional response) need to be treated with the same care as parameters.

Food-web models are usually closed (i.e., the modelled system is assumed to be closed) and typically ignore any form of resource competition among basal species. In our case we kept the system open at the prey field level for the consumer species by including alternative prey to the modelled ones. These other prey sources were simply constant prey biomasses available to the predators, but their incorporation avoided the unrealistic assumption that the predators only fed upon the species explicitly included in the model. The other factor that we incorporated was a competitive effect between the basal species. This incorporation greatly improved the performance of our models, but in a more general sense this kind of competition is likely to be very common in nature. These features, although still rudimentary, enhance the representation of those inputs from the rest of the community that are affecting the behaviour of the modelled subsystem.

From an applied perspective, we prefer to see our results as a glass half-full rather than half-empty. In spite of all the variability and complexity, this work shows that there are reasonable ways to address the issues, putting us closer to management-quality multispecies models. Furthermore, the approach implemented here circumvents the problem of uncertainty in quantitative diet composition by making model parameterization less reliant on this source of information, and, at the same time, freeing available data for model validation. Finally, our approach shows how to cope with the fact that predictions from models with different functional responses can vary substantially, though more work in this

direction is needed. At the very least, we have clearly demonstrated that a single model structure cannot be considered per se a reliable source for making inferences about the modelled system.

Addendum

Peter Yodzis passed away on 28 March 2005, while this paper was in press. As scientists we will all miss his insights and clarity of thought; as a friend I will always miss his deep laugh and unbounded generosity. Until the next time, my friend.

Mariano Koen-Alonso

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Appendix A

Table A1. Database of biomasses and catches for squid (*Illex argentinus*), anchovy (*Engraulis anchoita*), hake (*Merluccius hubbsi*), and sea lion (*Otaria flavescens*) used for the fitting of the models presented in this paper.

Year	Biomass (t)				Catch (t)			
	Squid	Anchovy	Hake	Sea lion	Squid	Anchovy	Hake	Sea lion
1929								0.15
1930								1.72
1931								11.23
1932								47.28
1933								140.45
1934								316.15
1935								570.92
1936								865.72
1937								1143.12
1938								1352.97
1939								1468.73

Table A1 (*concluded*).

Year	Biomass (t)				Catch (t)			
	Squid	Anchovy	Hake	Sea lion	Squid	Anchovy	Hake	Sea lion
1940								1489.25
1941								1430.93
1942								1317.77
1943								1173.65
1944								1018.12
1945								865.06
1946								723.10
1947								596.70
1948								487.44
1949								395.03
1950								318.13
1951								254.94
1952								203.51
1953								161.96
1954								128.58
1955								101.89
1956								80.61
1957								63.71
1958								50.30
1959								39.69
1960								31.30
1970		1 589 287	3 700 000		69	2881	87 400	
1971			4 094 920		96	4346	92 000	
1972			4 140 564	2110	94	8685	102 800	
1973		1 020 100	2 300 000	2691	331	7264	70 400	
1974			3 286 369	2903	441	6429	74 200	
1975			3 149 437	3860	390	4051	50 000	
1976			2 600 000		927	4320	60 906	
1977			2 642 715		143	4605	134 848	
1978		1 892 045	2 823 409		23 638	3406	189 161	
1979			2 634 311		50 702	4199	255 905	
1980			2 562 585		5 944	2263	162 350	
1981		2 151 767	2 308 283	4140	14 401	2620	174 729	
1982	192 600	1 285 930	2 099 625	3487	96 925	2136	223 909	
1983		1 188 776	2 230 037	3780	80 058	2237	176 100	
1984		1 203 181	2 842 969	3305	120 772	2050	135 224	
1985		1 480 093	2 203 954	3720	133 166	2583	203 334	
1986			2 142 882		127 970	3323	182 858	
1987	181 977		1 960 388		155 681	4097	230 325	
1988			1 779 005		169 213	4117	233 526	
1989			1 639 150	5248	262 978	4384	263 533	
1990			1 643 631	5210	180 767	2771	288 398	
1991			1 737 620		155 681	4360	297 079	
1992	693 538		1 722 591		214 414	4080	255 369	
1993	479 571	764 710	1 836 000		277 622	5729	364 928	
1994	203 820	975 298	1 775 049	6084	185 403	2123	365 695	
1995	168 943	1 969 881	1 654 398	7146	129 093	6530	457 306	
1996	225 602	2 198 822	1 819 739	8897	244 617	4546	487 356	
1997	483 532		1 252 698	8428	523 341	4189	480 452	
1998	799 641	1 327 565	1 342 216	7407	267 255	4301	392 463	
1999	921 254	1 025 945	1 086 010		546 303	4301	365 000	

Appendix B

Table B1. List of symbols with their corresponding unit(s), where not dimensionless, and a brief description.

Symbol	Unit(s)	Description
N_i	Dimensionless	Total number of biomass estimates for species i contained in the database
B_i	tonne	Biomass of species i
r_i	year ⁻¹	Intrinsic biomass/production ratio of species i
K_i	tonne	Carrying capacity of species i
α_{ij}	Dimensionless	Competition coefficient of species j on species i
F_{ij}	year ⁻¹	Functional response of species j preying on species i
m_i	year ⁻¹	“Other mortality” rate of species i
H_i	tonne·year ⁻¹	Harvest rate of species i
f_{r_i}	Dimensionless	Fraction of its maximum physiological capacity for production realized by species i
a_{r_i}	year ⁻¹ ·kg ^{0.25}	Allometric coefficient of the maximum physiological capacity for production of species i . It depends on species i ’s metabolic type
w_i	kg	Mean individual biomass of species i
T_i	year ⁻¹	Mass-specific respiration rate of species i
e_{ij}	Dimensionless	Assimilation efficiency by species j of prey i
μ_i	year ⁻¹ ·tonne ^(1-v_i)	Density-dependent mortality coefficient of species i
v_i	Dimensionless	Density-dependent mortality exponent of species i
a_{T_i}	year ⁻¹ ·kg ^{0.25}	Allometric coefficient of the mass-specific respiration rate of species i ; it depends on species i ’s metabolic type
C_{ij}	time ⁻¹	Generic capture rate, i.e., consumption of species i by predator j per unit of j searching time
h_{ij}	time	Generic handling time, i.e., time spent by predator j off the search for prey after capturing one unit of prey i
J_i	year ⁻¹	Asymptotic maximum consumption rate of predator i ; within the bioenergetic and allometric framework it represents the realized maximum capacity of predator i to metabolize food, which is a fraction of its maximum physiological capacity to metabolize food ($a_{J_i} w_i^{-0.25}$)
f_{J_i}	Dimensionless	Fraction of its maximum physiological capacity to metabolize food realized by species i
a_{J_i}	year ⁻¹ ·kg ^{0.25}	Allometric coefficient of the maximum physiological capacity to metabolize food of species i ; It depends on species i ’s metabolic type
ξ_{ij}	year ⁻¹ ·tonne ⁻¹	Multispecies Holling Type II functional response positive coefficient corresponding to the consumption of predator j of prey i
Q_j	tonne	Multispecies Holling Type II with predator interference functional response positive parameter corresponding to the baseline level of predator interference when predator j tends to zero
q_j	Dimensionless	Multispecies Holling Type II with predator interference functional response predator interference exponent; this parameter determines the degree of predator interference ($q_j = 0$ implies no predator interference, while $q_j \rightarrow \infty$ implies that predator interference precludes foraging)
γ_{ij}	year ⁻¹ ·tonne ^{-b_j}	Generalized Holling functional response positive coefficient corresponding to the consumption by predator j prey i
b_j	Dimensionless	Generalized Holling functional response shape parameter (exponent) corresponding to predator j
ρ_{ij}	year ⁻¹ ·tonne ⁻¹	Frequency-dependent predation functional response positive coefficient corresponding to the consumption by predator j of prey i
p_{ij}	Dimensionless	Frequency-dependent predation functional response positive coefficient corresponding to the preference of predator j for prey i
β_j	Dimensionless	Frequency-dependent predation functional response shape parameter (exponent) corresponding to predator j
τ_{ij}	year ⁻¹ ·tonne ⁻¹	Evans functional response positive coefficient corresponding to the consumption by predator j of prey i
δ_j	tonne ⁻¹	Evans functional response shape parameter corresponding to predator j
a_{ij}	year ⁻¹ ·tonne ⁻¹	Ecosim functional response positive coefficient corresponding to the consumption by predator j of prey i ; within the Ecosim framework it represents the rate of effective search for prey i by predator j
v_{ij}	year ⁻¹	Ecosim functional response positive coefficient corresponding to the consumption by predator j of prey i ; within the Ecosim framework it represents the rate at which unavailable prey i becomes available for predation by j
v'_{ij}	year ⁻¹	Ecosim functional response positive coefficient corresponding to the consumption by predator j of prey i ; within the Ecosim framework it represents the rate at which available prey i becomes unavailable for predation by j

Table B1 (*concluded*).

Symbol	Unit(s)	Description
$-\ln[\ell(\theta)]$	Dimensionless	Minus loglikelihood
S_i^2	Dimensionless	Lognormal sample variance of the residuals of the species i biomass time series
B_{it}	tonne	Observed biomass of species i in year t
\hat{B}_{it}	tonne	Predicted biomass of species i in year t
AIC_c	Dimensionless	Akaike Information Criterion corrected for sample size
n_p	Dimensionless	Number of estimated parameters in a given model
N	Dimensionless	Total number of biomass estimates contained in the database
Δ_{AIC}	Dimensionless	Difference between the AIC_c of a given model and the AIC_c of the best ranked model (minimum AIC_c)
h_i	year ⁻¹	Harvesting mortality (= fishing mortality) of species i
$\tilde{\eta}(\theta)$	Dimensionless	Importance function
$\eta(\theta)$	Dimensionless	Posterior distribution
$w(\theta)$	Dimensionless	Importance weight
$\ell(\theta)$	Dimensionless	Likelihood
$\psi(\theta)$	Dimensionless	Prior distribution
$\hat{\eta}(\theta)$	Dimensionless	Estimate of the posterior distribution $\eta(\theta)$ obtained from the sample–importance–resample algorithm
θ_{MLE}	Variable	Generic representation of the maximum-likelihood estimator of a parameter
R_S	Dimensionless	Spearman's rank correlation coefficient
α_g	Dimensionless	Global significance level when multiple simultaneous comparisons are performed
α_c	Dimensionless	Significance level for each comparison when multiple simultaneous comparisons are performed
n_R	Dimensionless	Number of pairwise correlations performed among estimated parameters in a given model
B_{oi}	tonne	“Other prey” biomass available to predator i ; this is a constant biomass for a given predator
t_0	year	Initial year
B_{i0}	tonne	Initial biomass for prey i

Note: The order of the symbols coarsely follows their order of appearance in the text.