# Comparative analysis of trophic structure of commercial fishery species off Central Chile in 1992 and 1998

Sergio Neira [a,*], Hugo Arancibia [a], Luis Cubillos [b]

[a] *Departamento de Oceanografía, Universidad de Concepción, P.O. Box 160-C, Concepción, Chile*
[b] *Instituto de Investigación Pesquera, P.O. Box 350, Talcahuano, Chile*

## Abstract

Trophic interactions and community structure of commercial fishery species off Central Chile ($33°$–$39°$S) were analyzed and compared for 1992 and 1998 by ecotrophic modelling, using the Ecopath modelling software. The model encompasses the fishery, pinnipeds (sea lions), small pelagic fish (anchovy, pilchard), medium-sized pelagic fish (horse mackerel), demersal fish (e.g. Chilean hake, black conger), benthic invertebrates (carrot prawn, yellow prawn), and other groups such as zooplankton, phytoplankton, and detritus. Input information for the model was gathered from published and unpublished reports and our own estimates. Also, the effects of fishing and predation on fishery resources and on the most important components of the system were investigated, within an ecotrophic framework.

Predators consumed the greater part of the production of the most important fishery resources, particularly juvenile stages, and the fishery removed a large fraction of adult production. Mortality by predation is an important component of natural mortality, especially in recruit and prerecruit groups. Analysis of direct and indirect trophic impact shows that adult Chilean hake have a negative impact on juvenile Chilean hake through cannibalism, and on pilchard, anchovy, and carrot prawn through predation. Also, fishing has a strong impact on fishery resources, such as Chilean hake, pilchard, and anchovy. Total biomass in 1998 was 1.5 times higher than in 1992. However, total catches in 1998 were about 80% of those in 1992. Changes in biomass and total yields of the system between 1992 and 1998 can be observed in such properties as total flows, consumption, respiration, and production. It is concluded that ecotrophic modelling is an useful tool for fishery management, since it can improve our understanding of the predator–prey interactions among the exploited (fishery resources) and unexploited but potential fishery resources of the system.
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## 1. Introduction

Although short-term fishery management objectives may be partially fulfilled in the absence of ecosystem information, long-term strategies necessarily require placing fisheries in their ecosystem context, that is by incorporating knowledge of interspecific interactions of both exploited and unexploited populations, their physical environment and their habitat (Christensen et al., 1996; Sinclair et al., 1997).

The Humboldt Current system of Central Chile is a typical upwelling ecosystem that sustains some of the most productive fisheries of the world (FAO, 1995) due to coastal upwelling (Vergara, 1992).

Arancibia (1989, 1992) and Quiñones et al. (1997), analyzed interspecific relationships between fishery resources and their prey in Central Chile, and

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\* Corresponding author.
*E-mail address:* seneira@udec.cl (S. Neira).

concluded that most species that are fishery resources play important ecological roles in the marine system. Nonetheless, research on the trophic relationships between the main components, such as Chilean hake (*Merluccius gayi*) and horse mackerel (*Trachurus symmetricus*), have been both sporadic and short-term (Arancibia, 1987, 1991; Miranda et al., 1998). Additionally, some species that are not fishery resources could have important roles as either predators or preys (Neira and Arancibia, 2000).

Since the early 1980's, the development and later westward expansion of an important purse-seine horse mackerel fishery has influenced total landing in Central Chile. During the 1990's horse mackerel landings ranged from 2.4 million tonnes to a historical maximum of more than 4 million tonnes in 1995 (Fig. 1a). During 1997–1998, remarkable changes occurred in the length structure of jack mackerel catches, as juveniles dominated the fishing grounds. This has been attributed to both the entrance of one or two strong year classes and changes in oceanographic conditions

associated with the ENSO event of 1997–1998 (Cubillos et al., 1999; Arcos et al., 2001). The dramatic drop in horse mackerel landings in the later years was accompanied by an increasing trend in landings of other important fishery resources, such as Chilean hake, pilchard (*Strangomera bentincki*), and anchovy (*Engraulis ringens*) (Fig 1b). The ecosystem effects of these changes in landings of the most important fishery resources—especially those of horse mackerel—are still poorly understood in Central Chile.

Consequently, the objective of this paper is to investigate changes in the trophic interactions and the community structure of the Central Chile marine ecosystem (33°–39°S) between early 1990's—when the horse mackerel fishery was plenty—and late 1990's—when the horse mackerel fishery had collapsed. To accomplish this objective, we constructed two mass-balanced ecotrophic models summarizing biomass, catches and production of the main trophic groups, with emphasis on fishery resources in the Central Chile marine ecosystem in 1992 and 1998.

## 2. Materials and methods

The study area is located off Central Chile (33°–39°S) and extends 65 km offshore, covering a total surface area of 50,042 km$^2$ (Fig. 2). The area defined is the main fishing ground of both the purse-seine and the trawling industrial fishing fleets.

To reduce the time-scale limitations of the mass-balance model Ecopath (Christensen and Pauly, 1992a), changes have been analyzed in one-year periods. The analyses covered the years 1992 and 1998 as the best records were available for those years.

The model comprised 21 functional groups, including the main trophic components of the system and with emphasis on fish species—both targeted and by-catch species (Table 1). We used the Ecopath model (Polovina, 1984; Christensen and Pauly, 1992a, 1995), which emphasizes the relationships among economically important groups of fish and other species, and their most important prey groups. The system contains other groups that may have important roles as predators, competitors or prey and which may af-
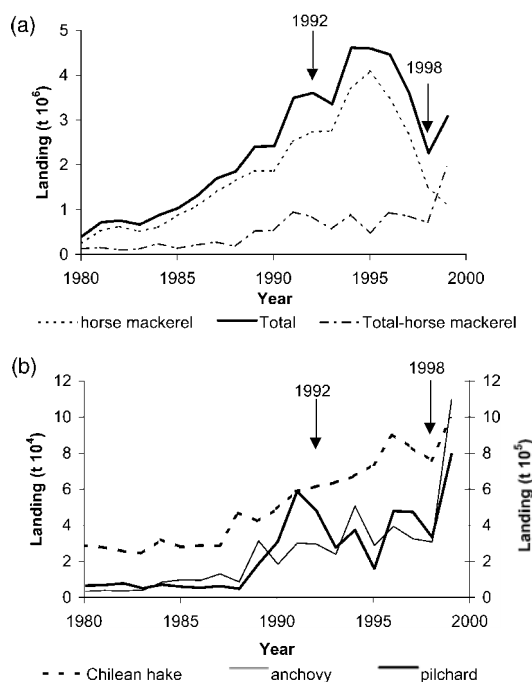


Fig. 1. Landings of the most important fishery resources in Central Chile 1980–2000. (a) Total landings, total landings without horse mackerel, and horse mackerel landings; (b) Chilean hake (first Y exe), anchovy and pilchard (secondary Y exe) landings.
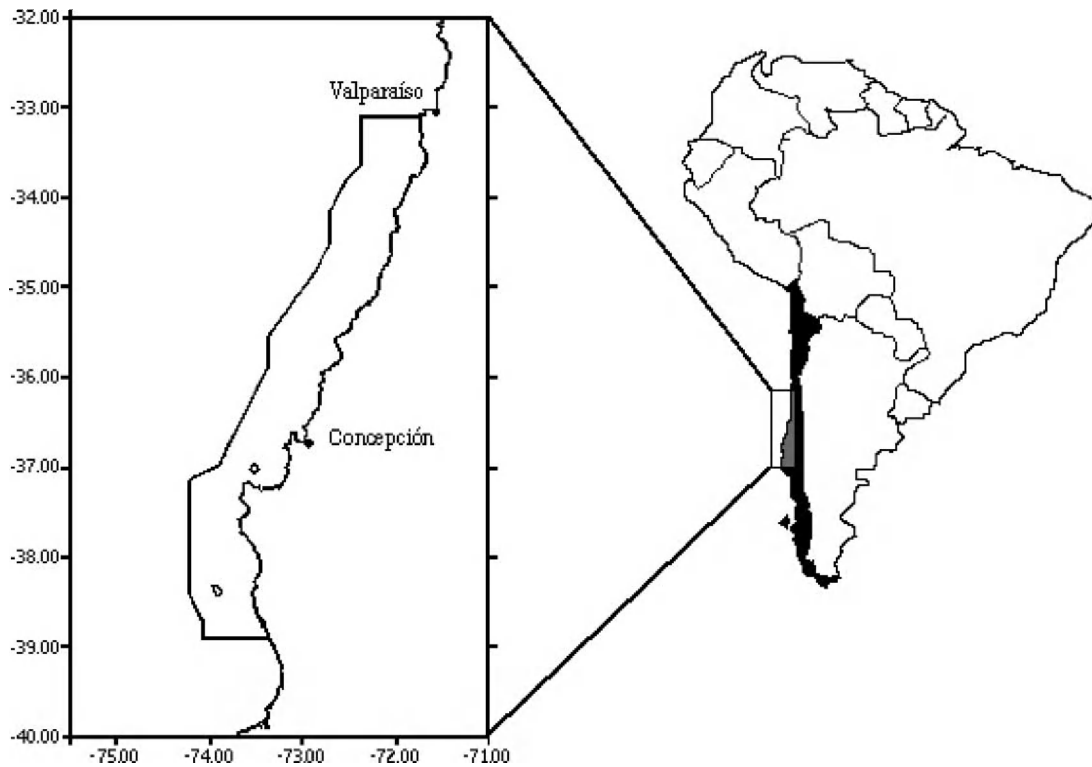
Fig. 2. Study area, the Central Chile marine ecosystem.

fect fishery yields. Such is the case with gelatinous plankton, marine birds and mammals and large pelagic fish (swordfish). However, the trophic and community structuring role of these organisms has not been appropriately studied within the Central Chile marine ecosystem. Taking these facts into consideration, and the incomplete knowledge of their biomass, rates and diet matrices, their inclusion in the model was inadvisable: the many assumptions would have decreased the accuracy of results.

Assuming steady-state for the years 1992 and 1998, the production of each group in the system should be balanced by predation by other components (predation mortality), exports (fishing mortality and other exports) and mortality other than from predation and yields. Then,

production of $i$ = all predation on $i$

+ biomass losses not due to predation on $i$

+ yields of $i$ + other exports of $i$

The terms of the equation can be replaced by Christensen and Pauly (1992a):

$$\frac{B_i P_i}{B_i}, \text{[production of } i]$$

$$= \sum_j \left( \frac{B_j Q_j}{B_j \mathrm{DC}_{ij}} \right) \text{[losses not due to predation on } i]$$

$$+ (1 - \mathrm{EE}_i) \times \frac{B_i P_i}{B_i}, \text{[*other losses'' of } i]$$

These lead to the following linear equation:

$$\frac{B_i P_i}{B_i \mathrm{EE}_i} - \sum_j \left( \frac{B_j Q_j}{B_j \mathrm{DC}_{ij}} \right) - \mathrm{EX}_i = 0$$

where $i$ is a model component or group, $j$ indicates any of the predators of $i$, $B_i$ is the biomass of $i$, $P_i/B_i$ is the production of $i$ per biomass unit (equivalent to total mortality $Z$ under steady-state conditions, sensu Allen, 1971), $Q_i/B_i$ is the consumption by $i$ per biomass unit, $\mathrm{DC}_{ij}$ is the fraction of $i$ in the diet of $j$ (in mass units), $\mathrm{EE}_i$ is the ecotrophic efficiency of $i$ (the total fraction

Table 1
Functional groups included in modelling the Central Chile marine ecosystem

| Common name | Scientific name (age group) |
|---|---|
| 1. Sea lion | *Otaria flavescens* |
| 2. Chilean hake (j) | *Merluccius gayi* (0–3) |
| 3. Chilean hake (a) | *Merluccius gayi* (4+) |
| 4. Pilchard (j) | *Strangomera bentincki* (0) |
| 5. Pilchard (a) | *Strangomera bentincki* (1+) |
| 6. Anchovy (j) | *Engraulis ringens* (0) |
| 7. Anchovy (a) | *Engraulis ringens* (1+) |
| 8. Carrot prawn (j) | *Pleuroncodes monodon* (0) |
| 9. Carrot prawn (a) | *Pleuroncodes monodon* (1+) |
| 10. Yellow prawn | *Cervimunida johni* |
| 11. Horse mackerel | *Trachurus symmetricus murphyi* |
| 12. Black conger | *Genypterus maculatus* |
| 13. Rattail fish | *Coelorhyncus aconcagua* |
| 14. Big-eye flounder | *Hipoglossina macrops* |
| 15. Cardinal fish | *Epigonus crassicaudus* |
| 16. Pacific sand perch | *Prolatilus jugularis* |
| 17. Skates | *Raja* spp. |
| 18. Copepods | |
| 19. Euphausiids | |
| 20. Phytoplankton | |
| 21. Detritus | |

For nomenclature, see the text; j: juveniles; a: adults

of the production that is either eaten by predators or exported from the system), $EX_i$ are the exports of $i$ (by emigration or yields).

The energy balance of each component of the system is given by:

$$Q = P + R + U$$

where $Q$ is prey consumption, both from inside the system and from outside (imports), $P$ is production (it must be eaten by predators, exported from the system or contributed to detritus), $R$ is respiration, and $U$ is food not assimilated by predators.

This structure defines the parameters needed to complete the model. Each component requires estimates of biomass, the $P/B$ and $Q/B$ ratios, $DC_{ij}$, $EX_i$, assimilation and $EE_i$. Nevertheless, one of the parameters ($B_i$, $P_i/B_i$, $Q_i/B_i$ or $EE_i$) can remain unknown for each group, since it can be estimated (together with respiration) from the solutions of the system of linear equations.

The information to estimate input parameters for the Ecopath model for 1992 is from Neira and Arancibia (2000, see Appendix A), while the information for 1998 was obtained as follows:

Biomass ($B_i$) is the total mass of each $i$ group per unit of area (tonnes per square kilometer). Biomass data were either estimated by the authors or obtained from official reports of the Chilean Fishery Foundation. Horse mackerel biomass was estimated from the average density reported by Córdova et al. (1999), transformed to tonnes per square kilometers for the whole study area. The biomasses of Chilean hake (juveniles), carrot prawn (juveniles), euphausiids, copepods, and phytoplankton were estimated from the model, i.e. the model was used to estimate the biomass required to ensure sufficient production to sustain the other groups in the ecosystem and the catches.

Yield ($Y_i$) is the annual landing of $i$ (t km$^{-2}$). For fishery resources, the information was obtained from the Fishing Statistics Yearbooks of the National Fishery Service (SERNAPESCA, 1999). The annual yields ($Y_i$) of groups such as big-eye flounder, skates, rattail fish, black conger and Pacific sand perch—which are part of the by-catch of the Chilean hake fishery—were estimated as the nominal landings for each $i$ group ($D_i$), as reported by SERNAPESCA (1999), plus an estimate of the biomass discarded from the Chilean hake trawling fishery ($C_i$), or

$$Y_i = D_i + C_i$$

$C_i$ was estimated as:

$$C_i = Y_{\text{Chilean hake}} \times (L_i \times L_{\text{Chilean hake}}^{-1})$$

where $Y_{\text{Chilean hake}}$ is the annual landing of Chilean hake (SERNAPESCA, 1999), $L_i$ is the yield of the $i$ species during a fishery research cruise carried out during 1997, $L_{\text{Chilean hake}}$ is the yield of Chilean hake during the same cruise. The basic assumption was that all species had the same response to the Chilean hake trawling fishing gear.

The yield of horse mackerel for the study area was estimated assuming equilibrium conditions, such that

$$F = \frac{Y}{B}$$

where $F$ is the fishing mortality coefficient, $Y$ is yield, $B$ is biomass. Since $B$ and $F$ (0.15 per year; Ruben Pinochet, UnderSecretariat for Fisheries, Chile, personal communication) are known, it is possible to estimate $Y$ from

$$Y = B \times F$$

Production $(P_i)$ is the amount of tissue accumulated by group $i$. Production is estimated as the production/biomass ratio $(P_i/B_i$; per year). Total mortality $Z_i$ was estimated for every group $i$ where $P_i/B_i$ was unknown since, according to Allen (1971), for marine populations under equilibrium,

$$Z_i = \left(\frac{P}{B}\right)_i$$

$Z_i$ values were estimated by the authors using standard stock assessment methodology.

Consumption $(Q_i)$ is the amount of food ingested by the group $i$. It is estimated from the consumption/biomass ratio $(Q_i/B_i$; per year). The $Q_i/B_i$ values reported by Neira and Arancibia (2000) were used in this paper. In the absence of other information, we used a default value of 20% for the unassimilated food $(U)$ for every group $i$.

Food composition of the predators $(DC_{ij})$ is the fraction (in weight) of every prey $j$ in the stomach content of predator $i$. $DC_{ij}$ for sea lions was estimated from the information provided by Mario George-Nascimento (personal communication, Universidad Católica de la Santísima Concepción). The values for Pacific sand perch, black conger, and big-eye flounder were estimated from samplings of the by-catch of the Chilean hake fleet operating in the study area at the beginning of 1999. It was not possible to gather field information during 1998 to estimate $DC_{ij}$ for skates, rattail fish, and cardinal fish; thus, the 1992 estimates were used (Neira and Arancibia, 2000). Prey items that were not included in the model as functional group—due to incomplete knowledge of their biomass, rates and diet matrices—were incorporated to the $DC_{ij}$ as imports.

The model was balanced by checking the values of $EE_i$ and of the gross efficiency of food conversion $(GE_i)$. Obviously, $EE_i$ must be between 0 and 1, while $GE_i$, which is equal to $P_i/Q_i$, should lie between 0.1 and 0.3 (Christensen and Pauly, 1992b). For inconsistent values of $EE_i$ or $GE_i$, we make changes in input data $B_i$, $P_i/B_i$, or $DC_{ij}$ following criteria presented in Christensen et al. (2000) until we obtained acceptable runs, i.e. EE < 1 and 0.1 < GE < 0.3 for each group $i$.

Trophic interactions, such as predation and removal by fishing, were compared using predation mortality coefficient $(M_2)$, $F$ and "other mortality" mortality coefficient $(M_0)$. The relative importance of $M_2$ compared to both natural mortality $M$ $(M_2 + M_0)$, and total mortality $Z$ $(M + F)$, was analyzed, that is, $M_2/M$ and $M_2/Z$. The relative importance of $F$ with respect to $Z$ was analyzed, also.

Direct and indirect trophic interactions were analyzed using combined trophic impact (Ulanowicz and Puccia, 1990). We used the net trophic impact to reflect both the impact of prey over their predators and the impact of predators over their prey. Trophic impacts are relative but comparable among groups (Christensen and Pauly, 1992b).

The average trophic level (TL) for every $i$ group is estimated as follows: by definition, $TL = 1$ is assigned to primary producers and detritus; for predators, TL is estimated as $1 +$ (the weighed average of the TLs of the preys in the stomach content of the predator). The TL for the fishery is:

$$TL_f = \sum_{ij} TL_i \times \left(\frac{Y_i}{Y_T}\right)$$

where $TL_f$ is the average trophic level of the fishery, $TL_i$ is the trophic level of the $i$ group, $Y_i$ is the landing of the group $i$, and $Y_T$ is the total landing of all the groups without including discards. TL is a dimensionless index (Christensen and Pauly, 1992a).

The system was compared as a whole between 1992 and 1998 using global parameters of the system, such as total biomass $(B_T)$, total yield $(C_T)$ and total throughput $(T_T)$. These indices are characteristic of the size of an ecosystem (Jarre-Teichmann, 1998).

Finally, the results of the Central Chile marine ecosystem model were compared to those in other systems, especially from similar subsystems in the most important upwelling areas of the world.

## 3. Results

Tables 2 and 3 summarize the input parameters and the results of the balanced ecotrophic model for the Central Chile marine ecosystem in 1992 and 1998. Table 4 shows the diet matrices for the predators in the system for both years. Overall, pelagic species such as horse mackerel, pilchard, and anchovy dominated the system. Chilean hake was the dominant species in the demersal environment.

Table 2
Inputs (bold) and outputs of the Central Chile marine ecosystem model, 1992

| Group name/parameter | $B_i$ (t km$^{-2}$) | $P_i/B_i$ (per year) | $Q_i/B_i$ (per year) | $Y_i$ (t km$^{-2}$ per year) | $F_i$ (per year) | $M_{0i}$ (per year) | $M_{2i}$ (per year) | EE$_i$ | GE$_i$ |
|---|---|---|---|---|---|---|---|---|---|
| 1. Sea lion | **0.030** | **1.050** | **15.000** | **0.003** | 0.120 | 0.930 | 0.000 | 0.095 | 0.070 |
| 2. Chilean hake (j) | **4.827** | **2.497** | **8.323** | **0.243** | 0.050 | 0.610 | 1.830 | 0.755 | 0.300 |
| 3. Chilean hake (a) | **4.487** | **0.541** | **5.159** | **1.188** | 0.260 | 0.130 | 0.150 | 0.764 | 0.105 |
| 4. Pilchard (j) | **4.620** | 2.537 | **15.000** | **5.019** | 1.090 | 0.130 | 1.320 | **0.950** | 0.169 |
| 5. Pilchard (a) | **6.970** | 1.771 | **12.000** | **3.933** | 0.560 | 0.090 | 1.120 | **0.950** | 0.148 |
| 6. Anchovy (j) | **3.120** | 3.625 | **15.000** | **1.160** | 0.370 | 0.180 | 3.070 | **0.950** | 0.242 |
| 7. Anchovy (a) | **5.230** | 2.171 | **12.000** | **4.942** | 0.940 | 0.110 | 1.120 | **0.950** | 0.181 |
| 8. Carrot prawn (j) | 0.665 | **5.900** | **18.000** | **0.000** | 0.000 | 0.090 | 5.810 | **0.985** | 0.328 |
| 9. Carrot prawn (a) | **0.799** | **2.520** | **12.500** | **0.080** | 0.100 | 0.910 | 1.510 | 0.638 | 0.202 |
| 10. Yellow prawn | **0.416** | **2.184** | **11.600** | **0.059** | 0.140 | 0.750 | 1.290 | 0.657 | 0.188 |
| 11. Horse mackerel | **13.790** | **0.823** | **14.200** | **6.480** | 0.470 | 0.330 | 0.020 | 0.598 | 0.058 |
| 12. Black conger | **0.212** | **0.212** | **3.000** | **0.036** | 0.170 | 0.020 | 0.020 | 0.913 | 0.071 |
| 13. Rattail fish | **0.256** | 0.278 | **4.000** | **0.064** | 0.250 | 0.080 | 0.540 | **0.900** | 0.069 |
| 14. Big-eye flounder | **0.286** | 0.304 | **3.000** | **0.073** | 0.260 | 0.120 | 0.000 | **0.850** | 0.101 |
| 15. Cardinal fish | **0.780** | 0.320 | **4.500** | **0.021** | 0.030 | 0.190 | 0.100 | 0.198 | 0.071 |
| 16. Pacific sand perch | **0.759** | 0.358 | **7.000** | **0.231** | 0.300 | 0.220 | 0.000 | **0.850** | 0.051 |
| 17. Skates | **0.436** | 0.362 | **3.500** | **0.134** | 0.310 | 0.2200 | 0.000 | **0.850** | 0.103 |
| 18. Copepods | 48.956 | **35.000** | 154.519 | – | – | 1.750 | 33.250 | **0.950** | 0.227 |
| 19. Euphausiids | 73.627 | **2.960** | **16.200** | – | – | 0.140 | 2.820 | **0.953** | 0.183 |
| 20. Phytoplankton | 112.107 | **120.000** | 0.000 | – | – | 82.940 | 37.060 | **0.500** | – |
| 21. Detritus | 100.000 | – | – | – | – | – | – | – | – |

For parameter nomenclature, see the text; j: juveniles; a: adults.

Table 3
Inputs (bold) and outputs of the Central Chile marine ecosystem model, 1998

| Group name/parameter | $B_i$ (t km$^{-2}$) | $P_i/B_i$ (per year) | $Q_i/B_i$ (per year) | $Y_i$ (t km$^{-2}$ per year) | $F_i$ (per year) | $M_{0i}$ (per year) | $M_{2i}$ (per year) | EE$_i$ | GE$_i$ |
|---|---|---|---|---|---|---|---|---|---|
| 1. Sea lion | **0.052** | **1.050** | **15.000** | **0.005** | 0.100 | 0.950 | 0.000 | 0.092 | 0.070 |
| 2. Chilean hake (j) | 2.653 | **2.497** | **8.323** | **0.196** | 0.070 | 0.120 | 2.310 | **0.950** | 0.300 |
| 3. Chilean hake (a) | **8.560** | **0.504** | **5.159** | **1.324** | 0.150 | 0.190 | 0.160 | 0.621 | 0.098 |
| 4. Pilchard (j) | **2.157** | **1.411** | **15.000** | **1.222** | 0.570 | 0.310 | 0.540 | 0.774 | 0.094 |
| 5. Pilchard (a) | **7.351** | **1.650** | **12.000** | **5.191** | 0.710 | 0.700 | 0.240 | 0.568 | 0.137 |
| 6. Anchovy (j) | **2.322** | **1.276** | **15.000** | **0.599** | 0.260 | 0.320 | 0.700 | **0.750** | 0.080 |
| 7. Anchovy (a) | **13.163** | **1.113** | **12.000** | **7.358** | 0.560 | 0.140 | 0.420 | 0.877 | 0.093 |
| 8. Carrot prawn (j) | 1.346 | **5.900** | **18.000** | **0.000** | 0.000 | 0.090 | 5.810 | **0.985** | 0.328 |
| 9. Carrot prawn (a) | **1.402** | **1.061** | **12.500** | **0.239** | 0.170 | 0.050 | 0.860 | **0.950** | 0.087 |
| 10. Yellow prawn | **0.578** | **1.314** | **11.600** | **0.096** | 0.170 | 0.070 | 1.080 | **0.950** | 0.113 |
| 11. Horse mackerel | **19.624** | **0.450** | **14.200** | 2.944 | 0.150 | 0.300 | 0.000 | 0.333 | 0.032 |
| 12. Black conger | 0.305 | **0.212** | **3.000** | **0.059** | 0.190 | 0.020 | 0.000 | **0.913** | 0.071 |
| 13. Rattail fish | **0.100** | 0.197 | **4.000** | **0.018** | 0.180 | 0.020 | 0.000 | **0.912** | 0.049 |
| 14. Big-eye flounder | **0.091** | 0.259 | **3.000** | **0.016** | 0.180 | 0.080 | 0.000 | **0.680** | 0.086 |
| 15. Cardinal fish | **0.035** | 0.333 | **4.500** | **0.007** | 0.200 | 0.130 | 0.000 | **0.600** | 0.074 |
| 16. Pacific sand perch | **1.499** | 0.146 | **7.000** | **0.128** | 0.090 | 0.060 | 0.000 | **0.584** | 0.021 |
| 17. Skates | **0.093** | 0.258 | **3.500** | **0.018** | 0.190 | 0.060 | 0.000 | **0.750** | 0.074 |
| 18. Copepods | 70.782 | **35.000** | 154.519 | – | – | 1.750 | 33.250 | **0.950** | 0.227 |
| 19. Euphausiids | 106.315 | **2.960** | **16.200** | – | – | 0.140 | 2.820 | **0.950** | 0.183 |
| 20. Phytoplankton | 160.995 | **120.000** | | – | – | 60.000 | 60.000 | **0.500** | – |
| 21. Detritus | 100.000 | – | – | – | – | – | – | – | – |

For parameter nomenclature, see the text; j: juveniles; a: adults.

**Table 4**

Diet composition of the predators assumed in ecotrophic model of the Central Chile marine ecosystem in 1992 and 1998

| Prey/predator | 1 | | 2 | | 3 | | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | | 12 | | 13 | 14 | | 15 | 16 | | 17 | 18 | 19 |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | 1992 | 1998 | 1992 | 1998 | 1992 | 1998 | 1992–1998 | 1992–1998 | 1992–1998 | 1992–1998 | 1992–1998 | 1992–1998 | 1992–1998 | 1992 | 1998 | 1992 | 1998 | 1992–1998 | 1992 | 1998 | 1992–1998 | 1992 | 1998 | 1992–1998 | 1992–1998 | 1992–1998 |
| 1. Sea lion | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 2. Chilean hake (j) | 0.246 | 0.150 | 0.08 | 0.010 | 0.215 | 0.130 | | | | | | | | 0.013 | | | | 0.065 | | | | 0.065 | | | | |
| 3. Chilean hake (a) | 0.254 | 0.400 | | | 0.014 | 0.012 | | | | | | | | | | 0.036 | 0.562 | | | | | | | | | |
| 4. Pilchard (j) | 0.065 | 0.039 | 0.13 | 0.010 | 0.035 | 0.02 | | | | | | | | | | | | | | | | | | | | |
| 5. Pilchard (a) | 0.105 | 0.132 | 0.133 | 0.028 | 0.100 | 0.022 | | | | | | | | | | | | | | | | | | | | |
| 6. Anchovy (j) | 0.035 | 0.042 | 0.215 | 0.028 | 0.039 | 0.022 | | | | | | | | | | | | | | | | | | | | |
| 7. Anchovy (a) | 0.066 | 0.237 | 0.08 | 0.056 | 0.110 | 0.042 | | | | | | | | | | | 0.124 | | | | | | 0.200 | | | |
| 8. Carrot prawn (j) | | | 0.030 | 0.041 | 0.110 | 0.150 | | | | | | | | 0.004 | | 0.243 | 0.034 | | 0.015 | 0.198 | | | | 0.002 | | |
| 9. Carrot prawn (a) | | | 0.011 | 0.015 | | 0.014 | | | | | | | | | | 0.107 | 0.107 | 0.105 | 0.310 | 0.337 | | | | 0.210 | | |
| 10. Yellow prawn | | | | | 0.021 | 0.014 | | | | | | | | | | 0.002 | 0.024 | | 0.018 | | | | | 0.023 | | |
| 11. Horse mackerel | 0.162 | | | | 0.017 | | | | | | | | | | | | | | | | | | | | | |
| 12. Black conger | 0.004 | | | | | | | | | | | | | | | | | | | | | | | | | |
| 13. Rattail fish | | | | | 0.006 | | | | | | | | | | | | | | | | | | | | | |
| 14. Big-eye flounder | | | | | | | | | | | | | | | | | | | 0.001 | | | | | | | |
| 15. Cardinal fish | 0.063 | | | | | | | | | | | | | | | | | | | | | | | | | |
| 16. Pacific sand perch | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 17. Skates | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 18. Copepods | | | | | | | 0.020 | 0.020 | 0.020 | 0.020 | | | | | 0.010 | | | | | | | | | | 0.112 | 0.650 |
| 19. Euphausiids | | | 0.197 | 0.802 | 0.055 | 0.564 | | | | | | | | 0.983 | 0.923 | | | 0.002 | 0.011 | | 0.500 | 0.679 | | | | |
| 20. Phytoplankton | | | | | | | 0.980 | 0.980 | 0.980 | 0.980 | | | | | | | | | | | | | | | 0.800 | 0.350 |
| 21. Detritus | | | | | | | | | | | 1.000 | 1.000 | 1.000 | | | | | | | | | | | | | |
| Imports | | | 0.124 | 0.010 | 0.278 | 0.010 | | | | | | | | 0.017 | 0.067 | 0.838 | 0.045 | 0.861 | 0.656 | 0.389 | 0.500 | 0.256 | 0.800 | 0.765 | 0.088 | |

Tabulated values represent the fraction of the food intake in weight; j: juveniles; a: adults. Predators 4–7 take 2% copepods and 98% phytoplankton, while predators 8–10 eat detritus only.
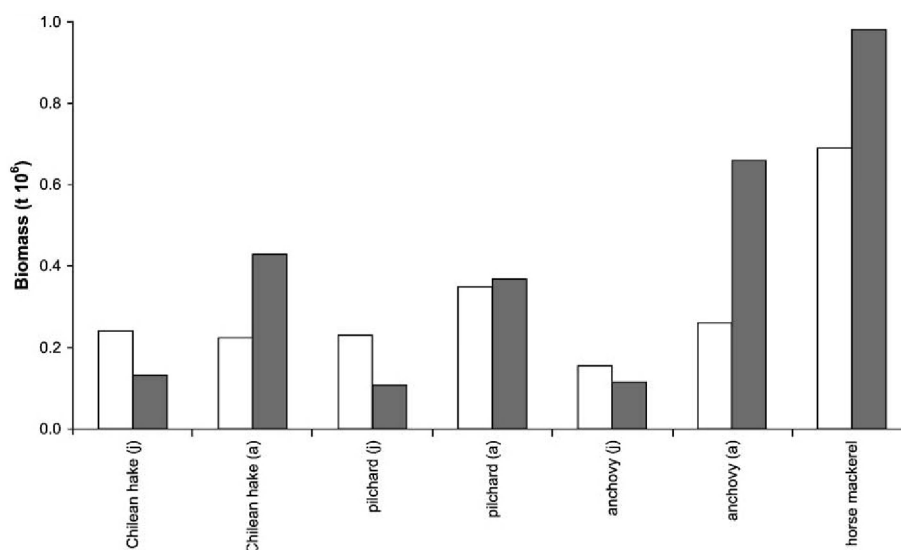
Fig. 3. Biomass of the most important fishery resources in central Chile. Biomasses in 1992 are shown in white bars, biomasses in 1998 in grey bars.

Closer examination shows changes in both biomass and yields for the main groups between 1992 and 1998 (Fig. 3). The biomass of horse mackerel, Chilean hake adults, and anchovy adults increased in 1998. The opposite was true for Chilean hake juveniles, pilchard juveniles, and anchovy juveniles. Other important differences between 1992 and 1998 were the increase in the biomass of yellow prawn, sea lions, black conger, and Pacific sand perch, and decrease in the biomass of most of the species that are part of the by-catch in the Chilean hake fishery (e.g. skates, big-eye flounder, and rattail fish).

Adult anchovy and pilchard were the most important fishery resources during 1998, with landing of 5.2 and 7.4 t km$^{-2}$ per year, respectively. Formerly, this place was occupied by horse mackerel, which had been the main fishery resource in Central Chile since late 1980s, with landings that peaked at 4.5 million tonnes in 1995 and fell to a low of 1.5 million tonnes in 1998. Although a fraction (about 0.1) of the pelagic fish catches, yields of Chilean hake adults were higher in 1998 than in 1992, and were by far the most important demersal fishery resource in Central Chile in both years.

In the Central Chile marine ecosystem model, $M_2$ was the main mortality factor for Chilean hake juveniles, carrot prawn juveniles and adults and yellow

prawn. Fishing mortality was the most important mortality factor for horse mackerel, black conger, big-eye flounder, cardinal fish, and skates (Tables 2 and 3), but it must be pointed out that these results could be due to the fact that the model did not include predators for these groups.

Table 5 summarizes the comparative analysis of the effects of fishing ($F$) and predation ($M_2$) mortality on

Table 5
Predation mortality ($M_2$) of the main fishery resources expressed as a percentage of both natural ($M$) and total mortality ($Z$), 1992 and 1998. For comparative purposes, fishing mortality ($F$) is included for each group as a percentage of $Z$, both for 1992 and 1998

| Group | 1992 | | | 1998 | | |
|---|---|---|---|---|---|---|
| | $M_2/M$ | $M_2/Z$ | $F/Z$ | $M_2/M$ | $M_2/Z$ | $F/Z$ |
| Chilean hake (j) | 75 | 73 | 2 | 95 | 93 | 3 |
| Chilean hake (a) | 54 | 28 | 48 | 46 | 32 | 30 |
| Pilchard (j) | 91 | 52 | 43 | 64 | 38 | 40 |
| Pilchard (a) | 93 | 63 | 32 | 26 | 15 | 43 |
| Anchovy (j) | 94 | 85 | 10 | 69 | 56 | 20 |
| Anchovy (a) | 91 | 52 | 43 | 49 | 24 | 50 |
| Carrot prawn (j) | 98 | 98 | 0 | 98 | 98 | 0 |
| Carrot prawn (a) | 62 | 60 | 4 | 95 | 79 | 16 |
| Yellow prawn | 63 | 59 | 6 | 94 | 82 | 13 |
| Horse mackerel | 6 | 2 | 57 | 0 | 0 | 33 |

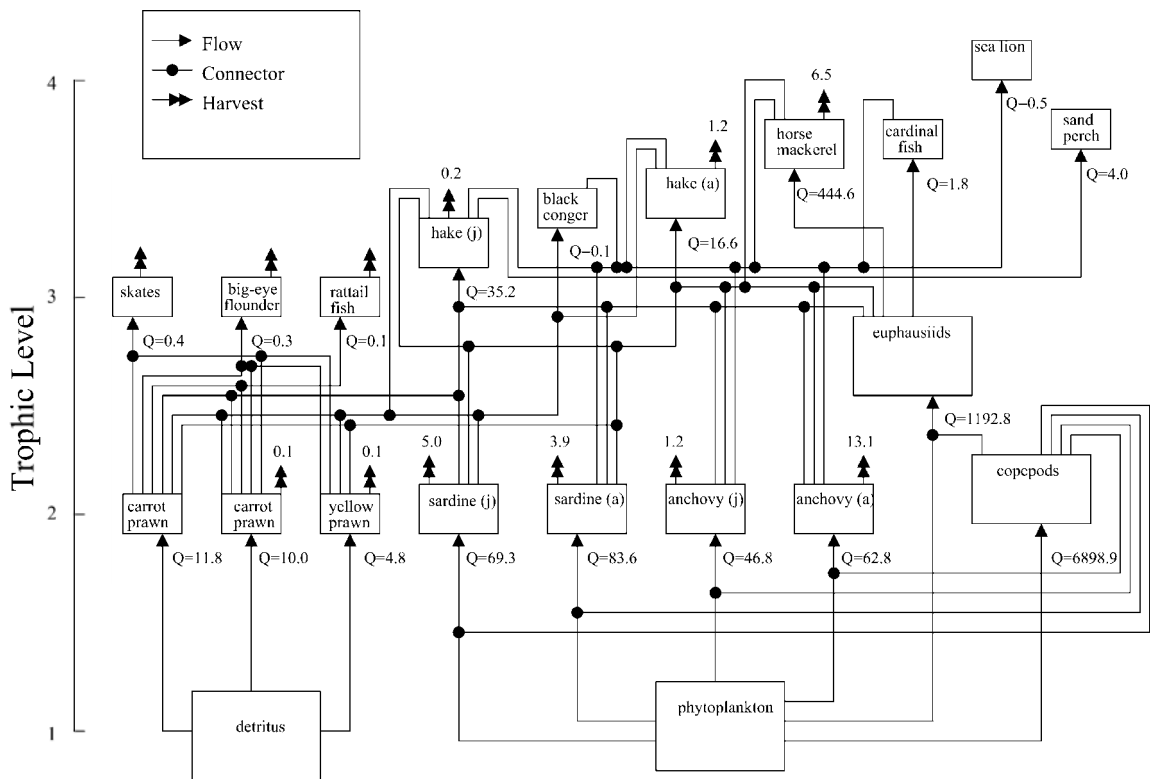For parameter nomenclature, see text; j: juveniles; a: adults.

Fig. 4. Flow diagram of the Central Chile marine ecosystem (33°–39°S), 1992. $Q$: consumption. Flows are expressed in t km$^{-2}$ per year.

the main fishery resources in 1992 and 1998. $M_2$ decreased markedly in pilchard and anchovy juveniles and adults in 1998. The opposite was observed for Chilean hake juveniles, carrot prawn adults, and yellow prawn.

The diagram that describes the main flows in the Central Chile marine ecosystem is shown in Fig. 4 for 1992. Groups are ordered according to their average TLs above the basal level (TL = 1), up to the highest trophic levels, those of carnivorous fish and sea lions.

The main input flows in the Central Chile marine ecosystem were between planktonic invertebrates (copepods and euphausiids) and primary producers, as has been reported for other upwelling ecosystems (Jarre-Teichmann, 1998). Other important flows within the pelagic environment were from euphausiids and copepods to horse mackerel, and primary producers and copepods to pilchard and anchovy (juveniles and adults). Within the demersal environment, the

main flows were from pilchard, anchovy, prawns, and euphausiids to Chilean hake (juveniles and adults).

The overall structure of the system with regard to flow pathways was similar in the two years analyzed, although there were differences in the magnitude of flows. The inputs for pilchard and anchovy juveniles in 1998 were lower by a factor of 1.5–2.0 than in 1992. For pilchard adults, flows remained almost constant, while for anchovy adults they increased by a factor of 2.5 over the two years investigated. Inputs for benthic invertebrates increased, but decreased for most of the species of the Chilean hake fishery by-catch, except for black conger and cardinal fish. Flows for Chilean hake adults increased by a factor of almost three in 1998. Inputs to horse mackerel also increased.

In both 1992 and 1998, predators took the majority of total production of the main resources (Table 6), particularly for Chilean hake, adult pilchard and anchovy juveniles. For instance, during 1998 fisheries captured the greater part of the production of pilchard

Table 6
Utilisation of the production of the main fishery resources considered in ecotrophic model of the Central Chile marine ecosystem in 1992 and 1998, including both fishery ($Y$) and predator consumption ($Q$)

| Group | 1992 | | | 1998 | | |
|---|---|---|---|---|---|---|
| | $Y$ | $Q$ | $Y/(Y + Q)$ (%) | $Y$ | $Q$ | $Y/(Y + Q)$ (%) |
| Chilean hake (j) | 0.2 | 8.7 | 2 | 0.2 | 6.7 | 3 |
| Chilean hake (a) | 1.2 | 0.5 | 71 | 1.3 | 1.3 | 50 |
| Pilchard (j) | 5.0 | 6.1 | 45 | 1.2 | 1.3 | 48 |
| Pilchard (a) | 3.9 | 7.7 | 34 | 5.2 | 1.8 | 74 |
| Anchovy (j) | 1.2 | 9.5 | 11 | 0.6 | 1.7 | 26 |
| Anchovy (a) | 4.9 | 5.9 | 45 | 7.4 | 3.6 | 67 |
| Carrot prawn (j) | – | 3.8 | – | – | 7.9 | – |
| Carrot prawn (a) | 0.1 | 1.2 | 8 | 0.2 | 1.2 | 14 |
| Yellow prawn | 0.1 | 0.4 | 20 | 0.1 | 0.6 | 14 |
| Horse mackerel | 6.5 | – | 100 | 2.9 | – | 100 |
| Total | 23.1 | 43.8 | 34 | 19.1 | 26.1 | 42 |

Catches ($Y$) are also presented as a percentage of the total flow ($Y + Q$). Flows are expressed in $t\,km^{-2}$ per year; j: juveniles; a: adults.

and anchovy adults, and during 1992 and 1998 most of the Chilean hake adults.

The $Y/(Y + Q)$ ratio was markedly higher in 1998 that in 1992 for pilchard adults, anchovy (juveniles and adults), carrot prawn adults, and Chilean hake juveniles: the increase was smallest in the hake (Table 6). The opposite was the case with Chilean hake adults and yellow prawn. For horse mackerel, the most of the production removed was taken as fishing yields, but it must be pointed out that these results could be due to the fact that the model only includes sea lion as predator for this group.

Even though total yields in the system were lower in 1998 than 1992, the $Y/(Y + Q)$ ratio was higher in 1998, because predators only used about half of the total production of the fishery resources in 1998 than they did in 1992 (Table 6).

Total biomass per trophic level was higher in 1998 than in 1992 (Table 7). The greatest changes happened at trophic levels V and VI, where they were between 2 and 3 times higher in 1998 than in 1992. This is the result of increases in sea lion and black conger biomass (Tables 2 and 3). However, the structure of the system—as biomass proportion at each trophic level with respect to total biomass—was almost constant in the two years. About 95% of the total biomass was concentrated in trophic levels I–III, and this show constancy between 1992 and 1998.

Total throughput per trophic level was higher in 1998 than 1992 (Table 8). However, the structure of the

system—as throughput proportion at each trophic level with respect to total throughput—was almost constant in the two years. About 98% of the total throughput was concentrated in trophic levels I–III, and this show constancy between 1992 and 1998.

The mixed trophic impact diagrams are shown in Fig. 5 for the 1992 model. Predators that had a negative impact on the system include juvenile and adult Chilean hake through cannibalism and predation on small pelagic fish, such as juvenile and adult pilchard and anchovy; horse mackerel through predation on euphausiids, and with indirect impact on other groups that prey on euphausiids (e.g. cardinal fish and Pacific sand perch, Table 4).

Some groups—black conger, rattail fish, big-eye flounder, cardinal fish, Pacific sand perch and skates—had slight or no impact on other groups, ei-

Table 7
Summary of total biomass per trophic level as an absolute value ($B$) and as a percentage of the total system biomass, 1992 and 1998

| Trophic level | 1992 | | 1998 | |
|---|---|---|---|---|
| | $B$ ($t\,km^{-2}$) | $B$ (%) | $B$ ($t\,km^{-2}$) | $B$ (%) |
| VI | 0.004 | 0.014 | 0.014 | 0.003 |
| V | 0.349 | 0.124 | 0.775 | 0.189 |
| IV | 12.313 | 4.360 | 19.013 | 4.641 |
| III | 61.454 | 21.761 | 85.194 | 20.793 |
| II | 96.136 | 34.043 | 139.065 | 33.942 |
| I | 112.107 | 39.698 | 165.655 | 40.432 |

Table 8
Summary of throughput per trophic level as an absolute value (T) and as a percentage of the total system throughput, 1992 and 1998

| Trophic level | 1992 | | 1998 | |
|---|---|---|---|---|
| | T (t km$^{-2}$ per year) | T (%) | T (t km$^{-2}$ per year) | T (%) |
| VI | 0.012 | $3.9 \times 10^{-5}$ | 0.055 | $1.3 \times 10^{-4}$ |
| V | 1.556 | 0.005 | 3.317 | 0.008 |
| IV | 141.160 | 0.461 | 202.852 | 0.461 |
| III | 877.484 | 2.867 | 1234.917 | 2.809 |
| II | 7447.925 | 24.324 | 10712.720 | 24.367 |
| I | 22151.600 | 72.343 | 31810.340 | 72.355 |

ther because these fish species had low biomass levels compared with the dominant groups of the ecosystem (Tables 2 and 3) or because their main prey were not part of the model but considered as imports (Table 4). These findings must be treated with caution; the biomass of these groups could be underestimated, because some of the primary data were gathered from fishing with hake trawling gear for the direct assessment of the biomass of Chilean hake (Lillo et al., 1993).
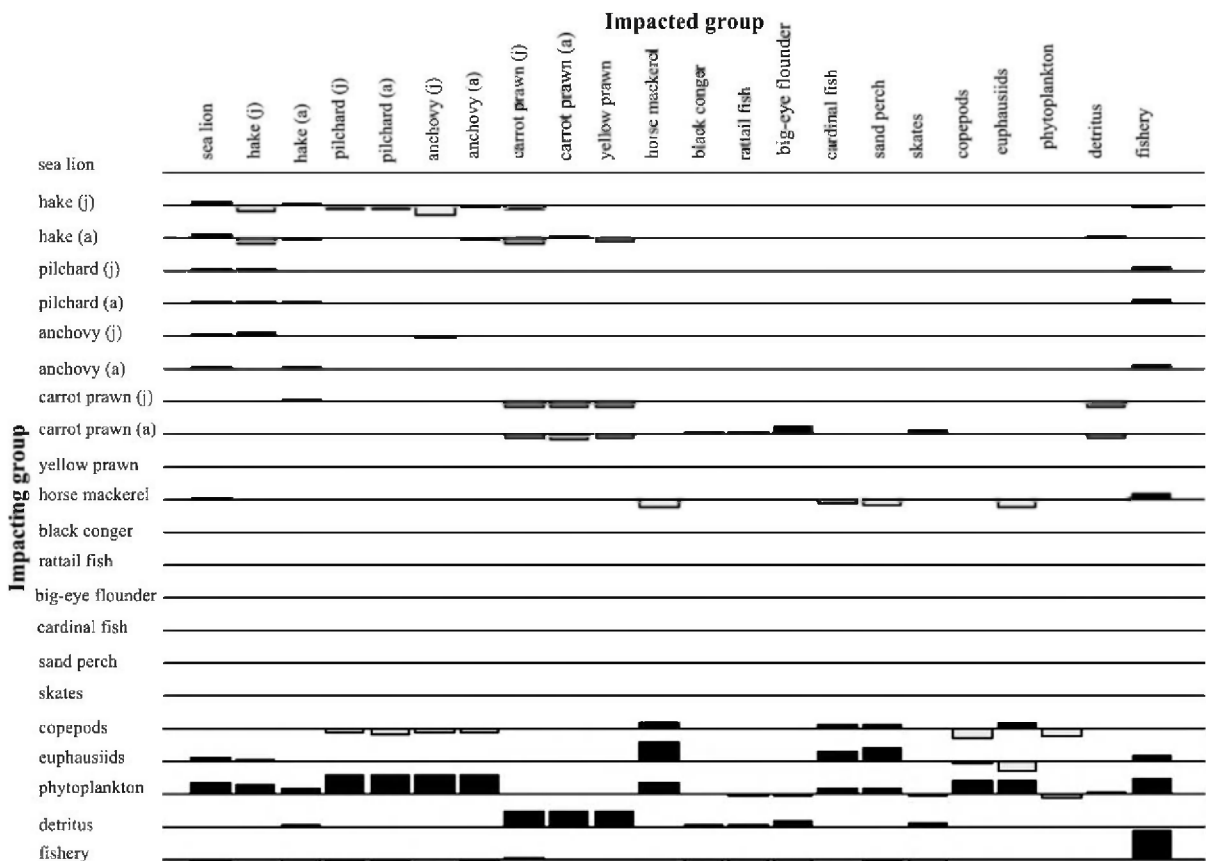


Fig. 5. Mixed trophic impact in the Central Chile marine ecosystem, 1992. The figure shows the direct and indirect impact on the living groups in the system caused by groups at the left. Positive impact is shown above the base line and negative below. The impacts are relative but comparable between groups.

The positive impact of fishing activities for groups like carrot prawn juveniles is explained by the removal through fishing of predators like Chilean hake (Tables 2–4). Nonetheless, fishing had a negative ecotrophic impact on such important fishery resources as Chilean hake (particularly adults), pilchard, anchovy, horse mackerel, and black conger, and also on species that are part of the Chilean hake fishery by-catch, like cardinal fish, Pacific sand perch, skates, and big-eye flounder.

One of the most important differences between 1992 and 1998 was the decrease in the magnitude of the impact (both positive and negative) of the juvenile groups of Chilean hake, pilchard and anchovy. This was due the decrease in biomass of these groups from 1992 to 1998. Groups whose biomass increased from 1992 to 1998, such as adult Chilean hake and adult anchovy, increased their impact. One of the most noticeable changes in trophic impacts was increase in cannibalism in Chilean hake during 1998.

The lower yields in 1998 are reflected the trophic level of the fishery ($TL_f$). The decrease in $TL_f$ from 3.607 in 1992 to 3.427 in 1998, is explained mostly by the decrease in horse mackerel yields, since it has a higher TL (3.7) than other resources, such as pilchard and anchovy (TL = 2; Figs. 2 and 3), which sustained the greatest yields in 1998 (Table 3).

## 4. Discussion

Fish and other fishery resources have trophic pathways with differing lengths for their sustenance (Fig. 4) and, like all groups in the ecosystem, have more than one predator and more than one kind of prey (Wyatt, 1976). This is an important point, since both competition and predation have been reported as biological interactions that can potentially decrease the biomass of species of economic importance (Lalli and Parsons, 1993; Sinclair et al., 1997). For instance, Chilean hake, horse mackerel, cardinal fish, and Pacific sand perch all share euphausiids as major prey, while the latter share copepods as prey with small pelagic fish (pilchard and anchovy). Consequently, only a fraction of every prey group—and ultimately of primary production—is available to be consumed by commercially exploited stocks. These interactions, and the energy lost towards the higher

levels of the trophic web, can be seen in Table 8 and Fig. 4.

Our results give a holistic, but incomplete, view of the system due to the model emphasizes only the relationships among economically important groups of fish and other species, and their most important prey groups. The most important effect of not including more predators in the model is that both mortality and biomass removal by predation could be strongly underestimated for most groups. Nevertheless, the results show that predation was an important cause of natural mortality in the ecosystem in both 1992 and 1998, with its greatest impact on recruits and prerecruits groups, i.e. Chilean hake juveniles (age groups 0–3), pilchard juveniles (age group 0), anchovy juveniles (age group 0), and carrot prawn juveniles (age group 0). Predators used the majority of the production of fishery resources, particularly in recruit and prerecruit groups of Chilean hake, pilchard, anchovy, and carrot prawn. Regarding Chilean hake, cannibalism was important in 1992 and 1998 (Table 4). This result is in agreement with previous reports showing that Chilean hake is a highly cannibal species (Arancibia, 1989), even in the long-term (Arancibia and Fuentealba, 1993).

The fisheries remove a large fraction of the production of adult Chilean hake (age group 4+), pilchard (1+), and anchovy (1+). These results are in agreement with previous reports showing that predation is the main biological interaction mechanism in marine ecosystems, particularly in early stages of the life cycle of organisms, such as eggs, larvae, and juveniles (Bax, 1991, 1998). Also, that more biomass is removed by predation than by fishing has been recognized for four subsystems in the most important upwelling ecosystems of the world (Jarre et al., 1991; Jarre-Teichmann, 1998), as well as for other highly exploited systems, such as the North Sea (Bax, 1991).

The fisheries also have indirect effects on the trophic web. The analysis of mixed trophic impacts (Fig. 5), shows that most of the fishery resource species are important trophic components in the system, with strong impacts on the other components as predators, prey, or competitors. Thus, changes in management measures for fishery resources can affect the whole trophic web. For instance, pilchard and anchovy have important roles in the ecosystem as prey, and some of their predators, like Chilean hake, are also important fishery

resources (Tables 4 and 5). There is evidence that catching species in the lower levels of trophic webs has caused alterations in the structure of ecosystems, compromising the sustainability of fisheries both of small pelagic fish and of their predators (Pauly et al., 1998).

Changes in total biomass and catches in the Central Chile marine ecosystem between 1992 and 1998 could be an expression of the changing state of the system,

reflected in properties like total flows, consumption, respiration, and production.

One of the most remarkable changes in the system was the major differences in biomass and catches of horse mackerel between 1992 and 1998. Biomass of horse mackerel in 1998 was higher than in 1992, whereas catches declined dramatically from 1992 to 1998 (Fig. 1a). This situation is explained by the entrance of one or two strong year classes, and con-
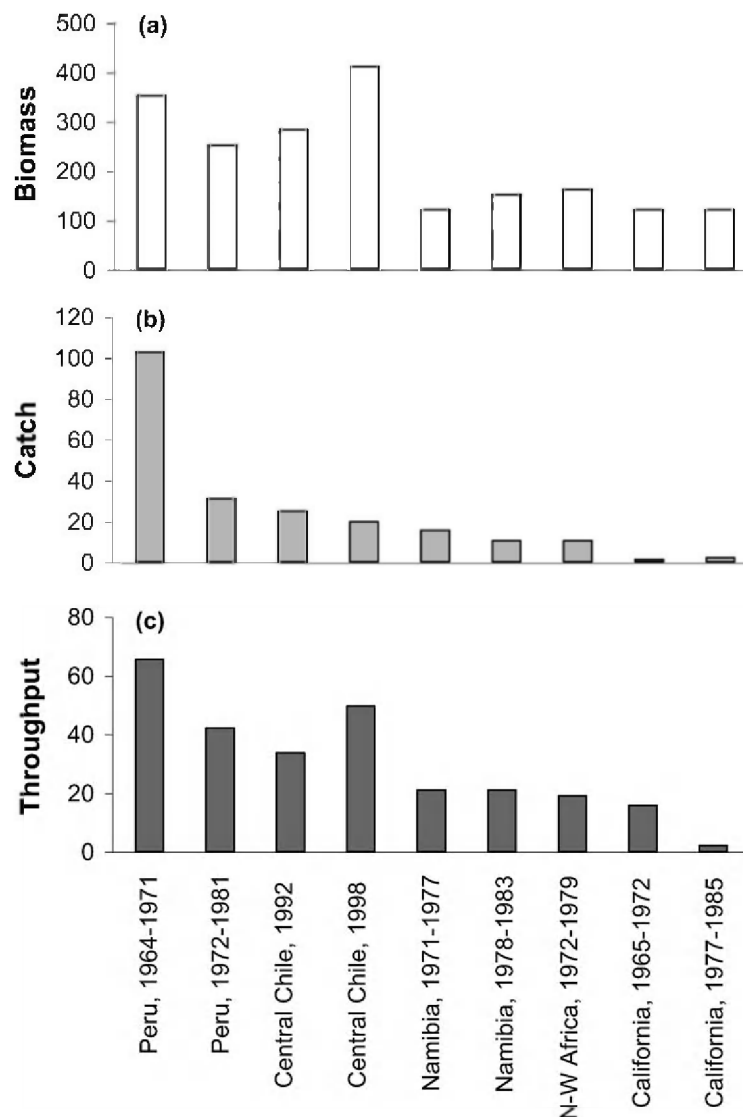


Fig. 6. Summary of total biomass, catch and throughput in the Central Chile marine ecosystem, 1992 and 1998, and those of four comparable ecosystems (Jarre-Teichmann, 1998). (a) Biomass; (b) catch, $Y$; (c) total throughput. Throughput is expressed in $10^3$ t km$^{-2}$ per year, catches in t km$^{-2}$ per year and biomass in t km$^{-2}$.

secutive fishing bans implemented by the Chilean fishery managers in order to protect the high proportion of juveniles captured in the Central Chile fishing grounds (Cubillos et al., 1999; Arcos et al., 2001). Nevertheless, the distribution of biomass and throughput across trophic levels was almost constant in 1992 compared to 1998. The above result may suggest that trophic structure of the system did not differ dramatically in 1992 and 1998.

Changes in the size composition of marine populations can vary due to exploitation/production rates and recruitment fluctuations. As a result, the inter-dependent ratios $P/B$ and $Q/B$ vary. Taking this into account, the $Q_i/B_i$ ratios for 1992 and 1998 may not be the same as we have assumed in this study, since both production and consumption rates are size dependent (Allen, 1971), so that $Q/B$ could be either under- or overestimated for some groups. In the case of horse mackerel, the ratio could be underestimated, because the unusual presence of juveniles in the study area. Thus, the changes in trophic flows between 1992 and 1998 could be even higher than suggested from results of this study.

A comparison of the results of ecotrophic modelling of the Central Chile marine ecosystem and those from similar subsystems in the most important upwelling areas of the world—Peru, Namibia, the Canary Current, and California (Jarre et al., 1991; Jarre-Teichmann, 1998; Fig. 6)—shows that the Central Chile system is one of the most important upwelling ecosystems in terms of biomass, yields and total flows. The year 1998 stands out because of the high biomass in the system, higher even than that reported for the Peru system before the breakdown of the Peruvian anchovy fishery (Jarre-Teichmann, 1998; Fig. 6). A possible explanation is that the biomass of phytoplankton, copepods, and euphausiids,

calculated from the Ecopath model, may have been overestimated. Although $P/B$ ratios used in this study as input for zooplankton and phytoplankton are in accordance with those informed for the same groups in comparable ecosystems (e.g. Jarre et al., 1989; Jarre-Teichmann et al., 1998), accurate information on plankton biomass and productivity is still lacking for Central Chile. Nevertheless, recent measurements indicate that annual and daily primary productivity levels off Central Chile are among the highest values reported for the open ocean (Daneri et al., 2000).

We conclude that ecotrophic modelling is an useful tool for fishery management, since it can improve our understanding of the predator–prey interactions among the exploited (fishery resources) and unexploited but potential fishery resources of the system. Therefore, research efforts are required to understand predator–prey relationships, particularly those involving fishery resources in Central Chile, then assuring the future exploitation of various species and the ecosystem biodiversity and integrity.

## Appendix A

Sources for inputs in the Central Chile marine ecosystem model, 1992

| Group name/parameter | $B_i$ (t km$^{-2}$) | $P_i/B_i$ (per year) | $Q_i/B_i$ (per year) | $Y_i$ (t km$^{-2}$ per year) | DC | $EE_i$ |
|---|---|---|---|---|---|---|
| 1. Sea lion | GE | GE based on Jarre-Teichmann et al. (1998) | GE | GE | GC | EO |
| 2. Chilean hake (j) | SA | SA | Arancibia et al. (1998) | GE | GC | EO |
| 3. Chilean hake (a) | SA | SA | Arancibia et al. (1998) | OR | GC | EO |

## Appendix A (*Continued*)

| Group name/parameter | $B_i$ (t km$^{-2}$) | $P_i/B_i$ (per year) | $Q_i/B_i$ (per year) | $Y_i$ (t km$^{-2}$ per year) | DC | EE$_i$ |
|---|---|---|---|---|---|---|
| 4. Pilchard (j) | SA | EO | GE based on Jarre et al. (1989) | OR | Arrizaga et al. (1993) | GE based on Jarre et al. (1989) |
| 5. Pilchard (a) | SA | EO | GE based on Jarre et al. (1989) | OR | Arrizaga et al. (1993) | GE based on Jarre et al. (1989) |
| 6. Anchovy (j) | SA | EO | GE based on Jarre et al. (1989) | OR | Arrizaga et al. (1993) | GE based on Jarre et al. (1989) |
| 7. Anchovy (a) | SA | EO | GE based on Jarre et al. (1989) | OR | Arrizaga et al. (1993) | GE based on Jarre et al. (1989) |
| 8. Carrot prawn (j) | EO | GE | GE based on Wolff (1994) | – | – | EO |
| 9. Carrot prawn (a) | SA | SA | GE based on Wolff (1994) | OR | – | EO |
| 10. Yellow prawn | SA | SA | GE based on Wolff (1994) | OR | – | EO |
| 11. Horse mackerel | SA | SA | Jarre et al. (1989) | OR | GC | EO |
| 12. Black conger | GE | GE | GE | GE | GC | GE |
| 13. Rattail fish | GE | GE | GE | GE | GC | GE |
| 14. Big-eye flounder | GE | GE | GE | GE | GC | EO |
| 15. Cardinal fish | GE | GE | GE | GE | GC | GE |
| 16. Pacific sand perch | GE | GE | GE | GE | GC | GE |
| 17. Skates | GE | GE | GE | GE | GC | GE |
| 18. Copepods | EO | GE based on Jarre et al. (1991) | GE based on Jarre et al. (1989) | – | Jarre et al. (1989) | GE based on Jarre et al. (1989) |
| 19. Euphausiids | EO | GE | GE | – | Hutchings et al. (1991) | GE based on Jarre et al. (1989) |
| 20. Phytoplankton | EO | GE | – | – | – | – |
| 21. Detritus | EO | | – | – | – | – |

Nomenclature: j: juveniles; a: adults; SA: stock assessment; GE: guess estimate; OR: official report from the National Fishery Service; GC: gut content; EO: Ecopath output.

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