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Research Article

Trophic interactions in northern Chile upwelling ecosystem, year 1997

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ABSTRACT. A food web model is constructed to describe predator-prey interactions, community structure and trophic flows in northern Chile upwelling ecosystem (18°20'S, 24°S), for the year 1997. The model is built using the Ecopath with Ecosim software version 6.4, and encompasses 21 functional groups, ranging from primary producers (phytoplankton) to top predators (birds and marine mammals), the principal fishing resources and the fishery. Input parameters required to build the model were gathered from specialized literature, grey literature and our own estimates. The results indicated that the total biomass (B_T) was estimated at 624.7 ton km^{-2}. The combined biomass of small pelagic fish represented 26% of B_T, while the combined biomass of demersal fish represented only 0.1% of B_T. These results highlight the importance of pelagic fish in this system. Predation mortality resulted to be the main source of mortality. Nevertheless, fishing mortality was important in anchovy, mackerel, common dolphinfish and jack mackerel. The mean trophic level of the fishery was estimated as 3.7, with landings sustained mainly by anchovy. Primary production required to sustain the landings (PPR) was estimated at 7.5% of calculated total net primary production, which is lower than PPR estimates in other upwelling ecosystems. The average trophic transfer efficiency was 18%, which is in the range (10-20%) informed for marine ecosystems. Results indicate that in 1997 the northern Chile marine ecosystem was characterized for being a system far from maturity, dominated in terms of biomass and flows by the pelagic realm.

Keywords: upwelling, trophic level, trophic interaction, Ecopath, Ecosim, northern Chile.

Interacciones tróficas en el ecosistema de surgencia del norte de Chile, año 1997

RESUMEN. Se construye un modelo de trama trófica para describir las interacciones predador-presa, estructura comunitaria y flujos tróficos en el ecosistema de surgencia del norte de Chile (18º20'S, 24ºS), en el año 1997. El modelo se construye utilizando el programa computacional Ecopath con Ecosim versión 6.4, y considera 21 grupos funcionales que abarcan desde productores primarios (fitoplancton) hasta predadores tope (aves y mamíferos marinos), incluyendo los principales recursos pesqueros y la pesquería. Los parámetros de entrada requeridos para implementar el modelo fueron obtenidos de literatura especializada, literatura gris y estimaciones propias. Los resultados indican que la biomasa total del sistema (B_T) se estimó en 624.7 ton km^{-2}. La biomasa combinada de pelágicos pequeños representó 26% de B_T, mientras que la biomasa combinada de peces demersales representó sólo 0,1% of B_t. Estos resultados realzan la importancia de los peces pelágicos en este sistema. La mortalidad por depredación resultó ser la principal fuente de mortalidad en el sistema. Sin embargo, la mortalidad por pesca fue importante en anchoveta, caballa, palometa o dorado de altura y jurel. El nivel trófico promedio de la pesquería fue estimado en 3.7, con desembarques sustentados principalmente por anchoveta. La producción primaria requerida para sustentar los desembarques (PPR) se estimó en 7,5% de la producción primaria neta calculada, que es inferior a estimados de PPR en otros sistemas de surgencia. La eficiencia promedio de transferencia de energía fue 18%, que se encuentra en el rango (10-20%) informado para ecosistemas marinos. Los resultados indican que en 1997, el ecosistema marino del norte de Chile se encontraba en condición alejada de la madurez, dominado en términos de biomasa y flujos por el ambiente pelágico.

Palabras clave: surgencia, nivel trófico, interaccion trófica, Ecopath, Ecosim, norte de Chile.

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INTRODUCTION

In the last three decades scientists and managers have been recognizing the need for incorporating wider ecosystem considerations into fisheries management (FAO, 2003; Parsons 2005; Constable 2011). The necessity of an ecosystem approach to fisheries (EAF) results from i) the increasing knowledge on stock dynamics and their relationships with their physical and biological environment (Pauly *et al.*, 1998; Neira & Arancibia, 2002; Shannon & Cury, 2003), and ii) the pervasive negative impacts of fishing on target species and their ecosystems (Pauly *et al.*, 2000; Shannon & Cury, 2003; Heymans *et al*., 2004).

Multispecies, community and ecosystem models are expected to complement the traditional fisheries management based only on single-species models, and then increasing societal capacity to attain sustainable fisheries (Bostford *et al*., 1997). Several modelling platforms have been developed and applied to marine ecosystems with the aim of better understanding their structure and function, and to support EAF (Plaganyi, 2007). Among them, the Ecopath with Ecosim approach (EwE) is a useful family of models that allow the analysis of trophic interactions in aquatic systems (Polovina, 1984; Christensen & Pauly, 1992; Walters *et al*., 1997; Christensen & Walters, 2000). EwE is useful and practical for summarizing information about the main components in a system and their trophic relationships, allowing descriptions and comparisons among ecosystems (Christensen & Pauly, 1993; Jarre-Teichmann & Christensen, 1998; Jarre-Teichmann *et al*., 1998; Shannon & Jarre-Teichmann 1999; Neira, 2003; Neira & Arancibia, 2004; Arancibia *et al*., 2010).

The upwelling ecosystem off northern Chile (UENCh) sustains an important purse-seine fishery targeting anchovy (*Engraulis ringens*), sardine (*Sardinops sagax*), mackerel (*Scomber japonicus*) and jack mackerel (*Trachurus murphyi*). However, in the 90's decade, landings of these pelagic species exhibited a sustained declining trend (Fig. 1). This situation has strongly impacted the local economy in northern Chile, with a series of fusions (first) and closing (more recently) of several fishing companies, which resulted in a noticeable contraction of the fleet (Aliaga *et al.,* 2001; Cañón, 2004).

Fluctuations of fish populations can be explained by several factors such as fishing pressure, trophic interactions and environmental variability such as intensity of the upwelling front and temperature change produced by El Niño Southern Oscillation (ENSO) events, among others (Serra, 1986; Bernal, 1990; Yáñez *et al*., 2001; Blanco *et al*., 2002). The inter-annual variability in the oceanographic and atmospheric conditions in the UENCh are determined by large-scale events such ENSO (Montecinos *et al*., 2003), which presents a warm phase (known as El Niño) and a cold phase (known as La Niña). In the Chilean coast, the warm phase of ENSO is determined mostly by ocean-atmosphere processes, allowing the transport of equatorial waters towards the south (Thomas *et al*., 2001; Ulloa *et al*., 2001). However, fisheries studies carried out in northern Chile do not normally assess ecological interactions among populations or the effects of the physical environment on the dynamics of target species. On the other hand, it is necessary to advance our understanding on the trophic relationships of target species, the community structure in which they inhabit, and the potential effects of the fishery on target species in this system.

Medina *et al.* (2007) modelled the pelagic food web in the upwelling ecosystem of northern Chile (18º20'-24º00'S), to describe trophic interactions and energy flows among 13 functional groups during 1989, a period of rather normal oceanographic conditions (*i.e.*, non ENSO). In this paper we built a model representing the same food web in year 1997, which is a period characterized by the presence of ENSO (McPhaden, 1999; Escribano *et al*., 2004). The aim of this paper is to describe prey-predator relationships, community structure and trophic flows in the UENCh in 1997 and compare these system features with those in year 1989 informed by Medina *et al.* (2007).

MATERIALS AND METHODS

Study area and study period

The study area corresponds to the upwelling ecosystem in northern Chile (UENCh) that extends from 18º20'S to 24º00'S, and from the coastline to 60 nm westward, encompassing a total surface area of 65,000 km^2 (Fig. 2). This area has been delimited considering the distribution of the fishing fleets (Serra, 1986), and the influence of the coastal upwelling (Thiel *et al*., 2007). The oceanography of the study area is influenced by the Humboldt Current System, which is characterized by high biological and fish production (Carr, 2002). This is also the main fishing area for the industrial and artisanal purse-seine fleets targeting pelagic fish such anchovy, mackerel, jack mackerel and sardine (Castillo *et al*., 1997, 1999; Braun *et al*., 1999). In year 2011, the UENCh provided about 31% of total fish landings in Chile (www.sernapesca.cl).

The main oceanographic features in the study area are low turbulence, a quasi permanent positive anomaly of the sea surface temperature with a narrow coastal band of cold water (Bernal, 1990; Cubillos *et al*., 1998),

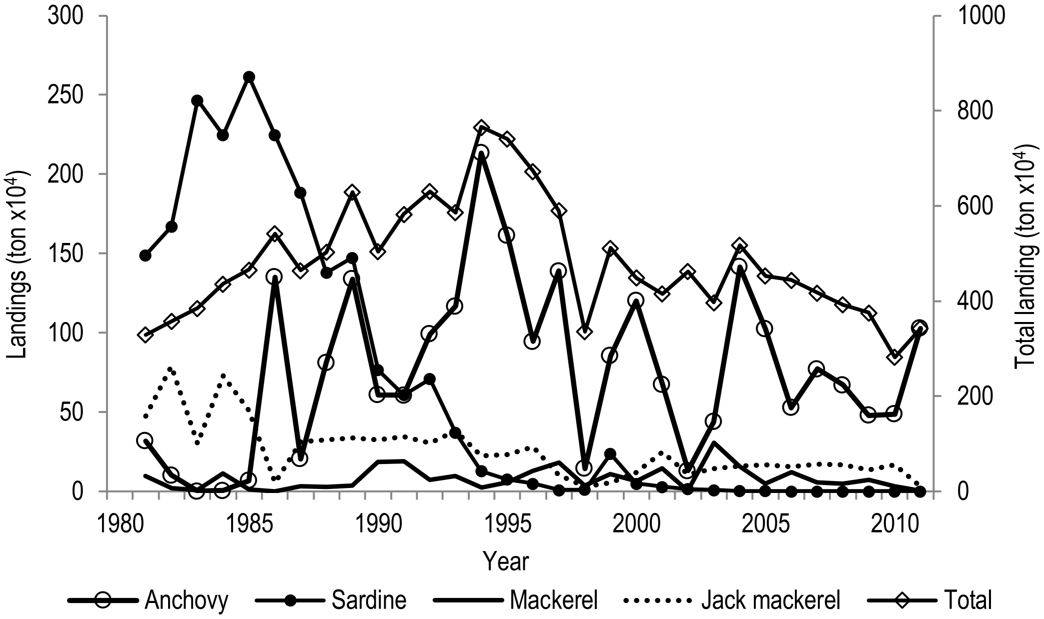

Figure 1. Landings of the main pelagic resources in the upwelling system of northern Chile (18º20'-24º00'S). First axis: total north Chile landings for anchovy, sardine, mackerel and jack mackerel. Secondary axis: total landings Chile.

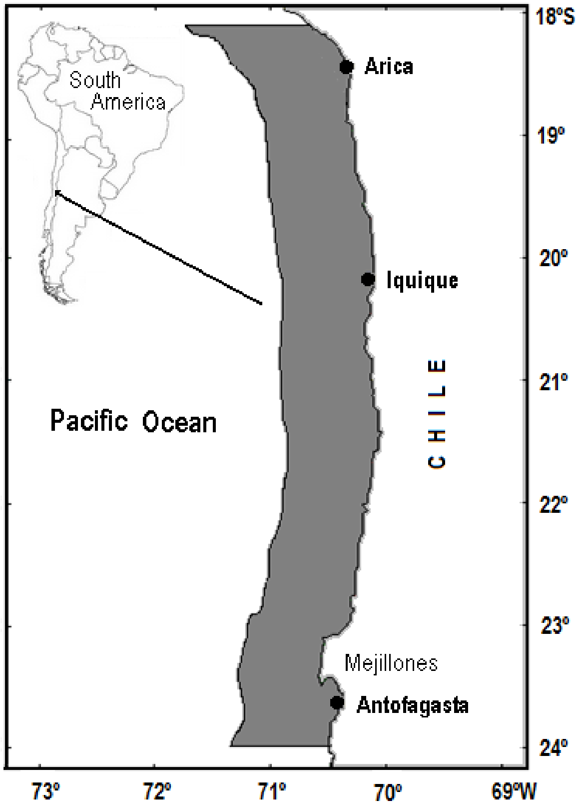

Figure 2. Study area corresponding to the upwelling system of northern Chile from 18º20'S to 24º00'S, and from the coastline up to 60 nm towards the west.

low frequency events (ENSO) with inter-annual periodicity (Fuenzalida, 1992), while high frequency events (*e.g.*, upwelling) are permanent throughout the year (Fuenzalida, 1990, Shaffer *et al.*, 1999; Blanco *et al.*, 2001).

In this paper we selected the year 1997 to build the food web model because of the presence of a strong ENSO conditions in the whole area. However, considering that the snapshot model corresponds to one year, we assume steady-state conditions and mass-balance for all functional groups (*sensu* Christensen & Pauly, 1993).

Describing the food web model for northern Chile

EwE is an ecotrophic model that incorporates interactions among functional groups in an ecosystem. It is based in two main equations focusing on (1) the usage of the production, and (2) the mass-balance of each group included in the model.

The production of each group *i* can be split in the following components:

Production = catches + predation mortality + biomass accumulation + net migration + other mortalities

The mathematical equation is:

$$P_i = Y_i + B_i M2_i + E_i + BA_i + B_i(1 - EE_i) \quad (1)$$

where: P_i is total production rate for group *i*; Y_i is total catch for *i*; *Bi* is total biomass of *i*; *M2*$_i$ is predation mortality of for *i*; *Ei* is the net migration rate for *i* (emigration minus immigration); BA_i is the biomass accumulation for *i*; $Pi\ (1\text{-}EE_i) = BM0i$ is other mortalities for *i*, those independent from predation and catches. Equation (1) can be re-expressed as:

$$B_i\left(\frac{P}{B}\right)_i - \sum_{j=1}^{n} B_j\left(\frac{Q}{B}\right)_i DC_{ij} - \left(\frac{P}{B}\right)_i B_i\left(1 - EE_i\right) - Y_i - E_i - BA_i = 0 \qquad (1a)$$

where *(P/B)i* is the production to biomass ratio equal to total mortality (*Z*) under steady-state conditions (*sensu* Allen, 1971); $(Q/B)_i$ is consumption to biomass ratio; DC_{ji} is the fraction (in weight) of the prey *i* in the diet of the predator *j*; EE_i is the ecotrophic efficiency of *i* that corresponds to the fraction of the production of group *i* that is utilized within the system as predation and/or catches; E_i corresponds to the exports of *i* (either as emigration or catches).

The mass-balance for each group is given by:

$$Q = P + R + U \qquad (2)$$

where *Q* is prey consumption, *P* is production, *R* is respiration, *U* is unassimilated food. This equation defines the consumption as the sum of gonadal and somatic growth, metabolic costs and excretion products.

Building the food web model

The model considers 21 functional groups from primary producers to top predators. The model is focused on target species and their main prey and predators. The groups are: phytoplankton, microzooplankton, mesozooplankton (copepods), macrozooplankton (euphausiids), gelatinous zooplankton (siphonphores and salps), mackerel (*Scomber japonicus*), sardine (*Sardinops sagax*), anchovy (*Engraulis ringens*), mesopelagic fish (Myctophidae), jack mackerel (*Trachurus murphyi*), demersal fish (black cusk-eel *Genypterus maculatus* and *Genypterus chilensis* red cusk-eel (check www.fishbase.org); southern grut *Cilus gilberti* and rock seabass *Paralabrax humeralis*), jumbo squid (*Dosidicus gigas*), palm ruff (*Seriolella violacea*), Eastern Pacific bonito (*Sarda chilensis*), common dolphinfish (*Coryphaena hippurus*), swordfish (*Xiphias gladius*), pelagic sharks (short fin mako *Isurus oxirynchus* and blue shark *Prionace glauca*), sea lions (*Otaria flavescens*), cetaceans (small cetaceans and dolphins), marine birds (guanay cormorants *Leucocarbo bougainvilli*, Peruvian booby *Sula variegata* and pelicans *Pelecanus thagus*), and detritus.

The model was built using available information on landings, life history parameters and biomass assessments for each functional group in the ecosystem model. The information was obtained from published literature, reports and thesis. We estimate some parameters using empirical equations that integrate information reported for the study area. Table 1 presents the corresponding source and estimation method for input parameters in each functional group.

When parameters were unknown, they were calculated by solving equations 1 and 2 under the assumption that $EE_i = 0.999$. The above implies that EwE calculates the unknown parameter (*e.g.*, Bi, P/Bi, Q/Bi) for each *i* assuming that M0 for that group is 0.001.

The mass-balance assumption for each group was verified considering: i) that $0 < EE_i < 1$; and that ii) the gross food conversion ($GE_i = P_i/Q_i$) was 0.1<GE<0.35 (Christensen & Pauly, 1992). When either EE or GE was beyond the accepted range, we performed changes in inputs parameters (B, P/B, Q/B and DC) following criteria proposed by Christensen *et al.* (2005).

Network analysis routines proposed by Ulanowicz (1986, 1995) and Ulanowicz & Kay (1991) included in EwE were run to calculate ecological indicators and flow indices based on theoretical concepts developed by Odum (1969) and Ulanowicz (1986). With these routines we calculated and compared the distribution of biomass and flows by aggregated trophic level and the trophic transfer efficiency between trophic levels. We quantified and compared the total system flow (F_T), the Finn's cycling index (*FCI*), which corresponds to the fraction of F_T used for cycling (Finn, 1976 *fide* Christensen & Pauly, 1992), and the connectance index (*CI*), which is the ratio between the actual trophic unions in the model and the maximum theoretical number that could be realized. The mixed trophic impact routine (*MTI*) included in EwE was used to quantify direct and indirect interactions among functional groups (*ITC*), including the fishery (Ulanowicz & Puccia, 1990).

Results of this model were compared with results obtained by Medina *et al.* (2007) that represent a different state of the same system, *i.e.*, a sardine dominated non-ENSO period (Medina *et al.*, 2007) *versus* an anchovy dominated ENSO period (this study).

RESULTS

Table 2 shows input parameters and those estimated using EwE for each functional group in the balanced model for the UENCh in year 1997 and the Table 3 shows the diet composition (in weight) for predators in the same model.

In general terms, total biomass (B_T) (*i.e.*, system biomass excluding detritus) sustained by the UENCh was estimated at 624.7 ton km^{-2}. Overall, pelagic species such as mackerel (11.01 ton km^{-2}), jack mackerel

Table 1. Functional groups included in the model representing the upwelling system of northern Chile, year 1997, and the source of input parameters. B: biomass, P/B: production to biomass ratio, Q/B: consumption to biomass ratio, Y: total catch, EE: ecotrophic efficiency = 0.999, DC: fraction (in weight) of the prey in the diet of the predator, assuming that the functional group is highly predated and/or exploited by the fishery.

Parameter / Group name	B ton km^{-2}	P/B yr^{-1}	Q/B yr^{-1}	Y ton km^{-2}	EE	DC
Phytoplankton	a	Daneri *et al.* (2002)			González *et al.* (1998)	
Microzooplankton	a	Moloney *et al.* (2002)	Neira & Arancibia (2004)		0.999	González *et al.* (1998)
Mesozooplankton	a	Escribano *et al.* (1999)	Vargas & González (2004)		0.999	González *et al.* (1998), Moloney *et al.* (2002)
Macrozooplankton	a	Moloney *et al.* (2002)	Vargas & González (2004)		0.999	González *et al.* (1998), Moloney *et al.* (2002)
Gelatinous zooplankton	Vargas & González (2004)	Moloney *et al.* (2002)	Vargas & González (2004)			González *et al.* (1998)
Mackerel	Braun *et al.* (2000)	Ganoza *et al.* (2002)	e	f		Medina & Arancibia (1992), Vargas & González (2004)
Sardine	Braun *et al.* (2000)	c: Ganoza *et al.* (2002)	e	f		Espinoza *et al.* (1998), Espinoza & Bertrand (2006)
Anchovy	Braun *et al.* (2000)	Ganoza *et al.* (2002)	e	f		Alamo (1997), Alamo & Espinoza *et al.* (1998), Espinoza & Bertrand (2006)
Mesopelagic fish	a	Moloney *et al.* (2002)	e		0.999	Palma (1993)
Jack mackerel	Braun *et al.* (1999)	Ganoza *et al.* (2002)	Robotham *et al.* (1995)	f		Medina & Arancibia (1992, 1995)
Demersal fish	a	Oyarzún *et al.* (1999); Slanzi (2003); Tascheri *et al.* (2003)	e: Oyarzún *et al.* (1999); Slanzi (2003); Tascheri (2003)		0.999	Medina *et al.* (2004), Oyarzún *et al.* (1999), Pizarro & Medina (2006)
Jumbo squid		Moloney *et al.* (2002)	Arancibia *et al.* (2007)	f		Arancibia *et al.* (2007), Clarke & Paliza (2000)
Palm ruff	b: Ganoza *et al.* (2002); f	c: Wolff & Aron (1992)	e	f		Ganoza *et al.* (2002)
Eastern Pacific bonito	a	c: Núñez (1993)	e	f	0.999	Blaskovic *et al.* (2002a, 2002b, 2002c)
Common dolphinfish	a	Olson & Watters (2003)	Olson & Galván-Magaña (2002)	f		Olson & Galván-Magaña (2002)
Swordfish	Bernal (1990)	Olson & Watters (2003)	e			Daza (2002)
Pelagic sharks	b: Arancibia *et al.* (2002); SERNAPESCA	Arancibia *et al.* (2002)	e	f		Olson & Watters (2003)
Sea lions	Sielfeld *et al.* (1997)	Moloney *et al.* (2002)	Moloney *et al.* (2002)	f		Sielfeld *et al.* (1997)
Cetaceans	Moloney *et al.* (2002)	Moloney *et al.* (2002)	Moloney *et al.* (2002)			Olson & Watters (2003)
Marine birds	Moloney *et al.* (2002)	Moloney *et al.* (2002)	Moloney *et al.* (2002)			Goya & Garcia-Godos (1999)

The reference indicates the origin of information, in bold indicate the values of the parameters.

Key: a) Estimated by Ecopath, b) Estimated using the equation B = Y/F (Baranov, 1918), where F = obtained from literature, Y = Fisheries Statistics National Fisheries Service (SERNAPESCA), c) Estimated using the equation Z = F+M (Beverton & Holt, 1957), d) Estimated using the empirical equation of Hoening (1983): Ln(Z) = 1.44-0.982*ln(Tmax); Tmáx (maximum age), e) Estimated using the empirical equation of Palomares & Pauly (1998): $\log Q/B = 7.964 - 0.204 \log W_{inf} - 1.965T' + 0.083Ar + 0.532h + 0.398d$, f) SERNAPESCA.

Table 2. Input parameters and outputs (bold) of the balanced model representing the food web in the upwelling system of northern Chile in 1997. TL: trophic level, B: biomass, P/B: production to biomass ratio, Q/B: consumption to biomass ratio, F: fishing mortality, Y: catches, EE: ecotrophic efficiency and GE: gross efficiency.

Group name	TL	*B*	*P/B*	*Q/B*	*F*	*Y*	*EE*	*GE*
		(ton km^{-2})	(yr^{-1})	(yr^{-1})	(yr^{-1})	(ton km^{-2})		
1. Phytoplankton	**1**	**319.68**	120.00		-	-	0.70	-
2. Microzooplankton	**2.21**	**17.48**	482.00	1928.00	-	-	1.00	**0.25**
3. Mesozooplankton	**2.48**	**47.02**	45.00	128.57	-	-	1.00	**0.35**
4. Macrozooplankton	**2.75**	**68.51**	13.00	31.71	-	-	1.00	**0.41**
5. Gelatinous zooplankton	**3.42**	6.90	0.58	2.45	-	-	**0.31**	**0.239**
6. Mackerel	**4.19**	11.01	1.20	7.00	0.25	2.766	**0.88**	**0.171**
7. Sardine	**3.49**	26.88	1.46	17.60	0.01	0.139	**0.10**	**0.083**
8. Anchovy	**3.57**	39.09	2.01	21.90	0.55	21.387	**0.94**	**0.092**
9. Mesopelagic fish	**3.53**	**67.31**	1.20	12.00	0	0	**1.00**	**0.1**
10. Jack mackerel	**4.38**	15.39	0.36	8.12	0.11	1.618	**0.41**	**0.044**
11. Demersal fish	**4.88**	**0.57**	0.31	4.12	0.01	0.006	**1.00**	**0.075**
12. Jumbo squid	**4.68**	3.60	3.50	8.64	0	0	**0.50**	**0.405**
13. Palm ruff	**3.86**	0.30	1.46	4.20	0.03	0.009	**0.41**	**0.348**
14. Eastern pacific bonito	**4.11**	**0.26**	0.99	5.50	0.02	0.004	**1.00**	**0.179**
15. Common dolphinfish	**4.95**	0.00	1.20	5.60	0.50	0.001	**0.42**	**0.214**
16. Swordfish	**5.23**	0.42	0.44	7.20	0	0.001	**0.00**	**0.061**
17. Pelagic sharks	**5.21**	0.06	0.49	6.10	0.10	0.006	**0.21**	**0.08**
15. Sea lions	**4.85**	0.09	0.30	20.00	0.03	0.003	**0.10**	**0.015**
19. Cetaceans	**5.03**	0.06	0.15	10.00	-	-	**0.00**	**0.015**
20. Marine birds	**4.92**	0.06	0.10	62.00	-	-	**0.00**	**0.002**
21. Detritus	**1**	1			-	-	**0.28**	-
Total		**624.70**				**25.94**		

(15.4 ton km^{-2}), sardine (26.9 ton km^{-2}), anchovy (39.1 ton km^{-2}), and mesopelagic fish (67.3 ton km^{-2}) dominated the system (Table 2), representing 26% of B_T, while the combined biomass of demersal fish represented 0.1% of B_T.

Table 2 presents the production/biomass ratio (*P/B* = *Z*) for all groups and fishing mortality (*F*) for target species. Fig. 3 shows the contribution (percentage) in which each mortality coefficient (*F*; *M2* and *M0*) contributes to Z. Fishing mortality is important in species such common dolphinfish (42%), jack mackerel (30%), anchovy (27%), mackerel and pelagic sharks, both with 21%. In groups such Eastern Pacific bonito, mesopelagic fish and demersal fish, the main source of mortality is predation (*M2*) exceeding 90%; the coefficient of other mortalities (*M0*) is important in sardine and swordfish, also about 90%. Overall, in 1997 predators consumed more production of functional groups than the fishery (Fig. 3).

Fig. 4 shows the main flows in the UENCh in year 1997 and the distribution of the functional groups according to their trophic level (*TL*), from *TL* = 1 (phytoplankton and detritus) up to apical predators with *TL* > 4.0 such jumbo squid (*TL* = 4.68), sea lions (*TL* = 4.85), marine birds (*TL* = 4.91), common dolphinfish (*TL* = 4.95), cetaceans (*TL* = 5.0), pelagic sharks (*TL* = 5.2) and swordfish (*TL* = 5.2). The most important flows of consumption occur between primary producers (phytoplankton) and plankton invertebrates (micro-, macro- and mesozooplankton), and from the latter groups towards small pelagic fish (anchovy and sardine). Other important flows occur from mesozooplankton towards mesopelagic fish, and from anchovy and sardine towards predators such demersal fish, jumbo squid, sea lions and marine birds.

The 21 functional groups in the model representing the UENCh were grouped into seven discrete trophic levels, with discrete *TL* I and discrete TL II concentrating the bulk of total flows. Just like in other upwelling systems (*e.g.*, Jarre-Teichmann & Christensen, 1998; Neira & Arancibia, 2004), the UENCh exhibited a decline in flows (*Ft*) and biomass (*Bt*) towards higher trophic levels (Table 4). This is related to the rather low trophic transfer efficiency (*TTE*) calculated for aggregated trophic levels higher than TL IV. However, *TTE* was higher in *TL* II (*TTE* = 11.8%), *TL* III (*TTE* =

Table 3. Diet composition of the predators included in the balanced model representing the food web in the upwelling system of central Chile, year 1997.

	Prey	Predator																		
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Phytoplankton	0.728	0.200	0.500	0.092		0.0003	0.022												
2	Microzooplankton	0.171	0.400	0.038	0.055	0.011	0.222		0.058											
3	Mesozooplankton			0.400	0.514	0.135	0.500	0.514	0.681				0.13							
4	Macrozooplankton			0.063	0.339	0.190	0.278	0.464	0.220	0.21	0.001		0.06	0.54		0.01	0.04			
5	Gelatinous zooplankton									0.01										
6	Mackerel									0.05					0.054	0.14	0.15	0.05	0.01	0.40
7	Sardine										0.054	0.081		0.17	0.066	0.12		0.22	0.14	
8	Anchovy					0.269				0.21	0.164	0.081	0.08	0.29	0.075	0.12	0.15	0.40	0.26	0.45
9	Mesopelagic fish					0.259				0.31		0.704			0.465	0.05			0.10	
10	Jack mackerel														0.030		0.15	0.05	0.07	0.11
11	Demersal fish										0.0002							0.10		
12	Jumbo squid										0.089	0.134			0.310	0.50	0.33	0.05	0.34	
13	Palm ruff																0.03		0.04	0.04
14	Eastern Pacific bonito															0.06	0.15		0.04	
15	Common dolphinfish														0.0003					
16	Swordfish																			
17	Pelagic sharks																			
18	Sea lions																			
19	Cetaceans																			
20	Marine birds																			
21	Detritus	0.101	0.4																	
22	Import					0.137			0.041	0.21	0.692		0.73					0.13		
23	Total	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

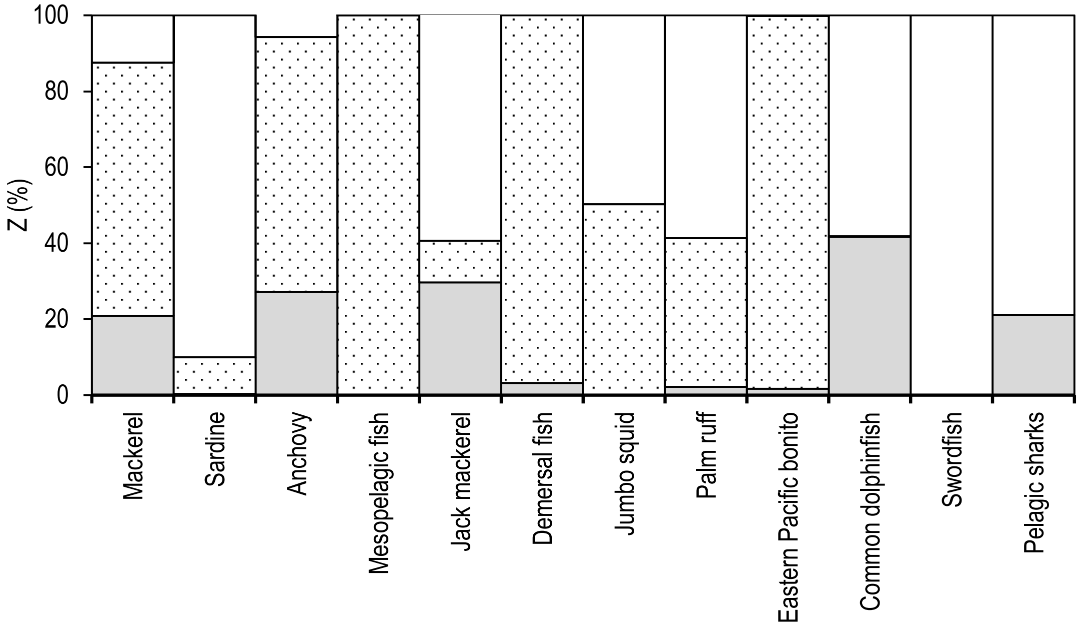

Figure 3. Mortality coefficients (as percentage of total mortality) for target species in the upwelling system of northern Chile, year 1997. Z: total mortality, F: fishing mortality (grey), M2: predation mortality (dotted), *M0:* other mortalities (white).

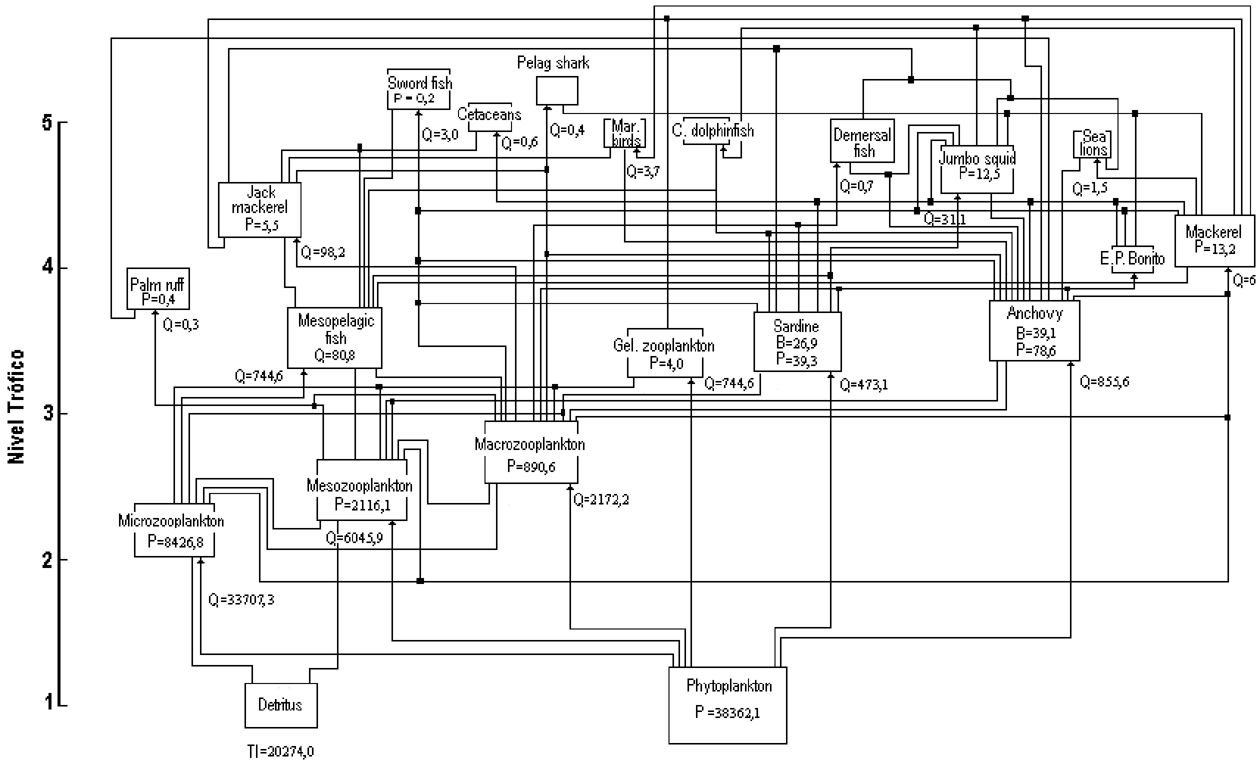

Figure 4. Flow diagram representing trophic flows among functional groups in the food web model representing the upwelling system in northern Chile in year 1997. P: production, Q: consumption, and B: biomass. Flows are expressed in ton km^{-2} yr^{-1}.

Table 4. Total biomass (B_t), total catches (Y_t), total flows (F_t) and trophic transfer efficiencies (*TTE*) by discrete trophic level in the model representing the upwelling system of northern Chile, year 1997. Trophic level (TL).

TL	B_t (ton km^{-2} yr^{-1})	Y_t (ton km^{-2} yr^{-1})	F_t (ton km^{-2} yr^{-1})	*TTE* (%)
I	320.0		58802.0	
II	83.7	0.5	32676.3	11.8
III	129.0	12.9	4353.6	28.0
IV	74.2	9.5	1184.0	17.6
V	16.8	2.9	195.3	7.1
VI	1.6	0.2	12.7	5.4
VII	0.1	0.0		1.4
Total	625.4	25.9	97058.0	17.8

28%) and *TL* IV (*TTE* = 17.8%). These results differ from what occurred in 1989 (Medina *et al.*, 2007), when *TTE* was high in *TL* II (*TTE* = 65.2%) and *TL* III (*TTE* = 9.5%), and the fishery was sustained by both anchovy and sardine. During 1997, instead, the fishery was sustained by functional groups located at *TLs* III and IV, including anchovy (84% of total landings), jack mackerel (11% of total landings), mackerel (6% of total landings) and sardine (0.5% of total landings).

Fig. 5 shows the mixed trophic impacts (*MTI*) between functional groups including the industrial and artisanal fleets operating in the study area in 1997. Overall, predators have direct negative impacts on prey, while preys have positive direct impacts on predators. Some MTIs can be highlighted from this figure. For example, the negative impact of cannibalism in jumbo squid and the negative MTIs of predators such jack mackerel, palm ruff, common dolphinfish, pelagic sharks and sea lions on anchovy.

The industrial fleet showed a negative impact on jack mackerel and positive impact on gelatinous zooplankton because fishing removes biomass of predators of this group. On the other hand, the artisanal fleet impacted negatively dolphinfish, sea lions and pelagic sharks with positive impact on demersal fish because this fleet removes biomass of their predators. The two fleets also impacted indirectly and positively some fishery resources (especially anchovy). This is the case of the positive impact of the artisanal fleet on demersal fish and palm ruff, which resulted from the fishing removal of sea lions and pelagic sharks. Mesopelagic fish showed an indirect negative impact on gelatinous zooplankton since both groups share mesozooplankton as preferred prey. The impacts of species such palm ruff, Eastern Pacific bonito and common dolphfish on other groups are almost unnoticeable.

Fig. 6 shows the trophic level (*TL*) calculated for the main predators in the UENCh model in 1989 (Medina *et al.*, 2007) and 1997 (this study). A noticeable difference in the magnitude of individual *TL* between the two periods is observed. In 1989, for instance, the most of the groups exhibited a *TL* < 4.0, with the exception of pelagic sharks. On the other hand, in 1997 most of the groups exhibited *TLs* > 4.0.

Table 5 presents network indices for the food web in the UENCh. The mean trophic level of the fishery (*TLm*) as a whole was estimated at 3.7. When examined by fleets, *TLm* of the artisanal fleet (*TLm* = 3.6) was slightly lower than the industrial fleet (*TLm* = 3.7). This is because both fleets caught mainly anchovy and sardine. The primary production required to sustain landings (*PPR*) was estimated at 2979.5 ton km^{-2} yr^{-1}, corresponding to 7.5% of the calculated net primary production of the system. The flows related to total transfers and total biomasses are indicators for the size of the ecosystem. The total transfers correspond to the sum of all flows in the system (consumption, exports, respiration and flow to detritus) and were estimated at 83,204 ton km^{-2} yr^{-1}. The main component resulted to be the consumption flow with 43% of total transfers. Total biomass without detritus was estimated at 624.7 ton km^{-2}.

One of the indicators to characterize system maturity is the primary production to respiration ratio (*PP/R*), which should approach to 1 in mature systems (Christensen & Pauly, 1992; Christensen *et al.*, 2005). In 1997, PP/R was estimated at 1.61 yr^{-1} meaning that this system was far from maturity or in an early stage of development. Other indicator of system maturity is the primary production to total biomass ratio (PP/B_T), which in mature ecosystems is low and in the UENCh was estimated at 61.40 in 1997.

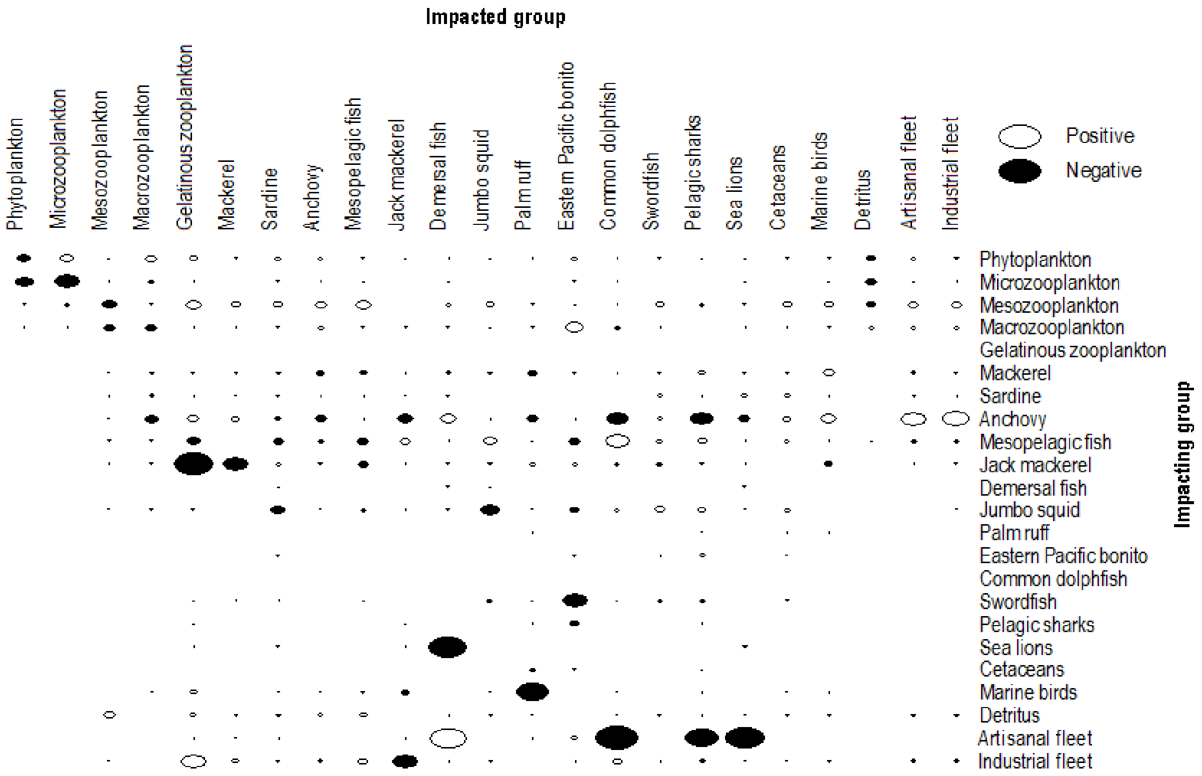

Figure 5. Mixed trophic impacts between the functional groups in the food web model that represents the upwelling system in of central northern Chile, in year 1997. Impacting groups are aligned in the "*x*" axis whiles impacting groups in the "*y*" axis.

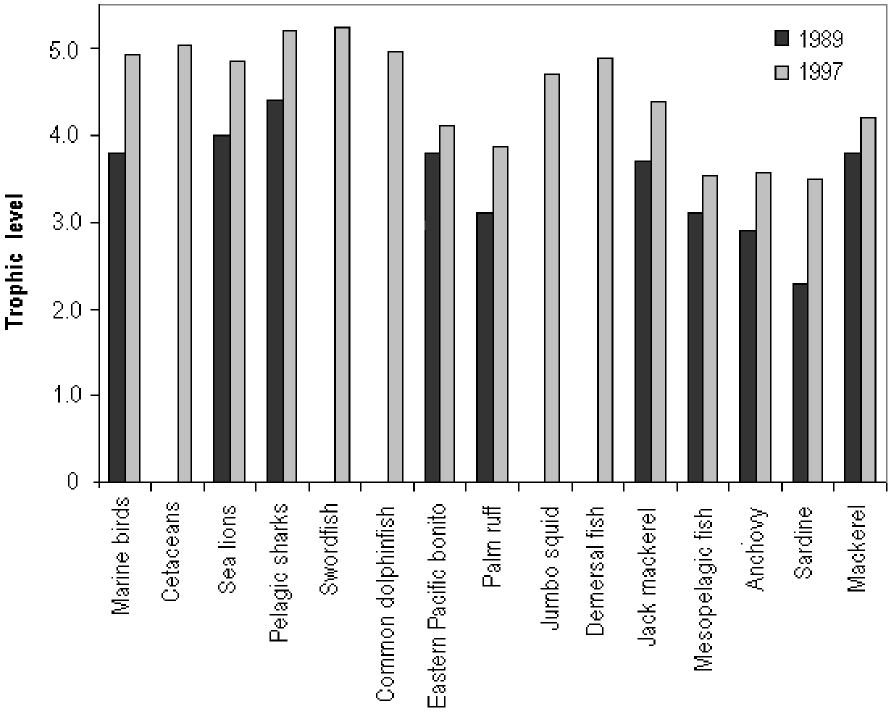

Figure 6. Trophic level of predators in the food web model representing the upwelling system in northern Chile, in years 1989 and 1997. Data on TL for 1989 are from Medina *et al.* (2007).

Table 5. Ecosystem indicators that describe the model representing the upwellig system of northern Chile, in year 1997 and its comparison to Medina *et al.* (2007) model representing the system in 1989.

Parameter	Year	
	1989	1997
System size		
Sum of all consumption (ton km^{-2} yr^{-1})	13091.8	44326.8
Sum of all the respiration flows (ton km^{-2} yr^{-1})	4244.0	24744.3
Sum of all flows to detritus (ton km^{-2} yr^{-1})	12060.2	20954.6
Total system flows (ton km^{-2} yr^{-1})	38674.0	106447.0
Total biomass (without detritus)(ton km^{-2})	707.7	645.4
Total catch (ton km^{-2} yr^{-1})	91.0	26.1
System maturity		
Sum of all the production (ton km^{-2} yr^{-1})	19684.0	50030.7
Calculated net primary production (PP_T) (ton km^{-2} yr^{-1})	13452.8	38362.1
Total primary production/total respiration (PP/R)	3.2	1.6
Total primary production /total biomass (PP/B_T)	19.0	61.4
Trophic transfer efficiency (%)	9.8	17.8
Finn's cycling index (*IF*) (%)	8.81	8.75
Fishing impact		
Mean trophic level of the catch	2.7	3.7
Primary production required to sustain landings *PPR* (ton km^{-2} yr^{-1})	1321.4	2834.4
(*PPR*) (%)	6.7	7.3

DISCUSSION

The model representing the UENCh in 1997 includes eight additional groups compared to the model built by Medina *et al.* (2007) for the same area in year 1989. These groups are microzooplankton, mesozooplankton, macrozooplankton, gelatinous zooplankton, demersal fish, jumbo squid, common dolphinfish, and swordfish. In addition, both models represent two different conditions: i) during non-ENSO conditions (year 1989) and ii) during ENSO conditions (year 1997). Regardless the difference in model structure and system conditions, comparing indicators derived from both models is still valid and interesting. Moreover, if more predators are included in a new, updated model, then the predation mortality in a prey group will be higher than the previous model.

Even in heavily exploited upwelling systems, predation mortality (*M2*) is the main source of mortality for fish species (Jarre-Teichman *et al.*, 1998; Jarre-Teichman & Christensen, 1998; Neira & Arancibia, 2004; Neira *et al.*, 2004). Results of our work are in agreement with this observation and *M2* explained the most of *Z*, meaning that the most of the production of functional groups in the UENCh was removed by predators and secondarily by fishing. However, Medina *et al.* (2007) informed that in 1989 the main source of mortality in the system was fishing and not predation. This may be explained by the increase in fishing effort from 1985 onwards after anchovy recovery, likely driven by strong recruitments (Aliaga *et al.,* 2001).

The highest *Z* values in the 1997 model were found in anchovy and jumbo squid. This is explained because both species have low longevity and high productivity, and are also important prey items in the diet of several predators. For example, anchovy is the main prey for jack mackerel, horse mackerel, palm ruff, Eastern Pacific bonito, pelagic sharks, sea lions and cetaceans. Anchovy sustained also the fishing landings in 1997. In turn, jumbo squid is important prey for cetaceans, dolphinfish, swordfish, and exhibits strong cannibalism (Table 3).

In the 1997 model, predators exhibited $TL > 4.0$. When comparing this result with the 1989 model (Medina *et al*., 2007) (Fig. 6), we observed an increase in *TL*s from one period to another (Fig. 6). A switch in sardine and anchovy diet may explain this change. During 1989, anchovy diet was based on zooplankton (85%) and phytoplankton (15%) (Alamo *et al.*, 1997) and the diet of sardine on zooplankton (26%) and phytoplankton (74%) (Oliva *et al*., 1987 *fide* Medina *et al*., 2007). In 1997, a dramatic change in the diet of both species occurred, with zooplankton being the most important prey in both species (>97%). This value was obtained considering the diet (numbers) informed by Alamo *et al.* (1997); Alamo & Espinoza (1998) and the carbon contents of each prey item expressed in percentage of fish total wet weight obtained from

Espinoza & Bertrand (2006). During ENSO, a marked decline in the abundance of phytoplankton and a concomitant increase in the abundance of zooplankton have been observed (González *et al.*, 1998; Daneri *et al.*, 2000), and this could explain the change in the diet of small pelagic fish.

However, Espinoza & Bertrand (2006) monitored the gut content of 21,203 anchovies from acoustic surveys conducted in Peru from 1996 to 2003, reporting that zooplankton (mainly euphausiids and copepods) is the main component in anchovy diet, in opposition to previous studies by Pauly *et al.* (1998), Jarre *et al.* (1991) and Jarre-Teichman *et al.* (1998) who indicate a similar importance of phytoplankton and zooplankton in the diet of anchovy. Nevertheless, Espinoza & Bertrand (2006) highlight that their study was based on qualitative descriptions, *i.e.*, frequency of occurrence and percentage in number of the items, rather than stomach content expressed in weight.

Therefore, the increase in *TL* in anchovy and sardine, which in turn are the main prey for predators and the bulk of the catch in the UENCh in 1997, resulted in an increase in trophic level of the fishery as a whole with $TLm > 3$. In this year the landings of anchovy reached 27 ton km^{-2} yr^{-1}, and was higher than the landings of the same species in 1989 (Medina *et al.*, 2007), when the fishery had a $TLm = 2.7$ and landings were sustained mostly by sardine (26 ton km^{-2} yr^{-1}).

In the decade of 1990s, landings of sardine progressively declined and in 1997/1998 with an El Niño, landings have the lowest values. In 1982/1983 a strong ENSO event affected the study area (Aceituno, 1988), negatively impacting anchovy and horse mackerel (Braun *et al.*, 2000). However, landings of sardine were not affected by this condition (SERNAPESCA, 1980-1990). In this context, the impact of the ENSO 1997/1998 on fish stocks in the Humboldt Current System is not yet clear, since for example, the fisheries of anchovy and sardines in Peru were not noticeably affected by the 1982/1983 ENSO (Arntz & Fahrbach, 1996). Therefore, it is suggested that the strong decline in the landings/biomass of sardine during the 1990s could result from recruitment overfishing (Serra, 1986; Aliaga *et al.*, 2001; Cubillos & Arcos, 2002) and predation and in a minor degree to ENSO. Unfortunately, the model representing the system in 1989 (Medina *et al.*, 2007) did not include some important predators of anchovy and sardine, such demersal fish, jumbo squid, swordfish, dolphinfish and cetaceans. This shortcoming impedes observing which groups predated on these small pelagic fish in 1989 and quantifying the strength of this trophic interaction. This is the importance of including these groups in the 1997 model.

The mixed trophic impacts (*MTI*) allowed assessing the influence of direct and indirect trophic interactions (including food competition) in the UENCh. *MTI* was also useful in identifying strong and weak interacting groups in the food web. For example, anchovy, mesopelagic fish and jack mackerel are strong interactors impacting positively and negatively many groups in the systems. On the other hand, palm ruff, Eastern Pacific bonito and common dophinfish are weak interactors with little impacts on other groups in the system.

The primary production required to sustain fishery landings (*PPR*) is an ecological indicator to track the ecological cost of fishing in an ecosystem during a time period, along years and/or compare the ecosystem effect of fishing in different ecosystems (Pauly & Christensen, 1995; Jarre-Teichman *et al.*, 1998). During 1997, the fishery removed only a small fraction (*i.e.*, 7.5%) of total primary production in the UENCh. This value is slightly higher compared to the value ($PPR = 6.7\%$) informed by Medina *et al.* (2007) for 1989, but much lower than the $PPR = 68.7\%$ informed by Cubillos *et al.* (1998) for 1997, both for the same area. *PPR* in the UENCh in 1997 was also lower than the $PPR = 15\%$ informed by Neira & Arancibia (2004) for central Chile, and the global estimate for upwelling areas $PPR = 25.1\%$ (Pauly & Cristhensen, 1995). However, the value 7.4% is in the minimum range reported by Jarre-Teichmann *et al.* (1998), who compared the upwelling systems from Peru, South Africa, Namibia and California, with *PPR* ranging from 4 to 15% of net production.

In this work we obtained seven discrete trophic levels, while (Medina *et al.*, 2007) reported five. This is due to the most of the species that are present in the 1997 model but not in the 1989 model are in high trophic levels (cetaceans, swordfish, dolphinfish and jumbo squid). In fact, the mean trophic transfer efficiency among trophic levels was relatively high (18%) in the 1997 model. Nevertheless, TTE in the UENCh is in the range informed for aquatic systems 10-20% (Christensen & Pauly, 1993; Lalli & Parsons, 1993), but it is higher than the 10-15% reported for upwelling systems (Pauly & Christensen, 1995).

After analysing the food web and the fisheries in the UENCh, we consider that there is still necessary to advance our knowledge on biological parameters for species that are not target species (it might became in the future), but play an important role as prey or predators in the ecosystem. Some of the groups could reach high biomass levels in the system, *e.g.*, mesopelagic fish. In this study the biomass of this group was estimated under the assumption that $EE = 0.999$, and reached 67.3 ton km^{-2}, which is almost two times the biomass estimated by Braun *et al.* (2000) for this group in 1998 (*i.e.*, 33.7 ton km^{-2}). The difference between the mesopelagic fish biomass estimated by Braun *et al.* (2000) and this work could be method-dependent, *i.e.*, acoustic underestimates the biomass in relation to Ecopath.

Results of our study confirm conclusions by Medina *et al.* (2007) related to the low maturity (in terms of structure and flows) of the UENCh. However, in theoretical terms the system in 1997 seems to have been in a situation closer to maturity (*sensu* Odum, 1969) compared to 1989. This can be inferred from the *PP/R* values estimated at 1.60 yr^{-1} in 1997 (this study) and 3.2 yr^{-1} in 1989 (Medina *et al*., 2007). Another indicator that support the previous conclusion is the Finn's cycling index (*IF*), which indicate the fraction of total transfers that are cycled in the system (Christensen & Pauly, 1992) with more cycling related to higher system maturity (Odum, 1969). The *IF* in the USNCh was higher in 1997 model (8.75%) compared to 1989 (2.80%), and the *IF* obtained in central Chile (8.97%) (Neira & Arancibia, 2002).

In 1997 flows related to total transfers indicated that the system presented more flows (106,447 ton km^{-2} yr^{-1}) compared to 1989 (38,674 ton km^{-2} yr^{-1}) (Medina *et al*., 2007), which seems reasonable considering that the 1997 model includes more groups than the 1989 one. However, in 1989 total biomass (707.7 ton km^{-2}) and total landings (91 ton km^{-2}) were higher than the same parameters in 1997.

The impact of the 1997/1998 ENSO on fishing resources is not clear, and results of this study allow hypothesising that the strong decline in landings and biomass of pelagic resources, especially sardine and anchovy in the USNCh, might have resulted from a combination of overfishing (affecting recruitment) (Serra, 1986; Aliaga *et al*., 2001; Cubillos & Arcos, 2002), in addition to predation, and secondarily to the effects of ENSO. Therefore, we suggest a combined analysis of the effect of fishing (*F*), predation (*M2*) and the environment (changes at ENSO scale), on sardine and anchovy that allow identifying the strength of each factor and their combined effects on the dynamics of these important fish species.

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