



Trophic modeling of the Northern Humboldt Current Ecosystem, Part I: Comparing trophic linkages under La Niña and El Niño conditions

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ABSTRACT

The El Niño of 1997–98 was one of the strongest warming events of the past century; among many other effects, it impacted phytoplankton along the Peruvian coast by changing species composition and reducing biomass. While responses of the main fish resources to this natural perturbation are relatively well known, understanding the ecosystem response as a whole requires an ecotrophic multispecies approach. In this work, we construct trophic models of the Northern Humboldt Current Ecosystem (NHCE) and compare the La Niña (LN) years in 1995–96 with the El Niño (EN) years in 1997–98. The model area extends from 4°S–16°S and to 60 nm from the coast. The model consists of 32 functional groups of organisms and differs from previous trophic models of the Peruvian system through: (i) division of plankton into size classes to account for EN-associated changes and feeding preferences of small pelagic fish, (ii) increased division of demersal groups and separation of life history stages of hake, (iii) inclusion of meso-pelagic fish, and (iv) incorporation of the jumbo squid (*Dosidicus gigas*), which became abundant following EN. Results show that EN reduced the size and organization of energy flows of the NHCE, but the overall functioning (proportion of energy flows used for respiration, consumption by predators, detritus and export) of the ecosystem was maintained. The reduction of diatom biomass during EN forced omnivorous planktivorous fish to switch to a more zooplankton-dominated diet, raising their trophic level. Consequently, in the EN model the trophic level increased for several predatory groups (mackerel, other large pelagics, sea birds, pinnipeds) and for fishery catch. A high modeled biomass of macrozooplankton was needed to balance the consumption by planktivores, especially during EN condition when observed diatoms biomass diminished dramatically. Despite overall lower planktivorous fish catches, the higher primary production required-to-catch ratio implied a stronger ecological impact of the fishery and stresses the need for precautionary management of fisheries during and after EN. During EN energetic indicators such as the lower primary production/total biomass ratio suggest a more energetically efficient ecosystem, while reduced network indicators such as the cycling index and relative ascendancy indicate of a less organized state of the ecosystem. Compared to previous trophic models of the NHCE we observed: (i) a shrinking of ecosystem size in term of energy flows, (ii) slight changes in overall functioning (proportion of energy flows used for respiration, consumption by predators and detritus), and (iii) the use of alternate pathways leading to a higher ecological impact of the fishery for planktivorous fish.

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1. Introduction

The northern part of the Humboldt Current Ecosystem (HCE) off Peru has been modelled with carbon and nitrogen budget models (Dugdale and MacIsaac, 1971; Walsh and Dugdale, 1971; Walsh,

1981), mass balance models (Jarre et al., 1989, 1991; Jarre and Pauly, 1993; Ballón, 2005), a size-based carbon flow model (Carr, 2003) and an empirical carbon flow model (Jahncke et al., 2004). Mass balance models have also been applied in the southern HCE off Chile (Wolff 1994; Ortiz and Wolff, 2002; Arancibia et al., 2003; Neira et al., 2004; Neira and Arancibia, 2004). These models have permitted comparisons between the HCE and other eastern boundary current ecosystems (Jarre, 1998; Jarre and Christensen,

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1998; Jarre et al., 1998; Moloney et al., 2005). However, none of these models have focused on the impact of the interannual variability associated with El Niño (EN).

According to Alheit and Niquen (2004), a regime shift occurred in Peruvian waters between 1968 and 1970, wherein waters warmed and zooplankton and anchovy (*Engraulis ringens*) biomass decreased, followed by an increase in sardine (*Sardinops sagax*) stocks. However, another regime shift back to cold conditions occurred during 1984–1986, in this case characterized by an increase of phytoplankton and zooplankton biomasses (see Ayon et al., 2008) associated with excellent recruitment of anchovy but decreases in sardine biomass.

Arntz and Fahrbach (1991) summarized the effects of the 1982–83 EN on the Northern Humboldt Current Ecosystem (NHCE). During EN, in the NHCE near surface temperature increases and the thermocline deepens, causing a collapse of the diatom-based trophic web, with emigration of anchovy and immigration of tropical and oceanic species. Gutierrez (2001) and Bertrand et al. (2004) described the effects of the 1997–98 EN on anchovy distribution and abundance, confirming that anchovy move to deeper waters but finding that the main spatial effect was concentration of stocks very nearshore. These authors attribute an apparent reduction in anchovy biomass to decreased effectiveness of acoustic sampling, unfavorable environmental conditions, increase of natural mortality due to poor feeding conditions, and to a much lesser degree, to mortality due to predation and fishing. Bouchon et al. (2001) analysed the ichthyofauna fluctuations over an El Niño Southern Oscillation (ENSO) cycle and concluded that in cold years the pelagic community is characterized by a high productivity and a low diversity (abundant diatoms and anchovy), but in warm years this pattern is reversed due to the immigration of offshore and tropical species and the reduction of anchovy. While responses of the main fish resources to EN-related perturbations are relatively well known (Aguilar, 1999; Tarazona et al., 2001), understanding the ecosystem response as a whole requires a multispecies ‘ecotrophic’ approach. Given the observed changes in biomass and species composition, it is expected that a strong EN impacts the food web, reducing or redistributing the main energy channel that flows through anchovy under La Niña (LN) conditions.

Previous models of the NHCE (Jarre et al., 1991), which described the flow of energy through the ecosystem during three decades (1953–1959, 1960–1969, 1973–1979), brought great understanding of ecosystem functioning. Now however, biological changes, new data sets, and the advancement of trophodynamic modeling permit construction of more detailed models through the inclusion of additional ‘functional groups’ of organisms (see also Guenette et al., 2008). In this paper we divided the phytoplankton compartment into two groups (diatoms and dino- and silicoflagellates) and zooplankton into three groups (micro-, meso- and macro-zooplankton) to account for the feeding preferences of different small pelagic fish. We incorporated the groups of mesopelagic fish and jumbo squid (*Dosidicus gigas*), which have gained in importance since the last 1997–98 EN. We also increased the detail of demersal groups and separated the hake into three different life history stages. The ecotrophic model framework is a simplified approach where species are aggregated into functional groups. Each group is represented by two linear equations, each of which must balance. One equation ensures balance between groups in the model, the other equation, balances the flows within each group.

The objective of this study is to compare such improved mass balance trophic models for a cold LN conditions (1995–96) versus a warm EN (1997–98) conditions, with the *a priori* hypothesis that the EN perturbation should decrease ecosystem organization. This paper also provides the basis for further explorations of ecosystem dynamics (Taylor et al., this 2008a), wherein non-steady state sim-

ulations of ecosystem change during and following the 1997–98 EN are performed and evaluated. In dynamic models, biomass changes are expressed in form of coupled differential equations derived from mass balance models equations.

2. Methods

2.1. Input data

Our models of the Northern Humboldt Current Ecosystem (NHCE) extend from 4°S to 16°S, and 60 nm offshore, covering an area of approximately 165000 km² (Fig. 1). In agreement with the ENSO cycle, data from June 1995 to May 1996 and from May 1997 to April 1998 were used as inputs for the cold LN and warm EN mass balance models, respectively, covering a full “biological year” each (*i.e.* starting from about the middle of a calendar year).

The models included 33 functional groups, namely: (1) diatoms, (2) dino- and silicoflagellates, (3) microzooplankton (20–200 μm), (4) mesozooplankton (200–2000 μm), (5) macrozooplankton (2–20 mm), (6) gelatinous zooplankton, (7) macrobenthos, (8) sardine, (9) anchovy, (10) mesopelagics (*Vinciguerria lucetia*, *Lampanyctus* spp., *Leuroglossus* spp.), (11) jumbo squid, (12) other cephalopods (*Loligo gahi*, *Octopus vulgaris*, *Logigunculla* sp.), (13) other small pelagics (e.g. *Anchoa nasus*), (14) horse mackerel (*Trachurus murphyi*), (15) mackerel (*Scomber japonicus*), (16) other large pelagics (e.g. *Sarda chiliensis*, *Coryphaena hippurus*, *Thunnus albacares*), (17) small hake (*Merluccius gayi peruanus*, <29 cm), (18) medium hake (*M. gayi peruanus*, 30–49 cm), (19) large hake (*M. gayi peruanus*, >50 cm), (20) flatfishes (*Paralichthys adspersus*, *Hippoglossina* sp.), (21) small demersals (e.g. *Odonthestes regia*, *Labrisomus philippi*, *Ctenosciaena peruviana*), (22) benthic elasmobranchs, (23) butterfishes (*Trachinotus paitensis*, *Stromateus stellatus*, *Peprilus medius*), (24) congers, (25) medium demersal fishes (e.g. *Paralabrax humeralis*, *Hemanthias peruanus*, *Mugil cephalus*), (26) medium sciaenids, (27) sea robin (*Prionotus stephanophrys*), (28) catfishes (*Galeichthys*



Fig. 1. Study area covers from 4°S to 16°S, and up to 60 nm (grey shaded area), in the Northern Humboldt Current Ecosystem (dashed line) (modified from Alheit and Niquen, 2004).

peruvianus), (29) chondrichthyans, (30) seabirds (*Phalacrocorax bougainvillii*, *Sula variegata*, *Pelecanus thagus*), (31) pinnipeds (*Otaria flavescens*, *Arctocephalus australis*), (32) cetaceans, and (33) detritus.

Models were constructed using the Ecopath software (Ecopath with Ecosim version 5.1; Christensen et al., 2005). Mass balance models are based on two equations for each functional group i (Christensen and Pauly, 1992).

The energy balance equation

$$Q_i = P_i + R_i + UF_i \quad (1)$$

where Q_i = prey consumption, P_i = production, R_i = respiration, UF_i = unassimilated food (including excretion and egestion) and, the production components equation

$$P_i = B_i * MO_i + EX_i + B_i * M2_i + BA_i \quad (2)$$

where MO_i = non-predatory mortality (expressed as a function of ecotrophic efficiency, EE_i), $M2_i$ = predatory mortality (expressed as a function of diet composition, DC), EX_i = export (including catch C_i and net migration, NM_i), BA_i = biomass accumulation. EE_i is the proportion of the production that is utilized in the system and is defined as

$$EE_i = (B_i * M2_i + C_i + NM_i + BA_i) / P_i \quad (3)$$

Thus, for each functional group, required input data is: wet weight biomass (B , t km⁻²), production/biomass ratio (P/B , y⁻¹), consumption/biomass ratio (Q/B , y⁻¹), catch (C , t km⁻² y⁻¹) and diet composition (DC) for each functional group. One unknown parameter (either B , P/B , Q/B or EE) can be estimated when solving the system of linear equations.

Input data for the models were gathered from published and unpublished sources (Table 1). Catch values were obtained from IMARPE (2006) landing statistics and the Sea Around Us (2006) database; some values of production/consumption ratio (P/Q) and unassimilated food (UF) were obtained from Moloney et al. (2005). Sea surface phytoplankton biomass was calculated from relationships of upwelling area vs. chlorophyll a (chl. a) threshold as calculated by Nixon and Thomas (2001). Conversion factors of carbon/chl. a = 40 (Brush et al., 2002) and wet weight/carbon = 14.25 (Brown et al., 1991) were used to estimate wet weights. Proportion of diatoms vs. silico- and dinoflagellates during LN and EN conditions were obtained from a time series (1992–2000) of species cell counts carried out by Universidad Nacional Mayor de San Marcos UNMSM at Ancón Bay, Central Peru (77°11' W–11°46' S). Phytoplankton cell counts were converted to biovolumes using the geometric formulas and software of Sun and Liu (2003); cell dimensions were obtained from the literature (e.g. Strickland et al., 1969; SERC, 2006; NODC, 2001) or measured under a microscope at the UNMSM. To convert biomass units from m³ to m², a mixed layer depth of 40 m was estimated by averaging vertical profiles of chl. a from several latitudes along the Peruvian coast with data from Calienes et al. (1985). Individual zooplankton body masses were estimated from abundance and biomass data (Ayón and Arones, 1997a,b) and zooplankton biovolumes were calculated from individual counts by taxonomic group using length:weight relationships from Rippe (1996) with body dimensions obtained from Santander et al. (1981) and Wangelin and Wolff (1996). Such biovolume conversions were also needed to convert stomach content data for sardine and anchovy (numbers of phytoplankton cells and zooplankton individuals per stomach by species) into fractions by weight.

In an Ecopath model, the Pedigree Index (P) permits assignment of quality or confidence ratings to each parameter. Qualitative pedigree index values were assigned as in Table 2. Based on the individual index values (I_{ij}) an overall Pedigree Index (P) is calculated using

$$P = \sum_{i=1}^n \frac{I_{ij}}{n} \quad (4)$$

where I_{ij} is the pedigree index value for group i and parameter j for each of the n living groups in the ecosystem. For the models constructed here, P was 0.638 (P scales between 0 and 1; $t^* = 4.54$, $n = 32$, $p < 0.001$), indicating good model quality with parameters mostly based on local data. For comparison, of 50 Ecopath models reviewed by Morissette (2007), only four models had higher pedigree indices than the present study (upper 7.5%).

Conservative estimates of biomass of some groups were calculated by the software assuming an ecotrophic efficiency of 0.95 (microzooplankton, macrozooplankton, gelatinous zooplankton, small pelagics, small demersals and other cephalopods). Ecotrophic efficiency ($0 < EE < 1$) and gross efficiency ($0 < GE < 0.4$) served as constraints for balancing the models. Gross food conversion efficiency is estimated using

$$GE_i = (P_i/B_i)/(Q_i/B_i) \quad (5)$$

Energy flow balance of models was achieved by tuning the diets of some groups. The dietary composition for functional groups is presented in Table 3. Based on the input data, the Ecopath software calculated ecosystem indicators which describe the state of an ecosystem in terms of energy flows. Behavior of trophic, fishery, energetic and network ecosystem indicators have been related to theories of ecosystem maturity (Odum, 1969) and health (Ulanowicz, 1997) (see Table 4 for a description). The trophic level of a group (TL) is calculated as the mean trophic level of its prey plus 1, assuming that primary producers and detritus groups have a trophic level of 1.0. Thus, trophic level is calculated using

$$TL_j = 1 + \sum (TL_i)(DC_{ij}) \quad (6)$$

where DC_{ij} is the fraction of prey i in the diet of the predator j .

The transfer efficiency (TE) of each discrete trophic level is defined as a measure of the fraction of input to each of the aggregated trophic levels that is passed on to the next level, that is, the fraction that is either consumed by predators or harvested

$$TE_n = (Q_{n+1} + EX_n)/Q_n \quad (7)$$

where n is the trophic level.

3. Results and discussion

3.1. Biomass and catch changes

Tables 5A and B presents results for LN and EN conditions, respectively. The model synthesizes available data and estimates additional parameters (bold type in Table 5) that define the relationships between the functional groups of organisms in the model. During the LN conditions diatoms, mesozooplankton, anchovy, horse mackerel, mackerel and jumbo squid dominated in biomass in their respective trophic levels. During EN conditions, biomasses of most groups decreased (anchovy, jumbo squid, horse mackerel, hake, demersal fishes, seabirds and pinnipeds), mainly due to a bottom-up control originating from biomass reduction in the lower trophic levels (diatoms, micro- and mesozooplankton). During EN conditions, macrobenthos biomass increased, mainly in the central zone off Peru (10–15°S; Quipuzcoa et al., 2001), probably because bottom oxygen concentrations increased, improving conditions for many organisms. However, biomasses of demersal fish species decreased (e.g. hake, small demersals).

Biomasses of some groups increased during EN (Fig. 2), possibly being favored by low nutrient conditions or higher temperatures (dinoflagellates, macrozooplankton) and/or immigration of some fish (mesopelagics, small pelagics, large pelagics and

Table 1
Input data for the models of the NHCE and their sources. Biomass (B), production (P), consumption (Q) and catch (C)

Functional group Period	B 1995–96	1997–98	P/B 1995–96	1997–98	Q/B 1995–98	C 1995–96	1997–98	Source
1. Diatoms	53.416	14.761	265	210				B, P/B calculated from Nixon and Thomas (2001) curve, 85% (1995–96) and 46% (1997–98) of diatoms calculated from Ancon, Central Peru (Ochoa, personal communication) and Sanchez (1996) data converted to biovolumes.
2. Silico- and dinoflagellates	9.426	17.328	265	210				B, P/B calculated from Nixon and Thomas (2001) curve, 15% (1995–96) and 86% (1997–98) of silico- and dinoflagellates calculated from data converted to biovolumes from Ancon, Central Peru (Ochoa, personal communication) and Sanchez (1996).
3. Microzooplankton (20–200 µm)			256	256				P/B from Sorokin and Kogelschatz (1979), diet from Shannon et al. (2003).
4. Mesozooplankton (200–2000 µm)	31.164	17	40	40				B calculated from IMARPE data (Ayon, personal communication), P/B from Moloney et al. (2005), diet from Shannon et al. (2003).
5. Macrozooplankton (2–20 mm)					46.55			Q/B from Antezana (2002a), diet from Shannon et al. (2003).
6. Gelatinous zooplankton			0.584	0.584				P/B from Jarre et al. (1998), diet from Shannon et al. (2003).
7. Macrobenthos	20.729	25.605	1.2	1.2	10			B calculated from IMARPE data (Gutierrez and Quipuzcoa, personal communication), P/B and Q/B from Walsh (1981) in Jarre et al. (1989), diet from Shannon and Jarre (1999).
8. Sardine (<i>Sardinops sagax</i>)	7.567	7.909	1.4	1.4		7.97	3.33	B calculated from IMARPE acoustic data (Gutierrez, personal communication), P/B from Patterson et al. (1992), diet calculated from Alamo et al. (1996a, 1996b), Alamo et al. (1997a, 1997b), Alamo and Espinoza (1998), Blaskovic et al. (1998), Espinoza et al. (1998a, 1998b), Blaskovic et al. (1999).
9. Anchovy (<i>Engraulis ringens</i>)	83.293	33.34	2	2		30.47	14.48	B from IMARPE VPA (Ñiquen, personal communication), P/B from Csirke et al. (1996), diet calculated from Alamo et al. (1996a, 1996b), Alamo et al. (1997a, 1997b), Alamo and Espinoza (1998), Blaskovic et al. (1998), Espinoza et al. (1998a, 1998b), Blaskovic et al. (1999).
10. Mesopelagics	6.882	22.375	1.4	1.4				B calculated from relationship between <i>Vinciguerria lucetia</i> and <i>Dosidicus gigas</i> from IMARPE acoustic data 1999–2005 (Gutierrez, personal communication), P/B calculated from maximum age, diet calculated from IMARPE data (Blaskovic, personal communication)
11. Jumbo squid (<i>Dosidicus gigas</i>)	0.524	0.243	8.91	8.91		0.19	0.01	B calculated from relationship between CPUE and B of <i>Dosidicus gigas</i> from IMARPE acoustic data 1999–2005 (Gutierrez, personal communication), P/B from Alegre et al. (2005), diet calculated from IMARPE industrial fleet data (Blaskovic, personal communication), Schetinnikov (1989), Nigmatullin et al. (2001).
12. Other Cephalopods			4.3	4.3		0.05	0.01	P/B from IMARPE VPA (Arguelles, personal communication), diet from Cardoso et al. (1998) and Villegas (2001).
13. Other small pelagics			1	1		0.69	2.36	P/B from Shannon et al. (2003) for saury (<i>Scorpaenopsis scorpaenoides</i>), flying fish (Exocoetidae), pelagic goby (<i>Sufflogobius bibarbatus</i>), diet based on Jarre et al. (1989).
14. Horse mackerel (<i>Trachurus murphyi</i>)	11.568	3.03	1.2	1.2		1.45	1.94	B from IMARPE acoustic data (Gutierrez, personal communication), P/B from Moloney (2005), diet calculated from IMARPE data (Blaskovic, personal communication)
15. Mackerel (<i>Scorpaenopsis scorpaenoides</i>)	8.488	6.892	0.85	0.85		0.10	1.34	B from IMARPE acoustic data (Gutierrez, personal communication), P/B from Jarre et al. (1989), diet calculated from IMARPE data (Blaskovic, personal communication)
16. Other large pelagics	0.589	1.757	0.85	0.4		0.25	0.35	B calculated from catch equal to 50% production, P/B from Jarre et al. (1989), diet calculated from IMARPE data (Blaskovic, personal communication)

(continued on next page)

Table 1 (continued)

Functional group	B		P/B	Q/B	C	Source	
17. Small hake (<i>Merluccius gayi</i> peruanus, <29 cm)	2.771	1.245	0.928	1.317	0.97	0.56	B from IMARPE VPA (Wosnitza, personal communication), <i>P/B</i> calculated as average of Z from VPA of the age groups involved (Ballon, personal communication), diet calculated from IMARPE data (Blaskovic, personal communication).
18. Medium hake (<i>M. gayi</i> peruanus, 30–49 cm)	0.414	0.163	1.627	1.946	0.22	0.11	B from IMARPE VPA (Wosnitza, personal communication), <i>P/B</i> calculated as average of Z from VPA of the age groups involved (Ballon, personal communication), diet calculated from IMARPE data (Blaskovic, personal communication).
19. Large hake (<i>M. gayi</i> peruanus, >50 cm)	0.055	0.028	1.044	1.516	0.02	0.01	B from IMARPE VPA (Wosnitza, personal communication), <i>P/B</i> calculated as average of Z from VPA of the age groups involved (Ballon, personal communication), diet calculated from IMARPE data (Blaskovic, personal communication).
20. Flatfishes	0.04	0.01	0.304	0.304	0.01	0.00	B from swept area data corrected with hake VPA (Wosnitza, personal communication), <i>P/B</i> from Neira et al. (2004), diet calculated from IMARPE data (Blaskovic, personal communication).
21. Small demersals			2.3	2.3	0.02	0.02	B from swept area data corrected with hake VPA (Wosnitza, personal communication), <i>P/B</i> from Wolff et al. (1998), diet calculated from IMARPE data (Blaskovic, personal communication).
22. Benthic elasmobranchs	0.078	0.045	1	1	0.03	0.04	B from swept area data corrected with hake VPA (Wosnitza, personal communication), <i>P/B</i> based on Shannon et al. (2003), diet calculated from IMARPE data (Blaskovic, personal communication).
23. Butter fishes	0.032	0.006	0.8	0.8			B from swept area data corrected with hake VPA (Wosnitza, personal communication), <i>P/B</i> from Wolff et al. (1998), diet calculated from IMARPE data (Blaskovic, personal communication).
24. Conger	0.019	0.004	0.75	0.75			B from swept area data corrected with hake VPA (Wosnitza personal communication), <i>P/B</i> from Wolff et al. (1998), diet calculated from IMARPE data (Blaskovic, personal communication).
25. Medium demersal fish	0.2	0.211	1.32	2.48	0.13	0.14	B from swept area data corrected with hake VPA (Wosnitza, personal communication), <i>P/B</i> calculated from catch curve for <i>Paralabrax humeralis</i> (Ballon, personal communication), diet calculated from IMARPE data (Blaskovic, personal communication).
26. Medium sciaenids	0.369	0.218	0.746	1.085	0.07	0.04	B from swept area data corrected with hake VPA (Wosnitza, personal communication), <i>P/B</i> calculated from catch curve for <i>Cynoscion analis</i> (Ballon, personal communication), diet calculated from IMARPE data (Blaskovic, personal communication).
27. Sea robin (<i>Prionotus stephanophrys</i>)	0.789	0.319	3.4	3.22			B from swept area data corrected with hake VPA (Wosnitza, personal communication), <i>P/B</i> calculated from catch curve (Ballon, personal communication), diet calculated from IMARPE data (Blaskovic, personal communication).
28. Catfish	0.577	0.65	0.9	0.9	0.07	0.54	B from swept area data corrected with hake VPA (Wosnitza, personal communication), <i>P/B</i> from Wolff et al. (1998), diet calculated from IMARPE data (Blaskovic, personal communication).
29. Chondrichthyans	0.027	0.078	0.486	0.486	0.01	0.02	B calculated from catch equal to 50% production, <i>P/B</i> calculated from Frisk et al. (2001) and Au and Smith (1997), diet calculated from IMARPE data (Blaskovic, personal communication).
30. Seabirds	0.067	0.01	0.04	0.04	60		B from IMARPE abundance data converted to biomass (Goya, personal communication), <i>P/B</i> and <i>Q/B</i> from Jarre et al. (1989), diet from Guillen (1990).
31. Pinnipeds	0.072	0.053	0.1	0.1	45.9		B from IMARPE abundance data converted to biomass (Goya, personal communication), <i>P/B</i> from Jarre et al. (1989), <i>Q/B</i> from Muck and Fuentes (1987) in Jarre et al. (1989), diet from Arias (2003).
32. Cetaceans	0.062	0.067	0.1	0.1	20		B calculated from modelled biomass of mysticetes, small and large odontocetes (Kaschner 2004), 1.1 sightings ratio 1997/1995 calculated from Bello et al. (1998), <i>Q/B</i> from Moloney et al. (2005), diet based on Jarre et al. (1998).

Table 2

Pedigree index values qualitatively assigned to model parameters. Biomass (*B*), production (*P*), consumption (*Q*), diet composition (*DC*) and catch (*C*). Lower pedigree index values correspond to guesstimates or other models, while higher pedigree index values correspond to high precision estimates locally based.

Functional group	<i>B</i>	<i>P/B</i>	<i>Q/B</i>	<i>DC</i>	<i>C</i>
1. Diatoms	0.7	0.5			
2. Dino- and silicoflagellates	0.7	0.5			
3. Microzooplankton	0	0.6	0.6	0.2	
4. Mesozooplankton	0.7	0.6	0.6	0.2	
5. Macrozooplankton	0.7	0.6	0.6	0.2	
6. Gelatinous zooplankton	0	0.2	0.6	0.2	
7. Macrobenthos	0.7	0.2	0.6	0.2	
8. Sardine	0.4	1	0.6	1	1
9. Anchovy	0.4	1	0.6	1	1
10. Mesopelagics	0.4	0.1	0.6	0.2	
11. Jumbo squid	0.4	1	0.6	0.5	1
12. Other Cephalopods	0.4	0.7	0.6	0	1
13. Other small pelagics	0	0.7	0.6	0	1
14. Horse mackerel	1	0.7	0.6	0.5	1
15. Mackerel	1	0.7	1	0.5	1
16. Other large pelagics	1	0.7	0.6	0.5	1
17. Small hake	1	1	0.6	1	1
18. Medium hake	1	1	0.6	1	1
19. Large hake	1	1	0.6	1	1
20. Flatfishes	0.4	0.8	0.6	0.7	1
21. Small demersals	0.4	0.2	0.6	0	
22. Benthic elasmobranchs	0.4	0.2	0.6	0.7	1
23. Butter fishes	0.4	0.2	0.6	0.7	
24. Conger	0.4	0.6	0.6	0.7	
25. Medium demersal fish	0.4	0.8	0.6	0.7	1
26. Medium sciaenids	0.7	0.8	0.6	0.7	1
27. Sea robin	0.7	0.8	0.6	0.7	
28. Catfish	0.4	0.1	0.6	0.7	1
29. Chondrichthyans	0	0.5	0.6	0.7	1
30. Seabirds	1	1	0.6	1	
31. Pinnipeds	1	1	0.6	1	
32. Cetaceans	0.4	0.6	0.6	0	

chondrichthyans). During the 1997–98 EN, Delgado et al. (2001) found dinoflagellates (e.g. *Ceratium breve*, *Ceratium praelongum*), and Ayón et al. (1997) found fish larvae (e.g. *Hoplunnis pacifica*, *Monolene maculipinna*) south of their characteristic ranges, immigrating with the intrusion of warm water masses.

For fish, catch reductions accompanied biomass reductions (Fig. 3), with the exception of sustained high catch changes of mackerel and catfish during EN (whose fishing mortalities were quite low in the cold period). Total catches decreased 41% during EN and the ratio of total catch to biomass decreased 19% (Table 6). A slope < 1.0 in Fig. 3 indicates that biomass changes do not translate immediately or fully into catch changes. Future management measures, should consider that EN-related reduction of catches should be at least proportional to the reduction of biomasses, allowing the exploitation rate (*F/Z*) to be maintained. The general biomass and catch reductions during EN can also be appreciated in the pyramids given in Fig. 4.

Separation of phytoplankton into two functional groups (diatoms and silico-dinoflagellates) permits description of alternate pathways and differential responses of consumers. The reduction of diatom biomass during EN forced remaining omnivorous planktivorous fishes (anchovy and other small pelagics) to prey more on zooplankton in the model, (increasing their trophic level). Espinoza and Bertrand (2008) found a higher fraction of zooplankton during EN than in 1996 in anchovy stomachs. Modelled TL of anchovy increased from 2.35 to 3.17 from LN to EN conditions (Table 5). Consequently, the TL of piscivorous groups (large pelagics, seabirds, pinnipeds) also increased. Anchovy biomass reduction left sardine consumption of diatoms and dinoflagellates to increase slightly during EN, possibly in compensation for the increased competition with remaining anchovy for zooplankton, and because sardines are

more efficient removers of small particles than anchovy (van der Lingen et al., 2006).

IMARPE zooplankton sampling (300 µm mesh size nets towed from 0 to 50 m depth) captures mainly mesozooplankton, while macrozooplankton, specifically euphausiids, are undersampled due to their deeper distribution. For this reason, biomass of macrozooplankton was estimated within the model, resulting in 21.1 t km⁻² during 1995–96, and 34.8 t km⁻² during 1997–98. These high estimates are nevertheless conservative given that they were back-calculated using an ecotrophic efficiency of 0.95. Back calculations must be taken with caution and should ultimately be complemented with dynamic approaches using Ecosim, preferably with long time series of functional groups biomasses, in order to better constrain the estimates (Guenette et al., 2008; Taylor et al., 2008a). Nevertheless, the existence of such a high macrozooplankton biomass is supported by Antezana (2002a) who described *Euphausia mucronata* with SHCE biomass values up to 500 g wet weight per 1000 m³ within the oxygen minimum layer (Antezana, 2002b). Neira et al. (2004) also estimated high biomasses of euphausiids to meet the consumption requirements of model predators. Their estimates ranged from 73.6 to 106.3 t km⁻² off central Chile. Moreover, the temporal variation of the diet of anchovy reported by Espinoza and Bertrand (2008) emphasized the importance of zooplankton over phytoplankton. All these evidences point to a high biomass of macrozooplankton in the NHCE as a prey of several species, especially during EN conditions when diatoms biomass diminishes. The apparent paradox of a high macrozooplankton biomass during EN conditions despite low phytoplankton biomass is explained by the lower consumption of diatoms by anchovy, leaving remaining phytoplankton for other species.

3.2. Trophic flows

A comparison of ecosystem indicators of both models (1995–96 and 1997–98) is presented in Table 6. According to Ulanowicz (1997), the ‘size’ of an ecosystem can be measured by its total activity in terms of energy flows, or by the total system throughput. In addition to the total biomass reduction (–26.7%), total system throughput reduced dramatically (–58.7%), along with a reduction of absolute energy flows for prey consumption, exports, respiration and to detritus. This reduction in the size of the modelled ecosystem in terms of total energy flows during EN is well-reflected in the energy flow pyramids (Fig. 4), where the volume of each compartment representing a trophic level is proportional to the total throughput of that level, and the top angle of the pyramids was made inversely proportional to the geometric mean of the transfer efficiencies between trophic levels.

A large decrease in total primary production during EN (–59.5%) exerted a bottom-up control and decreased ecosystem ‘size’ or total system throughput in the model. During EN the percentage contributions of total system throughput (Table 6) shows slight changes, on one hand an increase in consumption, and on the other hand a reduction in exports and flows into detritus. The relative reduction in exports and flows into detritus apparently reflects an increase in grazing by meso- and macro-zooplankton on phytoplankton in the model. These percentage flow changes were however small, indicating that although EN dramatically alters the system’s absolute size, the relative flow of energy between functional groups seems largely unaltered.

While a comparison between ecotrophic models should ideally be based on a common model structure (Moloney et al., 2005), it is noteworthy that the total system throughput (ca. 60000 t km⁻² y⁻¹) in the 1964–71 model before the anchovy collapse (Jarre et al., 1998) is similar to the value (55689 t km⁻² y⁻¹) obtained here for the LN model. Total system throughput is rather

Table 3

Diet composition of functional groups after the model was balanced, during LN (1995–96) and EN (1997–98). Values represent the fraction of the food intake in wet weight.

Prey/ predator	Years	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32			
1. Diatoms	1995–96	0.300	0.850	0.500			0.042	0.692				0.300		0.002						0.600		0.423												
	1997–98	0.200	0.300	0.500			0.123	0.017				0.300								0.600		0.447												
2. Dino- and Silicoflagellates	1995–96	0.100	0.050	0.100			0.003	0.004																										
	1997–98	0.200	0.500	0.400			0.051	0.000																										
3. Microzoo- plankton	1995–96	0.200	0.100	0.400			0.037	0.000						0.000																				
	1997–98	0.150	0.200	0.100				0.003																										
4. Mesozoo- plankton	1995–96				0.640		0.704	0.281	0.021	0.075		0.650		0.029						0.400		0.186					0.004							
	1997–98				0.640		0.566	0.603	0.021	0.056		0.650	0.002	0.003						0.400														
5. Macrozoo- plankton	1995–96				0.120		0.214	0.023	0.979	0.222	0.850		0.560	0.862		0.070	0.003	0.132			0.019	0.028		0.256	0.001	0.975	0.108					0.300		
	1997–98				0.120		0.260	0.377	0.979	0.184	0.850		0.469	0.265	0.002	0.201	0.006	0.000			0.061			0.076	0.000	0.611		0.021				0.300		
6. Gelatinous zooplankton	1995–96				0.040																				0.004									
	1997–98				0.040																		0.053											
7. Macrobenthos	1995–96					0.070						0.030			0.090	0.001	0.001	0.200		0.565	0.179	0.114	0.383	0.641	0.025	0.572								
	1997–98					0.070						0.020	0.020		0.190	0.069	0.004			0.552	0.500	0.114	0.861	0.473	0.171	0.950	0.083							
8. Sardine	1995–96															0.060					0.031				0.013									
	1997–98													0.017							0.017				0.004					0.447				
9. Anchovy	1995–96								0.043			0.200		0.699	0.358	0.645	0.005	0.500		0.078			0.100	0.184		0.198	0.213	0.877	0.539	0.100				
	1997–98								0.040				0.401	0.623	0.069	0.082	0.023	0.455		0.082			0.018	0.190		0.208	0.377	0.377	0.100					
10. Mesopelagics	1995–96								0.387					0.005			0.011							0.001							0.004			
	1997–98								0.337					0.001	0.151	0.173	0.002													0.058				
11. Jumbo squid	1995–96								0.120						0.071	0.112					0.022			0.005			0.667					0.200		
	1997–98								0.242								0.012	0.111			0.005						0.042					0.200		
12. Other Cephalopods	1995–96								0.077			0.120	0.102	0.088	0.070		0.002			0.114		0.037	0.043	0.008			0.009							
	1997–98													0.069		0.035	0.005	0.005			0.015		0.037	0.002	0.031		0.125							
13. Other small pelagics	1995–96								0.044			0.040		0.001	0.005	0.055				0.002			0.001	0.037		0.001		0.036	0.009					
	1997–98								0.040			0.029	0.199	0.210	0.163	0.205	0.020				0.005		0.011	0.051	0.218			0.126	0.008					
14. Horse mackerel	1995–96																				0.001							0.015	0.015	0.200				
	1997–98																				0.005		0.005						0.021		0.011	0.200		
15. Mackerel	1995–96																																0.200	
	1997–98																																0.200	

Table 4
Ecosystem indicators and their definitions.

Ecosystem indicator	Definition (Christensen et al. 2005)
<i>Trophic indicators</i>	
Total system throughput	Sum of all flows in a system, represents the size of the system in terms of flows
Total net primary production	Summed production from all primary producers. Primary producers are groups that capture energy through photosynthesis (e.g. phytoplankton and benthic algae)
Mean transfer efficiency	Geometric mean of transfer efficiencies for trophic levels II–IV
Connectance index	Ratio of the number of actual links to the number of possible links. It can be expected to be correlated with maturity
Mixed trophic impact	Combined direct and indirect trophic impacts that an infinitesimal increase of any of the groups is predicted to have on the other groups of the ecosystem
<i>Fishery indicators</i>	
Mean trophic level of the catch	Sum of trophic levels of species in the catch weighted by their contribution to the catch
Gross efficiency of the fishery	The sum of all realized fisheries catches relative to the total net primary production
Primary production required to sustain catches (PPR)	Flows in each path towards the catch of a group are converted to primary production equivalents using the product of catch, production/consumption and the proportion of each group in the path in the diets of the other groups
<i>Energetic indicators</i>	
System primary production/respiration	Ratio between total primary production and total respiration. In mature systems, the ratio should approach 1
System primary production/biomass	Ratio between total primary production and total biomass. In mature systems, the ratio should decline
System biomass/throughput	Ratio between total biomass and total system throughput. In mature systems, the ratio should increase
<i>Network indicators</i>	
Finn's cycling index	Fraction of an ecosystem's throughput that is recycled
Relative ascendancy	Ratio between ascendancy and developmental capacity, a measure of ecosystem network efficiency (organization)

insensitive to changes in trophic web topology, but is strongly affected by energy flow changes.

Analysis of modeled prey consumption rates of predators (not shown) showed that horse mackerel, mackerel, hake and seabirds, consumed 28% and 46% of anchovy production during LN and EN conditions, respectively. Medium hake mainly preyed upon anchovy, sea robin, small pelagics and small demersals, while jumbo squid preyed upon mesopelagics and macrozooplankton.

Transfer efficiencies during LN conditions were similar as for other upwelling systems with most transfer efficiencies under 10% (Christensen and Pauly, 1995), except for a peak value at trophic level III (17%) due to high utilization of anchovy production (Fig. 5). The slight reductions of transfer efficiencies at high trophic levels during the EN conditions could reflect bottom-up control effects of anchovy over pinnipeds and seabirds. Majluf (1989) mentioned that reductions in the availability of anchoveta cause fur seals have to take a wider range of prey. Tovar et al. (1987) concluded that a lack of food is the ultimate cause for the mass mortalities of seabirds, as for every EN there is a corresponding decline of guano bird numbers. In general, during EN there was an increased utilization of energy at lower levels, while higher trophic levels have similar transfer efficiencies.

Consumption of macrozooplankton increased by 65% during EN conditions, assuming it was the main prey group in both periods for mesopelagic fishes. During EN, several immigrants come from equatorial and oceanic waters, such as chondrichthyans, mesopelagics (lightfish and lanternfish), other small pelagics and other large pelagics, which could impact different trophic levels. Mesopelagic *Vinciguerria* sp. are known to move towards the coast during EN, providing prey for jumbo squid. The increasing trend of jumbo squid, after 1997–98 EN, occurred in parallel to an increase of mesopelagics, thus a possible bottom-up control of mesopelagics over jumbo squid was explored with dynamic simulations (Taylor et al., 2008a).

3.3. Ecosystem indicators

Percentage changes of modelled ecosystem indicators from LN to EN (Table 6) showed that the overall reduction in primary production during EN, produced coherent changes in trophic, fisheries,

energetic and network indicators. Fishery indicators showed a reduction in catches, accompanied by lower catch/biomass ratio and pelagic catch/demersal catch ratio, but higher trophic level of the catch and primary production required/catch ratio. In the NHCE, the mean trophic level of the catch increased temporarily (+19%) during EN, mainly due to the increase of anchovy trophic level and a higher proportion of other species in the catch (e.g. mackerel, horse mackerel and other large pelagics). When only demersal fishes are taken into account, trophic level of the catch decreased during EN (from 3.66 to 3.34). However, at a larger spatio-temporal scale, the mean trophic level of the catch showed a decreasing trend from 1980 to 1994 in the South Eastern Pacific (Pauly et al., 1998), suggesting a fishing down the food web process, probably due to the recovery of anchovy, the main target species at low trophic level. Primary production required to sustain the fishery is a function of the trophic level of the species that are caught, as more primary production is required to produce one tonne of a high-level trophic fish, than of a low-level trophic fish.

Thus, despite lower catches during EN (−41%), the increased trophic level of target species resulted in a higher primary production required/catch (+39%), which implies an ecologically costly fishery and stresses the need for precautionary management during and after EN.

Most energetic indicators (net system production, net primary production and primary production/biomass ratio) decreased during EN (Table 4), except the higher system biomass/throughput ratio, apparently indicating a more energetically efficient ecosystem (Odum, 1969) during EN. However, network indicators such as lower Finn's cycling index and relative ascendancy indicated a less "organized" ecosystem during EN, which according to Ulanowicz (1986) reflects lower ecosystem growth and development. This result is similar to that of Jarre and Pauly (1993) who estimated a seasonal decrease of cycling in winter and spring, due to lower biomass and activity of zooplankton and benthos as the principal consumers of detritus. During the LN conditions trophic flows were more articulated, channelling energy flows mainly through anchoveta and showing better adaptation of cold water species to upwelling conditions. Using models before and after the anchovy collapse, Pauly (1987) also mentioned that the Peruvian upwelling ecosystem was better organized before 1972–73 EN than thereaf-

Table 5

Model outputs of the NHCE during (a) LN and (b) EN. Trophic level (*TL*), biomass (*B*), production (*P*), consumption (*Q*), ecotrophic efficiency (*EE*), gross efficiency (*GE*), catch (*C*), fishing mortality (*F*), non-predatory mortality (*MO*) and predatory mortality (*M2*). Parameters in bold were estimated by the model.

(a) LN Functional group/parameter	<i>TL</i>	<i>B</i> (t km ⁻²)	<i>P/B</i> (y ⁻¹)	<i>Q/B</i> (y ⁻¹)	<i>EE</i>	<i>GE</i>	<i>C</i> (t km ⁻² y ⁻¹)	<i>F</i> (y ⁻¹)	<i>MO</i> (y ⁻¹)	<i>M2</i> (y ⁻¹)
1. Diatoms	1.00	53.416	265.000	–	0.801	–	0.000	0.000	52.690	212.310
2. Dino- and silicoflagellates	1.00	9.426	265.000	–	0.960	–	0.000	0.000	10.643	254.357
3. Microzooplankton	2.25	20.484	256.000	1024.000	0.950	0.250	0.000	0.000	12.800	243.200
4. Mesozooplankton	2.13	31.164	40.000	125.000	0.515	0.320	0.000	0.000	19.397	20.603
5. Macrozooplankton	2.50	21.096	19.085	46.550	0.950	0.410	0.000	0.000	0.954	18.131
6. Gelatinous zooplankton	2.98	0.017	0.584	2.920	0.950	0.200	0.000	0.000	0.029	0.555
7. Macrobenthos	2.06	20.729	1.200	10.000	0.994	0.120	0.000	0.000	0.007	1.193
8. Sardine	3.16	7.567	1.400	14.000	0.853	0.100	7.969	1.053	0.206	0.141
9. Anchovy	2.35	83.293	2.000	20.000	0.469	0.100	30.474	0.366	1.063	0.572
10. Mesopelagics	3.49	6.882	1.400	14.000	0.575	0.100	0.000	0.000	0.595	0.805
11. Jumbo squid	4.18	0.524	8.910	25.457	0.940	0.350	0.186	0.354	0.534	8.021
12. Other Cephalopods	3.50	6.584	4.300	12.286	0.950	0.350	0.055	0.008	0.215	4.077
13. Other small pelagics	2.77	7.804	1.000	10.000	0.950	0.100	0.688	0.088	0.050	0.862
14. Horse mackerel	3.57	11.568	1.200	12.000	0.130	0.100	1.451	0.125	1.044	0.031
15. Mackerel	3.59	8.488	0.850	8.500	0.048	0.100	0.096	0.011	0.809	0.029
16. Other large pelagics	3.60	0.589	0.850	8.500	0.503	0.100	0.250	0.425	0.422	0.003
17. Small hake	3.77	2.771	0.928	6.187	0.623	0.150	0.975	0.352	0.350	0.226
18. Medium hake	3.66	0.414	1.627	10.847	0.394	0.150	0.218	0.526	0.987	0.114
19. Large hake	4.32	0.055	1.044	6.960	0.295	0.150	0.017	0.307	0.736	0.001
20. Flatfishes	3.60	0.040	0.304	2.027	0.821	0.150	0.006	0.158	0.055	0.091
21. Small demersals	2.45	7.089	2.300	15.333	0.950	0.150	0.019	0.003	0.115	2.182
22. Benthic elasmobranchs	3.48	0.078	1.000	6.667	0.401	0.150	0.031	0.401	0.599	0.000
23. Butter fishes	2.44	0.032	0.800	4.000	0.039	0.200	0.000	0.000	0.768	0.032
24. Conger	4.21	0.019	0.750	5.000	0.823	0.150	0.000	0.000	0.132	0.618
25. Medium demersal fish	3.38	0.200	1.320	8.800	0.997	0.150	0.125	0.626	0.005	0.690
26. Medium sciaenids	3.24	0.369	0.746	4.973	0.859	0.150	0.067	0.181	0.105	0.459
27. Sea robin	3.49	0.789	3.400	17.000	0.897	0.200	0.000	0.000	0.351	3.049
28. Catfish	3.31	0.577	0.900	6.000	0.893	0.150	0.068	0.118	0.096	0.686
29. Chondrichthyans	4.74	0.027	0.486	3.240	0.508	0.150	0.007	0.247	0.239	0.000
30. Seabirds	3.39	0.067	0.040	60.000	0.000	0.001	0.000	0.000	0.040	0.000
31. Pinnipeds	3.45	0.072	0.100	45.900	0.000	0.002	0.000	0.000	0.100	0.000
32. Cetaceans	4.25	0.062	0.100	20.000	0.000	0.005	0.000	0.000	0.100	0.000
33. Detritus	1.00	–	–	–	0.814	–	0.000	0.000	0.000	0.000
(b) EN 1. Diatoms	1.00	14.761	210.000	–	0.945	–	0.000	0.000	11.652	198.348
2. Dino- and silicoflagellates	1.00	17.328	210.000	–	0.841	–	0.000	0.000	33.286	176.714
3. Microzooplankton	2.18	6.572	256.000	1024.000	0.950	0.250	0.000	0.000	12.800	243.200
4. Mesozooplankton	2.24	17.000	40.000	125.000	0.947	0.320	0.000	0.000	2.104	37.896
5. Macrozooplankton	2.12	34.773	19.085	46.550	0.950	0.410	0.000	0.000	0.954	18.131
6. Gelatinous zooplankton	3.00	0.003	0.584	2.920	0.950	0.200	0.000	0.000	0.029	0.555
7. Macrobenthos	2.06	25.605	1.200	10.000	0.995	0.120	0.000	0.000	0.006	1.194
8. Sardine	2.99	8.318	1.400	14.000	0.396	0.100	3.334	0.401	0.846	0.153
9. Anchovy	3.17	33.340	2.000	20.000	0.679	0.100	14.477	0.434	0.642	0.924
10. Mesopelagics	3.12	22.375	1.400	14.000	0.137	0.100	0.000	0.000	1.208	0.192
11. Jumbo squid	4.14	0.243	8.910	25.457	0.853	0.350	0.014	0.058	1.305	7.547
12. Other Cephalopods	3.14	0.227	4.300	12.286	0.950	0.350	0.012	0.053	0.215	4.032
13. Other small pelagics	2.85	21.419	1.000	10.000	0.950	0.100	2.357	0.110	0.050	0.840
14. Horse mackerel	2.60	3.030	1.200	12.000	0.616	0.100	1.937	0.639	0.461	0.100
15. Mackerel	3.74	6.892	0.850	8.500	0.279	0.100	1.345	0.195	0.613	0.042
16. Other large pelagics	3.99	1.757	0.400	4.000	0.687	0.100	0.351	0.200	0.125	0.075
17. Small hake	3.59	1.245	1.317	8.780	0.909	0.150	0.556	0.447	0.120	0.751
18. Medium hake	3.89	0.163	1.946	12.973	0.354	0.150	0.107	0.656	1.257	0.033
19. Large hake	4.51	0.028	1.516	10.107	0.286	0.150	0.012	0.429	1.082	0.005
20. Flatfishes	4.14	0.010	0.304	2.027	0.882	0.150	0.001	0.100	0.036	0.168
21. Small demersals	2.49	4.897	2.300	15.333	0.950	0.150	0.016	0.003	0.115	2.182
22. Benthic elasmobranchs	3.33	0.045	1.000	6.667	0.933	0.150	0.042	0.933	0.067	0.000
23. Butter fishes	2.64	0.006	0.800	4.000	0.845	0.200	0.000	0.000	0.124	0.676
24. Conger	4.12	0.004	0.750	5.000	0.000	0.150	0.000	0.000	0.750	0.000
25. Medium demersal fish	3.11	0.211	2.480	16.533	0.905	0.150	0.144	0.682	0.236	1.561
26. Medium sciaenids	3.50	0.218	1.085	7.233	0.977	0.150	0.043	0.197	0.024	0.863
27. Sea robin	3.27	0.319	3.220	16.100	0.052	0.200	0.000	0.000	3.054	0.166
28. Catfish	3.01	0.650	0.900	6.000	0.937	0.150	0.544	0.837	0.057	0.006
29. Chondrichthyans	4.40	0.078	0.486	3.240	0.501	0.150	0.019	0.244	0.242	0.000
30. Seabirds	4.01	0.010	0.040	60.000	0.000	0.001	0.000	0.000	0.040	0.000
31. Pinnipeds	3.86	0.053	0.100	45.900	0.000	0.002	0.000	0.000	0.100	0.000
32. Cetaceans	4.05	0.067	0.100	20.000	0.000	0.005	0.000	0.000	0.100	0.000
33. Detritus	1.00	–	–	–	0.824	–	0.000	0.000	0.000	0.000

ter. On a smaller spatial scale, Taylor et al. 2008b also found a similar increase in energetic efficiency and decrease in ecosystem organization at Independencia Bay during EN.

In general, biomass and trophodynamic changes indicated that during 1997–98 EN, the ecosystem temporarily moved from its original optimum operating point (Kay, 1991), but returned to it, in

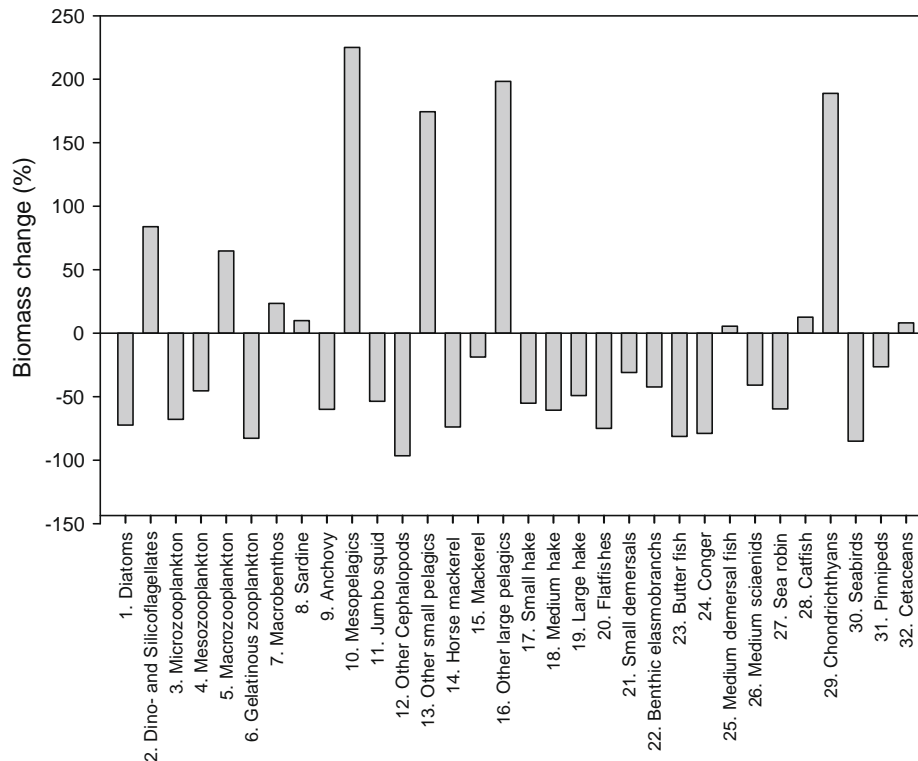


Fig. 2. Percentage biomass changes of functional groups from LN to EN.

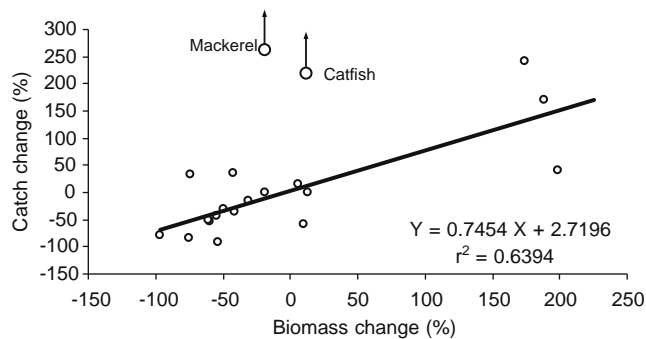


Fig. 3. Relationship between percentage biomass changes and percentage catch changes (excluding mackerel and catfish) from LN to EN.

agreement with the consideration that EN is a typical perturbation to the NHCE.

4. Conclusions

While past ecotrophic modeling efforts in the NHCE dealt with interdecadal changes (Jarre et al., 1991), this study focused on the interannual changes associated with El Niño and the Southern Oscillation (ENSO) cycle. The main finding of previous models was a decrease in relative ascendancy from the 1950s to the 1970s, after the decline of the anchoveta, which led to an increase in parallel energy transfer and food web connectance, as energy flows through anchovy were channeled through other species. Our models, with increased details in the planktonic and demersal groups, and incorporation of mesopelagic fishes and jumbo squid, determined three main impacts of EN on the food web: (i) dramatic

Table 6

Comparison of ecosystem indicators from models of the NHCE for both periods, including % change from LN to EN. Values in brackets are in percent of Total system throughput.

Ecosystem indicators	LN	EN	% Change
<i>Trophic indicators</i>			
Total system throughput ($t\ km^{-2}\ yr^{-1}$)	55,689	22,986	-58.7
Sum of all consumption ($t\ km^{-2}\ yr^{-1}$)	28,478 (51.1%)	12,259 (53.3%)	-57.0
Sum of all exports ($t\ km^{-2}\ yr^{-1}$)	2004 (3.6%)	718 (3.1%)	-64.1
Sum of all respiratory flows ($t\ km^{-2}\ yr^{-1}$)	14,688 (26.4%)	6065 (26.4%)	-58.7
Sum of all flows into detritus ($t\ km^{-2}\ yr^{-1}$)	10,519 (18.9%)	3944 (17.2%)	-62.5
Sum of all production ($t\ km^{-2}\ yr^{-1}$)	23,847	9957	-58.2
Total net primary production ($t\ km^{-2}\ yr^{-1}$)	16,653	6739	-59.5
Net system production ($t\ km^{-2}\ yr^{-1}$)	1965	674	-65.7
Total biomass (excluding detritus) ($t\ km^{-2}$)	302	222	-26.7
Mean transfer efficiency (II-IV)	10.17	11.72	15.2
Connectance index	0.168	0.174	3.6
System omnivory index	0.203	0.190	-6.4
<i>Fishery indicators</i>			
Total catches ($t\ km^{-2}\ yr^{-1}$)	42.70	25.31	-40.7
Mean trophic level of the catch	2.62	3.12	19.1
Gross efficiency (catch/total net primary production)	0.0026	0.0038	46.5
Total catch/total biomass	0.14	0.11	-19.2
Pelagic/demersal catches	26.98	16.28	-39.7
PPR ($t\ km^{-2}\ yr^{-1}$)	2420.1	1995.6	-17.5
PPR/total primary production (%)	14.5	29.6	103.8
PPR/catch	56.675	78.844	39.1
<i>Energetic indicators</i>			
System primary production/respiration	1.134	1.111	-2.0
System primary production/biomass	55.089	30.403	-44.8
System biomass/throughput	0.005	0.010	100.0
<i>Network indicators</i>			
Finn's cycling index	12.61	7.49	-40.6
Ascendancy/development capacity (%)	46.2	40.4	-12.6

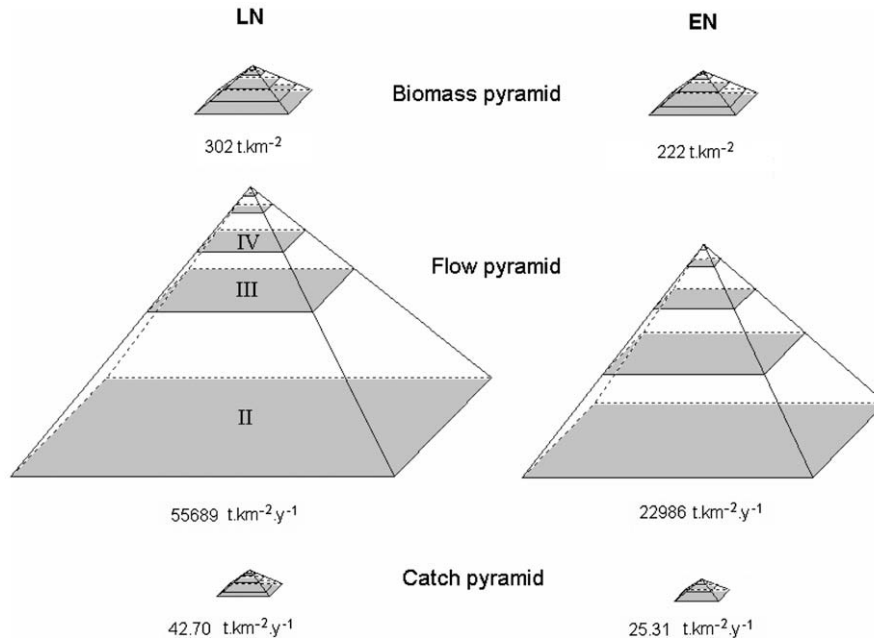


Fig. 4. Biomass (upper), energy flow (middle) and catch (lower) pyramids by discrete trophic levels in LN (left) and EN (right). The size of the pyramids is proportional to the values of biomass, energy flow or catch.

but temporary shrinking of ecosystem size in terms of flows and ecosystem organization, (ii) slight changes in overall functioning (i.e. proportion of energy flows used for respiration, consumption by predators, detritus and export), and (iii) use of alternate pathways through more zooplankton predation on primary producers, leading to a higher impact of the fishery on ecosystem flows. Con-

sequently, trophic level of piscivorous groups also increased. Sardine consumption of diatoms and dinoflagellates increased in order to compensate for the increased competition with anchovy for zooplankton, and because sardines are more efficient removers of small particles than anchovy (van der Lingen et al., 2006). A high biomass of macrozooplankton was needed to balance the con-

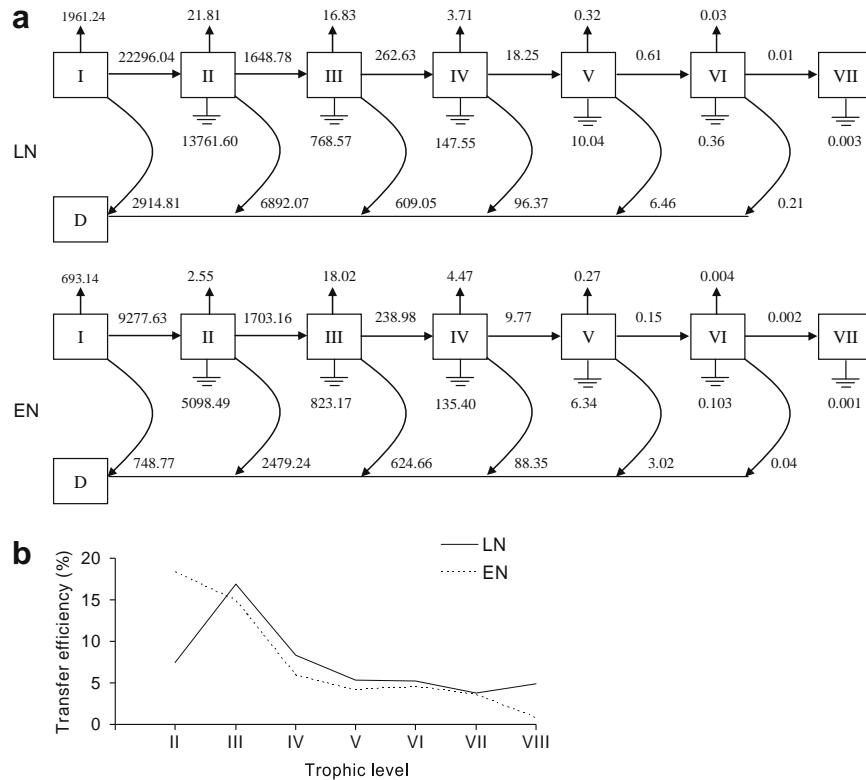


Fig. 5. Comparison of trophic structures in LN and EN: (a) NHCE canonical trophic food chains. Flow networks were aggregated into equivalent trophic chains with distinct trophic levels. Flows are in t.km⁻².y⁻¹, straight arrows indicate exports, ground symbols indicate respirational losses, and curved arrows indicate returns to detritus. (b) Transfer efficiencies by discrete trophic levels.

sumption by planktivores, especially during EN conditions when diatoms diminish dramatically. In these conditions, macrozooplankton consumed the remaining phytoplankton left by the reduced anchovy population. EN increased temporarily the trophic level of the catch, and despite lower catches, the higher PPR/catch ratio implied a stronger ecological impact of the fishery, which stresses the need for precautionary management during and after EN. Energetic indicators showed lower system primary production/biomass ratio during EN indicating a more energetically efficient ecosystem, however network indicators showed a lower cycling index, especially at higher trophic levels, and relative ascendancy suggesting a less organized ecosystem during EN conditions. These results give support to our general hypothesis that EN is a typical perturbation in the NHCE.

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