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Changes in trophic flow structure of Independence Bay (Peru) over an ENSO cycle

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ABSTRACT

During the strong warm El Niño (EN) that occurred in 1997/98, Independence Bay (14°S, Peru) showed a ca. 10 °C increase in surface temperatures, higher oxygen concentrations, and clearer water due to decreased phytoplankton concentrations. Under these quasi-tropical conditions, many benthic species suffered (e.g. macroalgae, portunid crabs, and polychaetes) while others benefited (e.g. scallop, sea stars, and sea urchins). The most obvious change was the strong recruitment success and subsequent proliferation of the scallop *Argopecten purpuratus*, whose biomass increased fiftyfold. To understand these changes, steady-state models of the bay ecosystem trophic structure were constructed and compared for a normal upwelling year (1996) and during an EN (1998), and longer-term dynamics (1996–2003) were explored based on time series of catch and biomass using Ecopath with Ecosim (EwE) software. Model inputs were based on surveys and landings data collected by the Instituto del Mar del Perú (IMARPE). Results indicate that while ecosystem size (total throughput) is reduced by 18% during EN, mainly as a result of decreased total primary production, benthic biomass remains largely unchanged despite considerable shifts in the dominant benthic taxa (e.g. scallops replace polychaetes as secondary consumers). Under normal upwelling conditions, predation by snails and crabs utilize the production of their prey almost completely, resulting in more efficient energy flow to higher trophic levels than occurs during EN. However during EN, the proliferation of the scallop *A. purpuratus* combined with decreased phytoplankton increased the proportion of directly utilized primary production, while exports and flows to detritus are reduced. The simulations suggest that the main cause for the scallop outburst and for the reduction in crab and macroalgae biomass was a direct temperature effect, whereas other changes are partially explained by trophic interactions. The simulations suggest that bottom-up effects largely control the system.

1. Introduction

The Humboldt Current System (HCS), located in the south east Pacific along the coasts of Chile and Peru, is one of the most productive marine systems in the world. This high productivity is the result of 'coastal upwelling' – a phenomenon driven by southerly trade winds that brings cold, nutrient-rich water from 40 to 80 m up into the euphotic zone where it supports phytoplankton growth (Barber et al., 1985; Arntz et al., 1991; Pennington et al., 2006). As a result, the system supports a large biomass of small planktivorous pelagic fish – comprising the bulk of catches by a large purse seining fleet. An important fishery also exists down to 15–30 m and in the intertidal areas (Arntz and Valdivia, 1985a; Arntz et al., 1988). Despite a relatively low annual harvest (ca. 200,000 t yr^{-1}) compared to the pelagic system, the exploited nearshore species are of high commercial value and the fishery supports thousands of fishers and their families (Wolff et al., 2003).

Under 'normal' upwelling periods, near-seafloor oxygen concentrations <0.5 ml l^{-1} are typical on the continental shelves of Peru (<100 m; Zuta et al., 1983). This is due to the oxygen minimum zone which occurs below the shallow, uplifted Peruvian thermocline (OMZ; 50–600 m) and the sinking of decomposing organic matter from the overlying euphotic zone (Arntz et al., 2006). Bacteria such as the filamentous 'spaghetti' bacteria (genus *Thioplaca*), are commonly found in association with the OMZ (Arntz et al., 1991). At shallower depths, oxygen concentrations increase and are able to support a higher benthic biomass.

These coastal phenomena propagate into Peru's bays, where much artisanal fishing occurs. This is seen in Independence Bay (~14°S) where the deeper regions of the bay (>30 m) are of low biomass while the bay's shallower perimeter is targeted by the artisanal fishery. These shallow areas contain valuable molluscan and crustacean species, but suspension feeding polychaetes dominate biomass (Tarazona et al., 1991).

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The HCS experiences 'natural' climate variations on seasonal, interannual, and decadal time scales, all of which affect the system's productivity and fisheries. Off Peru the strongest interannual perturbation is the warm "El Niño" (EN) phase of the El Niño Southern Oscillation (ENSO). ENs last about 18 months and occur irregularly every 3–5 years. During EN a Kelvin wave travels eastwards on the equator across the Pacific then north and south along the South American coast, where it depresses the normally shallow thermocline and a raises sea level (Pennington et al., 2006). Although Peruvian coastal upwelling continues during EN, water upwells from above the thermocline and is thus nutrient poor (Barber and Chavez, 1983). As a result, the area of 'productive habitat' supported by coastal upwelling is greatly reduced in area (>1.0 mg chl*a* m^{-3}; Nixon and Thomas, 2001), as is overall primary production (Carr, 2002). This reduction in production at the base of the food web negatively impacts many pelagic coastal species (Tam et al., 2008; Taylor et al., 2008).

EN can also produce significant positive faunal changes in benthic habitats, mainly as a result of increased oxygen levels (Arntz et al., 1991). This is especially the case in shallow depths, where faunal density, biomass, species richness, and diversity can all increase during EN (Tarazona et al., 1988). Several species from offshore, equatorial, and subtropical coastal areas also migrate to the Peruvian coast during EN, such as swimming crabs and penaeid shrimps (Arntz et al., 1991). In Independence Bay the resident scallop *Argopecten purpuratus* experiences much higher recruitment and growth during EN. Past El Nino densities have reached up to 8 kg m^{-2} and densities of 129 adult scallops $\cdot\ m^{-2}$ (Wolff, 1987; Arntz and Tarazona, 1990), which is about 50 times the normal level. Yearly surveys of the macrobenthos of Independence Bay (Fig. 1) conducted by the Instituto del Mar del Perú (IMARPE) have also observed EN biomass decreases in several functional groups (e.g. macroalgae, benthic detritivores, herbivorous gastropods, predatory gastropods, portunid crabs, and polychaetes); while scallops proliferate to nearly replace polychaetes as the main benthic consumer of plankton and detritus (Fig. 2).

During both of the strong ENs of 1982/83 and 1997/98, *A. purpuratus* became the principal target of the diving fishery, which experienced "gold rush" conditions with high catches and enormous revenues (Wolff, 1987, 1988, 1994; Wolff and Mendo, 2000; Mendo and Wolff, 2002). The fishing effort increased mainly due to migration of fishers from other areas. Catches largely reflect actual changes in the scallop population. Other high-price species associated with the scallop habitat are octopus and crab. Crab catches decreased during the 1997/98 EN, but octopus landings increased nearly 5-fold. Pelagic predatory fish migrated towards the coast during EN, such that catch of the line and net fishing fleet increased by about 2.5 times.

While we have a good basic understanding of the main changes to benthic communities associated with EN in Peru, trophic modeling of the effects of EN has not yet been employed. Here we describe and model the Independence Bay ecosystem from an energy flow perspective. First, we compare steady-state trophic models of the system for the upwelling and El Nino conditions, and secondly we explore the drivers of these changes (trophic vs. environmental) using dynamic simulations with performance measured against time series data of changing biomass. In particular, we address the following questions: (i) Are the positive impacts observed in the shallow benthic community during EN (increase in species richness, and diversity) also reflected in the entire ecosystem through indicators of system maturity? (ii) How is the system reorganized during EN? (iii) What insight can be gained into the management of the fishery during EN? (iv) Can changes in biomass and productivities be explained by direct responses to warming, or to trophic interactions? (v) What is the trophic effect of the increased scallop biomass, the reduced primary production (through biomass decrease of phytoplankton as well as macroalgae), and the reduced crab predator biomass on the system?

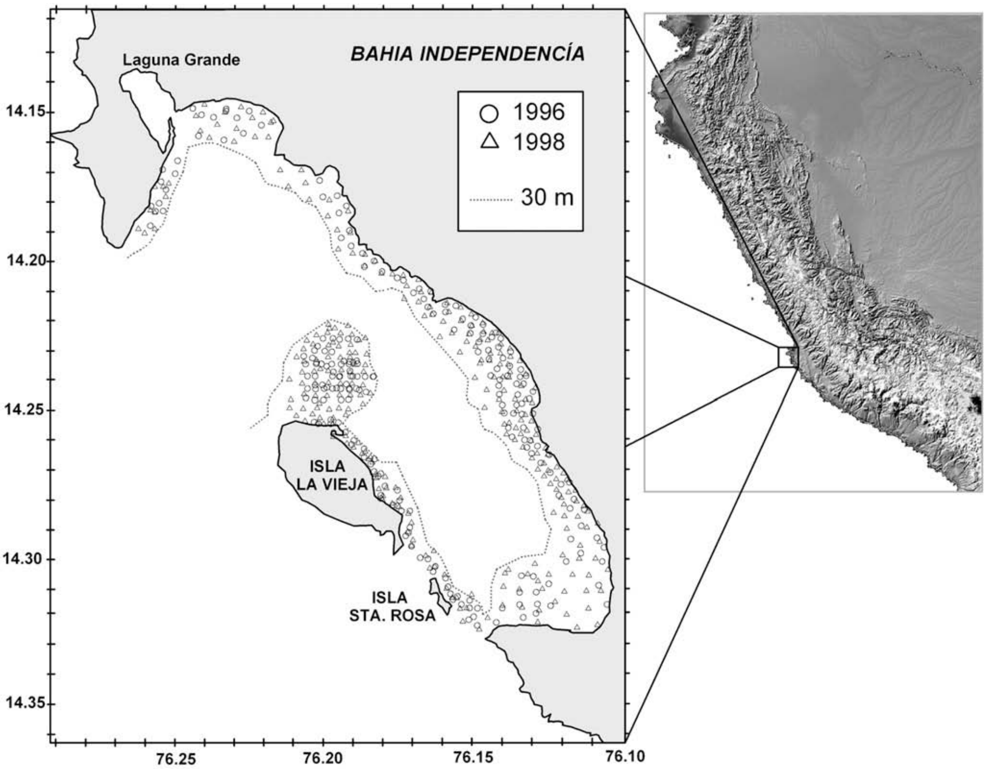

Fig. 1. Map of the Peruvian coast and the study site, Independence Bay. Macrobenthic fauna sampling stations are indicated by circles for 1996 ($n = 223$) and triangles for 1998 ($n = 252$). The 30 m depth isocline is indicated by a dashed line.

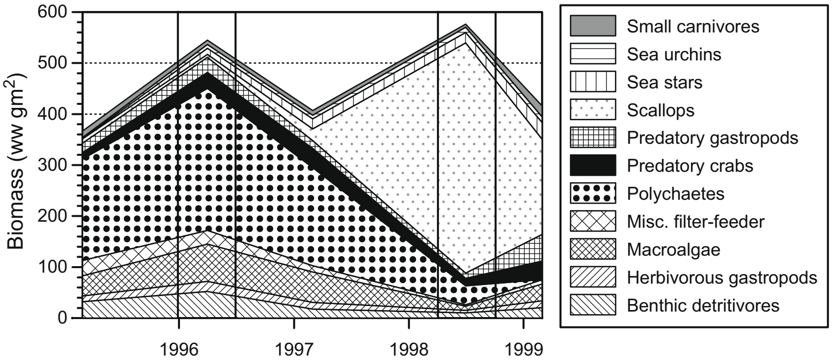

Fig. 2. Biomass changes of benthic macrofauna observed from 1995 to 1999 (IMARPE). Boxes indicate model periods.

2. Materials and methods

2.1. Study area

Independence Bay (14.238°S, 76.194°W) is located approximately 250 km southeast of Lima (Fig. 1). The bay is broadly open to the coastal ocean on either side of 'Isla La Vieja'. Conditions within the bay thus largely reflect the nearshore Peruvian upwelling system, characterized by low surface temperatures (14–18 °C) and high nutrient levels. Bottom (<30 m) oxygen concentrations averaging 3.5 mg L^{-1} during normal upwelling conditions, but in the deeper central part of the bay, low oxygen conditions prevail (<1.0 mg L^{-1}, >30 m) and benthic macrobiota is not abundant and microbial processes dominate. During a strong EN, temperatures increase as much as 10 °C and oxygen conditions are improved at the lower depths. Artisanal fisheries include a diving fishery using hookah and compressor, which operates around the bay's rocky and soft-bottom habitats less than 30 m, and a gillnet and line fishery that targets larger littoral and pelagic fish species.

2.2. Model definition

The two steady-state trophic models of Independence Bay were constructed for the soft-bottom habitats of <30 m depth that fringe the bay, covering about 38% of the total bay area (65.8 km^2 out of a total of 172 km^2; Fig. 1). This area was selected for the following reasons: (i) importance in overall bay macrobiota biomass, (ii) availability of data, and (iii) it encompasses the main activities of the artisanal fishery. Model periods are for 1996, representing a 'normal' upwelling year, and 1998, representing EN (end of the 1997/98 event; Fig. 2). The models were constructed with 20 functional groups including detritus, two primary producers (phytoplankton and macroalgae), zooplankton, six benthic primary consumers (polychaetes, scallops, sea urchins, herbivorous gastropods, benthic detritivores, and miscellaneous filter-feeders), five benthic carnivores (predatory gastropods, small carnivores, predatory crabs, sea stars, and octopus), three fish (littoral fish, small pelagic fish, and pelagic predatory fish), and two top predators (marine mammals and seabirds). These functional groups were designated according to ecological status – organisms within a group are characterized by similar diets, predators, productivities and individual body size (Table 1).

2.3. Basic modeling approach

A mass-balance modeling approach was applied using the software Ecopath with Ecosim 5.0 (EwE) (Christensen and Pauly, 1992; Walters et al., 1997), which quantifies trophic flows among functional groups within an ecosystem and also includes fishery catch. The model also permits the assessment of ecosystem dynamics under different scenarios of use or environmental change (http://www.ecopath.org). Ecopath links the production and consumption of all trophically connected groups within the model ecosystem, as

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

where P_i is the total production rate of (i), Y_i is the total fishery catch rate of (i), B_i the biomass of the group (wet weight), E_i the net migration rate (emigration–immigration), $M2_i$ is the total predation rate for group (i), BA_i is the biomass accumulation rate for (i). $P_i{}^{*}$ $(1 - EE_i)$ is the 'other mortality' rate ($M0_i$), where EE is the "Ecotrophic efficiency" and is the proportion of the group's production that is consumed by higher trophic levels or is taken by the fishery (for further information, see Christensen et al., 2000). In order to ensure mass balance between the groups, a second master equation is used:

$$\textit{Consumption} = \textit{production} + \textit{respiration} + \textit{unassimilated food}$$

Energy flow in the model requires definition of the diet for all consumers, which determines the fraction of each functional group which will serve as food of the other groups. This diet matrix is further used in the calculation of the trophic level of each group:

$$TL_j = 1 + \sum TL_i * DC_{ij} \qquad (2)$$

where DC_{ij} is the fraction of prey (i), in the diet of the predator (j). The trophic level of the predator TL_j is calculated as the mean trophic level of its prey ($\sum TL_i{}^{*} DC_{ij}$) plus 1.0. Primary producers and detritus groups are assigned a trophic level of 1.0.

2.4. Input parameters

Input parameters, detailed below, are derived from a number of sources which are listed in Table 2. Input values for 1996 and 1998 steady-state models can be found in 3.

2.4.1. Biomass

Benthic macrofauna biomass was from IMARPE surveys for the periods 19–29th April, 1996 and 15–24th July, 1998. A total of 223 and 252 1 m^2 quadrants were sampled during the two surveys, respectively. All epifauna and infauna of the upper 5 cm of sediment were collected by hand and placed in mesh bags of 5 mm mesh size. Organisms were later counted and weighed (for further information on sampling, see Samamé et al., 1985; Yamashiro et al., 1990). Groups of small epifauna (herbivorous gastropods, benthic detritivores, scallops, small carnivores) and polychaetes were increased by 25% to correct for undersampling. Miscellaneous filter-feeders (consisting mainly of infaunal bivalves) were increased by 100% to also correct for undersampling—much of this group's biomass is found deeper than 5 cm. These biomass correc-

Table 1
Functional groups and representative species. Species listed are not exhaustive (small benthos groups show the most important species, representing >95% of biomass and/or species averaging >1 g m^2); **, groups/species not found/recorded in captures in 1998; *, groups/species found in 1998 but low in biomass; bold: groups/species not found/recorded in captures in 1996.

Functional group	Species
2. Macroalgae	*Rhodymenia* sp.*, *Macrocystis* sp.*, *Gigartina* sp.*, *Codium* sp.**, *Ulva* sp.*, ***Caulerpa sp., Lessonia nigrescens***
4. Polychaetes	*Diopatra* sp., ***Chaetopteridae***
5. Scallops	*Argopecten purpuratus*
6. Sea urchins	*Tetrapigus niger*, *Arbacia spatuligera*, *Arbacia* sp., *Loxechinus albus*, ***Strongylocentrotus*** sp.
7. Herbivorous gastropods	*Crepipatella dilatata*, *Crepipatella* sp., *Tegula euryomphalus*, *Tegula atra*, *Tegula* sp., *Crucibulum* sp., *Aplysia* sp., *Mitrella* sp.
8. Benthic detritivores	*Ophiuroidea**, *Pagurus* sp., *Eurypanopeus sp.**, *Taliepus marginatus* **
9. Misc. filter-feeders	Ascidians, *Aulacomya ater*, *Glycimeris ovata*, *Actinia* sp., *Prothothaca thaca*, *Sponges*, *Semele solida*, *Chama* sp.
10. Predatory gastropods	*Bursa ventricosa*, ***Bursa nana***, *Bursa* sp., *Thais chocolata*, *Thaididae* sp., *Priene rude*, *Cymatium weigmani*, *Cymathidae* sp., *Argobuccinum* sp.**, *Sinum cymba*
11. Small carnivores	*Oliva peruviana*, *Oliva* sp., *Nassarius dentifer*, *Nassarius gayi*, *Nassarius* sp., *Trophon* sp.**, *Crassilabrum crassilabrum*, *Natica* sp.**, *Xantochorus* sp., ***Solenosteria gatesi, Solenosteria sp., Polinices uber***
12. Predatory crabs	*Cancer setosus*, *Cancer porteri*, *Cancer coronatus***, *Cancer sp.*, *Hepatus chilensis*,, *Platyxanthus cockeri***, ***Callinectes arcuatus***, ***Callinectes sp***.
13. Sea stars	*Luidia bellonae*, *Luidia magallanica*, *Luidia* sp., *Asterina chilensis.***, *Patiria chilensis*, ***Heliaster helianthus***
14. Octopus	*Octopus mimus*
15. Littoral fish	*Isacia conceptionis*, *Seriolella violacea*, *Paralabrax humeralis*, *Cheilodactylus variegatus*, *Labrisomus philippii*, *Hemilutjanus macrophthalmos*, *Acanthistius pictus*, *Paralichthys adspersus*, *Cynoscion analis*, *Sciaena deliciosa*, *Calamus brachysomus*, *Mugiloides chilensis*, *Diplectrum conceptione*, *Chloroscombrus orqueta*, *Sphyraena ensis*, *S. idiastes*, *Myliobatis peruvianus*, *Orthopristis chalceus*, *Mugil cephalus*, ***Diplectrum conceptione***, ***Chloroscombrus orqueta***, ***Sphyraena ensis***, ***Sphyraena idiastes***, ***Myliobatis peruvianus***
16. Small pelagic fish	*Sardinops sagax sagax*, *Ethmidium maculatum*, ***Trachinotus paitensis***
17. Pelagic predatory fish	*Trachurus picturatus murphyi*, *Cilus gilberti*, *Scomber japonicus*, ***Sarda chiliensis chiliensis***, ***Auxis rochei***, ***Scomberomorus sierra***
18. Marine mammals	*Otaria byronia*, *Arctocephalus australis*
19. Seabirds	*Leucocarbo bougainvillii*, *Sula variegata*, *Pelecanus thagus*

tions were based on complementary benthic evaluations conducted by the authors.

Estimates of phytoplankton biomass for the 1996 model were taken from Peruvian coastal averages under 'typical' upwelling conditions (settled volume, 3.0 mL m^{-3}) (Rojas de Mendiola et al., 1985) and EN conditions (Delgado and Villanueva, 1998; Villanueva et al., 1998). EN phytoplankton values were increased slightly over coastal averages (+15%) in order to balance the model. Settled volumes were converted to g m^{-2} by assuming 1 mL = 1 g and then multiplying by an average depth for the model area of 15 m by assuming a well-mixed water column.

Information on zooplankton in Independence Bay is of qualitative nature only (Yamashiro et al., 1990); thus zooplankton biomass was left open to be calculated by the steady-state model assuming an Ecotrophic efficiency (*EE*) of 0.95.

Biomass of mobile species such as octopus and fish were estimated from catch data by assuming that the fishery takes 50% of yearly produced biomass. Small pelagic fish are not a principal target of the artisanal fishery and so catch estimates are likely poor indicators of the available biomass. Small pelagic fish biomass was thus left open to be calculated by the steady-state model assuming an *EE* of 0.95 (Table 3).

2.4.2. Catches

Estimates of catch were derived from IMARPE catch statistics for the artisanal fishery from the two main landing sites for Independence Bay – San Andres and Laguna Grande. Unfortunately, landings data do not identify habitat of capture, so that it was necessary to estimate the relative sizes of the bay's habitats in the model (ca. 10% rocky, 90% soft-bottom) and correct for the fact that most rocky habitat catches are made outside the model area (ca. 10 × greater than within the model). Taking into account the associations of functional groups with particular habitats, their catch statistics were adjusted as follows: scallops and predatory crab catches come *only* from the soft-bottom habitats of the model and thus did not need correction; fish groups, octopus, and miscellaneous filter-feeders, *primarily* found in soft-bottom habitats, were reduced by only 10% to correct catches associated with rocky habitats. Conversely, catches of herbivorous gastropods, predatory gastropods, and sea urchins were mainly associated with broken shell or rocky substrates, and were thus reduced by 80% (Table 3).

2.4.3. Production/biomass (total mortality)

Direct estimates of production to biomass ratios (*P*/*B*) or Total mortality (*Z*) existed for several benthic invertebrate groups in the model – scallops, predatory crabs, and sea stars. Other groups were estimated using empirical relationships from Brey (2001) taking into account taxonomic group, mean body size, temperature of habitat, feeding modes, and habitat type. In most cases this provided realistic estimates; however, values for polychaetes and misc. filter-feeders were increased to 1.0 based on other estimates from the literature (Table 3).

P/*B* of phytoplankton was estimated using a modified Eppley curve (Eppley, 1972) as described by Brush et al. (2002):

$$G = G_{\max} * f * LTLIM * NUTLIM \tag{3}$$

where G = realized daily growth rate (d^{-1})(base e), f is the fraction of the day during which there is light, and *LTLIM* and *NUTLIM* are dimensionless ratios from 0 to 1 which describe light and nutrient limitation of growth, respectively (Kremer and Nixon, 1977). $G_{\max}$, as given by Eppley (1972) describes an exponentially-shaped envelope for growth rates of phytoplankton under culture conditions without light or nutrient limitation (as recalculated by Brush et al., 2002):

Table 2

Sources of input data. IE = IMARPE benthic macrofauna evaluation, EM = empirical model (Brey, 2001), EO = Ecopath output, GU = guess estimate, IC = iterative consumption routine (for opportunistic feeding; described herein), IS = IMARPE landings statistics.

Functional group/parameter	Biomass – B_i (t km^{-2})	Production rate – P_i/B_i (y^{-1})	Consumption rate – Q_i/B_i (y^{-1})	Conversion efficiency – GE_i	Ecotrophic efficiency – EE_i	Catches – Y_i (t km^{-2} y^{-1})	Diet composition – DC
1. Phytoplankton	GU based on Rojas de Mendiola et al. (1985), Delgado and Villanueva (1998)	GU based on modified Eppley curve (Eppley, 1972; Brush et al., 2002)	–	–	EO	–	–
2. Macroalgae	IE	GU based on Macchiavello et al. (1987)	–	–	EO	–	–
3. Zooplankton	EO	GU based on Mendoza (1993), Hutchings et al. (1995)	GU adapted from Polovina and Ow (1985)	EO	GU	–	GU
4. Polychaetes	IE	GU based on Martin and Grémare (1997)	EO	GU	EO	–	GU
5. Scallops	IE	Mendo et al. (1987), Stotz and Gonzalez (1997)	GU based on Wolff (1994)	EO	EO	IS	GU based on Rouillon et al. (2002)
6. Sea urchins	IE	EM	EO	GU	EO	IS	GU
7. Herbivorous gastropods	IE	EM	EO	GU 0.3 based on Mann (1982)	EO	IS	GU
8. Benthic detritivores	IE	EM	EO	GU	EO	–	GU
9. Misc. filter-feeders	IE	GU based on Wolff (1994)	EO	GU	EO	IS	GU
10. Predatory gastropods	IE	EO	GE based on Huebner and Edwards (1981)	GU 0.3 based on Huebner and Edwards (1981)	EO	IS	GU, IC
11. Small carnivores	IE	EM	EO	GU	EO	–	GU partially based on Keen (1972) for gastropod spp., IC
12. Predatory crabs	IE	Wolff and Soto (1992)	Lang (2000), Wolff and Soto (1992)	EO	EO	IS	GU based on Leon and Stotz (2004), IC
13. Sea stars	IE	Ortiz and Wolff (2002)	EO	GU	EO	–	GU, IC
14. Octopus	GU based on catch data	EO	Wolf and Perez (1992), Vega and Mendo (2002)	Wolf and Perez (1992), Vega and Mendo (2002)	EO	IS	GU, IC
15. Littoral fish	GU based on catch data	GU 1.2 based on Wolff (1994)	EO	GU	EO	IS	GU based on FISHBASE (2006)
16. Small pelagic fish	EO	GU	EO	GU 0.1 based on Moloney et al. (2005)	GU	IS	GU based on FISHBASE (2006)
17. Pelagic predatory fish	GU based on catch data	GU 0.85 based on Jarre et al. (1991)	EO	GU 0.1 based on Moloney et al. (2005)	EO	IS	GU based on FISHBASE (2006)
18. Marine mammals	GU	GU based on Jarre et al. (1991)	EO	GU	EO	–	GU
19. Seabirds	GU	GU based on Moloney et al. (2005)	EO	GU based on Moloney et al. (2005)	EO	–	GU
20. Detritus	EO	–	–	–	–	–	–

Table 3

Input-output parameters for steady-state models of Independence Bay in 1996 and 1998 after application of the Ecoranger resampling routine. In bold, Ecopath calculated parameters. B_i = Biomass, P_i/B_i = production rate, Q_i/B_i = consumption rate, EE_i = ecotrophic efficiency, GE_i = gross efficiency or conversion efficiency (P_i/Q_i), F_i = fishing mortality, $M0_i$ = non-predation mortality, $M2_i$ = predation mortality.

Functional group/parameter	Trophic Level		B_i (t km^{-2})		P_i/B_i (y^{-1})		Q_i/B_i (y^{-1})		EE_i		GE_i		Catch (t y^{-1})		F_i		$M0_i$		$M2_i$	
	1996	1998	1996	1998	1996	1998	1996	1998	1996	1998	1996	1998	1996	1998	1996	1998	1996	1998	1996	1998
1. Phytoplankton	**1.00**	**1.00**	51.398	24.816	255.228	366.172	–	–	**0.340**	**0.958**	–	–	0.000	0.000	0.000	0.000	168.495	15.261	86.734	350.911
2. Macroalgae	**1.00**	**1.00**	69.204	8.656	15.840	17.954	–	–	**0.136**	**0.375**	–	–	0.000	0.000	0.000	0.000	13.685	11.217	2.155	6.737
3. Zooplankton	**2.23**	**2.26**	**28.270**	**29.425**	45.827	38.767	175.677	145.755	0.890	0.916	**0.261**	**0.266**	0.000	0.000	0.000	0.000	5.027	3.240	40.800	35.527
4. Polychaetes	**2.06**	**2.06**	324.892	45.927	0.899	1.042	**5.611**	**4.844**	**0.603**	**0.299**	0.160	0.215	0.000	0.000	0.000	0.000	0.357	0.731	0.542	0.311
5. Scallops	**2.00**	**2.00**	7.049	434.504	1.576	2.305	10.037	**14.789**	**0.806**	**0.458**	**0.157**	0.156	2.230	235.421	0.316	0.542	0.306	1.248	0.954	0.515
6. Sea urchins	**2.10**	**2.10**	7.925	11.040	0.551	0.650	**2.589**	**2.891**	**0.949**	**0.563**	0.213	0.225	1.458	0.002	0.184	0.000	0.028	0.284	0.339	0.366
7. Herbivorous gastropods	**2.00**	**2.00**	25.244	5.952	0.925	1.101	**2.778**	**3.793**	**0.788**	**0.943**	0.333	0.290	0.177	0.012	0.007	0.002	0.196	0.063	0.722	1.036
8. Benthic detritivores	**2.00**	**2.00**	70.679	11.314	0.989	1.337	**5.425**	**5.287**	**0.845**	**0.801**	0.182	0.253	0.000	0.146	0.000	0.013	0.153	0.267	0.836	1.057
9. Misc. filter-feeders	**2.24**	**2.22**	82.134	12.111	1.018	0.987	**4.859**	**4.762**	**0.949**	**0.994**	0.210	0.207	1.389	1.935	0.017	0.160	0.052	0.006	0.949	0.821
10. Predatory gastropods	**2.93**	**2.98**	28.104	10.955	**1.653**	**1.407**	4.731	4.549	**0.805**	**0.640**	0.349	0.309	1.326	1.838	0.047	0.168	0.322	0.506	1.284	0.733
11. Small carnivores	**2.96**	**2.99**	9.974	7.595	0.897	0.790	**4.952**	**3.705**	**0.918**	**0.865**	0.181	0.213	0.000	0.000	0.000	0.000	0.073	0.106	0.824	0.684
12. Predatory crabs	**3.35**	**3.09**	27.781	14.870	2.165	2.191	9.889	9.092	**0.930**	**0.191**	**0.219**	**0.241**	3.417	1.673	0.123	0.113	0.151	1.772	1.891	0.306
13. Sea stars	**3.11**	**3.03**	11.567	20.286	0.692	0.734	**3.254**	**3.446**	**0.860**	**0.304**	0.213	0.213	0.000	0.000	0.000	0.000	0.097	0.511	0.595	0.223
14. Octopus	**3.57**	**3.15**	0.315	1.425	4.878	4.809	**11.441**	**12.361**	**0.846**	**0.614**	0.426	0.389	0.749	3.153	2.377	2.212	0.750	1.854	1.750	0.742
15. Littoral fish	**2.86**	**2.99**	1.774	0.353	1.307	1.139	**10.426**	**10.281**	**0.846**	**0.951**	0.125	0.111	0.977	0.206	0.551	0.584	0.201	0.056	0.555	0.500
16. Small pelagic fish	**2.24**	**2.26**	**5.869**	**23.144**	1.939	2.168	**20.868**	**17.957**	0.967	0.867	0.093	0.121	0.298	0.195	0.051	0.008	0.063	0.288	1.825	1.871
17. Pelagic predatory fish	**3.24**	**3.26**	1.360	11.516	0.771	0.845	**7.928**	**7.710**	**0.679**	**0.449**	0.097	0.110	0.584	4.349	0.430	0.378	0.248	0.466	0.093	0.002
18. Marine mammals	**3.45**	**3.39**	0.052	0.010	0.101	0.100	**49.087**	**38.278**	**0.000**	**0.000**	0.002	0.003	0.000	0.000	0.000	0.000	0.101	0.100	0.000	0.000
19. Seabirds	**3.30**	**3.33**	0.056	0.009	0.034	0.036	**62.560**	**52.151**	**0.000**	**0.000**	0.001	0.001	0.000	0.000	0.000	0.000	0.034	0.036	0.000	0.000
20. Detritus	**1.00**	**1.00**	–	–	–	–	–	–	**0.187**	**0.483**	–	–	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

$$G_{\max} = 0.97 * e^{0.0633*T} \tag{4}$$

where T = water temperature. The 'normal' upwelling phytoplankton production 1996 assumed a mean temperature of 16 °C with 50% light (from self-shading) and 0% nutrient limitation factors, while the EN condition of 1998 assumed a mean temperature of 26 °C with 80% light and 50% nutrient limitation factors. Calculated P/B ratios were high (245 and 365 for 1996 and 1998, respectively) yet the value of total production for the 1996 model in terms of carbon, i.e. ~800 g C m^{-2} yr^{-1}, using a wet weight:C conversion of 14.25:1 from Brown (1991), is conservative with respect to other estimates for the Peruvian coastal system under upwelling conditions, i.e. >1000 and >1500 g C m^{-2} yr^{-1} from Walsh (1981) and Chavez and Barber (1985), respectively. P/B values for other groups are taken from the literature (Table 2).

2.4.4. Consumption and Conversion efficiency

Direct estimates of consumption rates (Q/B) were available for a few of the benthic invertebrate groups (octopus, scallops, predatory gastropods, and predatory crabs). For most other groups, ratios of Conversion efficiency (GE) or the ratio between Production and Consumption (P/Q) were applied (Tables 2 and 3).

2.4.5. Diet matrices

Direct diet studies for Independence Bay are limited and thus general knowledge from literature was used in the construction of diet matrices (Table 2). Initial attempts to balance the 1996 model resulted in insufficient production of many smaller epifaunal herbivore and detritivore invertebrate groups (scallops, sea urchins, herbivorous gastropods, benthic detritivores, and misc. filter-feeders) to meet the initial consumption values of the carnivorous benthic invertebrate groups (predatory gastropods, small carnivores, predatory crabs, sea stars, and octopus). As macroinvertebrate groups are described to be rather unselective and opportunistic feeders, limited more by their modes of feeding (Wilson and Parkes, 1998), diet proportions were adjusted to reflect both predatory consumption rates and the available production of prey groups. This was accomplished by iteratively distributing the prey production to the predators in weekly consumption increments, assuming unselectivity. When the production of a single prey group was completely utilized, the following iteration would consider only those prey not fully utilized. Base values of detritus feeding were assumed and the calculated diets resulted in high proportions of polychaetes in their diets – reflecting their high biomass and production in the benthic system in 1996. The 1998 situation was less problematic due to a reduction of carnivorous benthic invertebrate biomass as well as an increase in scallop biomass as prey (see Section 3). Assuming that scallops would be favored prey, their proportion in diet was set high (60–75%) and the remaining diets were calculated as above (Table 4). Diets for fish species were obtained from FishBase (Froese and Pauly, 2006) and were adjusted to the fish groups based on relative species contribution from recorded catches.

2.5. Addressing parameter uncertainty

The balanced steady-state model for 1996 was subjected to the EwE resampling routine *Ecoranger* (Christensen and Walters, 2004) in order to assess the probability distributions of the input parameters. Using a Monte Carlo approach, the routine drew a set of random input variables from normal distributions for each basic parameter, and all resulting combinations that satisfied mass-balanced constraints were recorded. Originally we allowed the routine to use confidence intervals as derived from a pedigree of the data sources, where highest confidence is placed in locally-derived data; however, the initial results often gave parameter values

Table 4
Diet matrices for steady-state trophic models of Independence Bay for 1996 and 1998 after application of the Ecoranger resampling routine (values of 0.000 indicates a proportion of <0.0005).

Prey/predator	Model	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1. Phytoplankton	1996	0.702	0.293	0.787				0.709							0.802			
	1998	0.698	0.301	0.821				0.721							0.795			
2. Macroalgae	1996				0.811	0.783	0.191							0.235				
	1998				0.808	0.801	0.226							0.255				
3. Zooplankton	1996	0.190	0.051					0.195		0.002				0.513	0.198	0.470		
	1998	0.208	0.047					0.175		0.002				0.340	0.205	0.521		
4. Polychaetes	1996				0.090				0.398	0.462	0.292	0.384		0.207				
	1998				0.091				0.052	0.074	0.027	0.039		0.094				
5. Scallops	1996								0.018	0.011	0.011	0.014	0.065					
	1998								0.746	0.613	0.765	0.758	0.743					
6. Sea urchins	1996									0.030		0.032						
	1998									0.059		0.034						
7. Herbivorousgastropods	1996								0.046	0.037	0.032	0.033	0.069					
	1998								0.026	0.031	0.016	0.017	0.033	0.019				
8. Benthic detritivores	1996								0.159	0.149	0.094	0.106	0.194	0.003				
	1998								0.055	0.072	0.028	0.034	0.056	0.015				
9. Misc. filter feeders	1996								0.196	0.164	0.134	0.164	0.220					
	1998								0.049	0.056	0.025	0.029	0.030					
10. Predatory gastropods	1996										0.108	0.145	0.255	0.001				
	1998										0.033	0.037	0.050	0.031				
11. Small carnivores	1996								0.020	0.015	0.015	0.014	0.045	0.000				
	1998								0.021	0.030	0.012	0.016	0.027	0.024				
12. Predatory crabs	1996										0.191			0.001				
	1998										0.033			0.028				
13. Sea stars	1996										0.025			0.000				
	1998										0.031			0.093				
14. Octopods	1996												0.153					
	1998												0.060					
15. Littoral fish	1996													0.001			0.251	0.093
	1998													0.026			0.098	0.100
16. Small pelagic fish	1996													0.001		0.530	0.699	0.907
	1998													0.015		0.479	0.847	0.900
17. Pelagic predatory fish	1996																0.050	
	1998																0.055	
18. Marine mammals	1996																	
	1998																	
19. Seabirds	1996																	
	1998																	
20. Detritus	1996	0.108	0.655	0.213	0.099	0.217	0.809	0.096	0.164	0.129	0.097	0.109		0.038				
	1998	0.094	0.653	0.179	0.101	0.199	0.774	0.104	0.051	0.063	0.032	0.036		0.059				

outside of reasonable biological constraints (e.g. high conversion efficiencies, high cannibalism) and thus we decided to fix all confidence intervals at 20% variation as was similarly done by Arias-González et al. (1997). We allowed resampling until 10,000 runs passed the selection criteria. The 'best' run was then chosen as that with the smallest sum of square residuals between the input parameters and the mean value of all successful runs (for more information, see Christensen et al., 2000).

2.6. Outputs/system statistics

Statistics for comparison of the two system states fall under the categories of community energetics, cycling indices, and system organization. Comparisons of the 'health' and maturity of the two system states drew on statistics from all three areas. Further general descriptive statistics from the calculated outputs of the models included: (i) total throughput (T) – measure of the total sum of flows within the system and indicates the 'size' or activity of the system; (ii) contributions to T from different types of flows – consumption, export, respiration and flows to detritus; (iii) breakdown of biomass and flows from different components of the system – pelagic vs. benthic biomass and production; and (iv) changes in feeding modes – Herbivory: detritivory ratios.

2.6.1. Community energetics

Several indices of community energetics allowed for the comparison of ecological succession and relative maturity according to Odum (1969) and include: (i) total primary production (PP) to total respiration (R) ratio (PP/R); (ii) biomass (B) supported by total primary production (PP/B); (iii) biomass supported by total throughput (B/T); and iv) energy transfer efficiency (TE) between discrete trophic levels.

2.6.2. Cycling indices

The Finn's cycling index (FCI) (Finn, 1976) is calculated as Tc/T, where Tc is the amount of system flows that are recycled compared to the total system throughput, T. According to Odum (1969) recycling increases in more mature and less stressed systems.

2.6.3. Growth and development indices

Global measurements of system organization are calculated according to a network analysis based on flows among elements in the system as defined by Ulanowicz (1986). Indices include the aforementioned throughput (T), along with a measure of ascendancy (A), and development capacity (C). Ascendancy incorporates both size and organization of flows into a single measure and is calculated as throughput (T) multiplied by mutual information (I), which concerns the diversity and evenness of flows between compartments (Baird et al., 1998). Development capacity is the theoretical upper limit to ascendancy and thus the dimensionless A/C ratio allows for a comparable measure of ecosystem development and is predicted to be higher in more mature ecosystems (Ulanowicz, 1986). The difference between development capacity and ascendancy ($C–A$) is the system overhead (Φ) and gives a measure of the system's 'strength in reserve' from which it can draw to meet perturbations (Ulanowicz, 1986).

2.6.4. Fishery

Other statistics allow for the assessment of the fishery activity such as its Gross efficiency (catch/net PP), mean trophic level of the catch, and primary production needed to sustain the fishery.

2.7. Simulating transition from upwelling to El Niño state

The simulation runs conducted for this study with EwE calculate biomass changes through time by solving the set of differential equations:

$$dB_i/dt = g_i\left[\sum\nolimits_k Q_{ki}(t)\right] - \sum\nolimits_j Q_{ij}(t) - M0_iB_i - \sum F_{if}(t)B_i \tag{5}$$

For species or functional groups $i = 1,\ldots, n$. The first sum represents the food-consumption rate, Q, summed over prey types k of species i, and g_i represents the growth efficiency (proportion of food intake converted into production). The second sum represents the predation loss rates over predators j of i. $M0_i$ represents the instantaneous natural mortality rate due to factors other than modelled predation. The final sum represents the instantaneous fishing mortality rate, F, as a sum of fishing components caused by fishing fleets f.

The Q_{ij} are calculated by assuming that the B_i are divided into vulnerable and invulnerable components (Walters et al., 1997), and it is the flux rates v_{ij} and v'_{ij} that move biomass into the vulnerable and invulnerable pools, respectively. This assumption leads to the rate equation:

$$Q_{ij} = \frac{a_{ij}(t)v_{ij}(t)B_iB_j}{v_{ij}(t) + v'_{ij} + a_{ij}(t)B_j} \tag{6}$$

where the v_{ij} and v'_{ij} parameters represent rates of behavioral exchange between vulnerable and invulnerable states and a_{ij} represents rate of effective search by predator j for prey type i. The exact setting of the v_{ij}, remains uncertain, but the modeling software allows for adjusting the vulnerabilities by a fitting procedure through which the sum of squares between observed and simulated (log) biomasses are minimized (see Walters et al., 1997). In EwE, the vulnerabilities for each predator–prey interaction can be explored by the user and settings will determine if control is top-down (i.e., Lotka-Volterra; >2.0), bottom-up (i.e., donor-driven; <2.0), or intermediate (≈2.0). We applied this fitting routine with our time series, and the computed vulnerabilities were then discussed in the light of possible control mechanisms operating in the ecosystem.

As input for simulations of the ecosystem response to ENSO we used catch per unit of effort (CPUE) time series for the fishery

Table 5

Biomass data for model groups derived from IMARPE benthic surveys in Independence Bay (1996, 1997, 1998, and 1999). Longer time series (1996–2003) were calculated from estimates of catch per unit effort (CPUE). Relative CPUE changes were used to reconstruct the longer time series relative to the 1996 starting values from the steady-state model.

Year/groups	Pp-1	Ma-2	Po-4	Sc-5	Su-6	Hg-7	Bd-8	Mf-9	Pg-10	Sc-11	Pc-12	Ss-13	Oc-14	Lf-15	Ppf-17
1996	51.4	69.2	324.9	7.0	7.9	25.2	70.7	82.1	28.1	10.0	27.8	11.6	0.3	1.8	1.4
1997	28.6	56.6	224.2	28.5	7.4	16.5	24.2	37.7	14.5	10.6	31.4	19.6	0.7	1.5	1.8
1998	28.6	7.6	43.5	564.2	10.9	6.7	13.8	8.2	9.8	6.8	4.5	20.1	0.2	0.2	2.7
1999	51.4	31.1	0.2	233.3	11.7	17.1	27.8	26.7	49.2	25.2	13.9	32.3	0.1	1.7	1.3
2000	51.4			120.6							29.8		0.1	2.4	0.3
2001	51.4			16.1							73.8		0.1	2.4	9.3
2002	51.4			2.7							41.6		0.1	3.5	3.5
2003	51.4			3.7							39.2		0.1	3.8	3.9

resources for the period 1996–2003 (including the EN year 1998) as proxies for stock biomass, together with biomass data obtained from the benthic surveys done by IMARPE for the years 1996, 1997, 1998 and 1999 (Table 5).

To distinguish between trophic and non-trophic effects on functional group biomass changes, we forced biomass changes of several functional groups (drivers) in the model to measure their impact. Drivers included biomass changes in 4 highly-variable functional groups whose abundances are known to be at least partially controlled by non-trophic environmental changes associated with ENSO: phytoplankton (*PP*), macroalgae (*MA*), predatory crabs (*C*) and scallops (*S*). We successively forced the biomass changes of these groups for the simulated time period of 8 years (1996–2003) and recorded the changes in fit as calculated by the sum of squares between the predicted and observed estimates.

An initial exploration of the dynamics using the default predator–prey vulnerability settings for all interactions either decreased the fit of the simulation or made only small improvements. Thus, we decided to first introduce all four drivers in combination and allowed EwE to search for the best predator–prey vulnerability settings. Using these optimized vulnerability settings we again addressed the importance of each driver through single or combined introduction to force the model through time.

3. Results

3.1. General descriptive

Initial parameters of the balanced model can be found on the Pangaea website (Taylor et al., 2007a, b). The Ecoranger resampling routine resulted in balanced models in 0.75% and 2.20% of the runs for the 1996 (normal conditions) and 1998 (EN conditions) models, respectively. The 'best' fitting model parameters are shown in Table 3. Summary statistics are presented in Table 6. The 'size', as measured by the total system throughput (*T*), indicates that the 1996 state was larger than 1998 (34,208 vs. 24,827 t km^{-2} yr^{-1}) mainly as a function of higher primary production. Contributions to *T* from different types of flows indicate that the EN state is characterized by higher absolute and relative flows due to consumption (11,918 t km^{-2} yr^{-1} and 48.0% of *T*) and respiration (7097 t km^{-2} yr^{-1} and 28.6% of *T*) and lower absolute and relative flows into detritus (14.8% of *T*) and as exports (8.6% of *T*). These results indicate better utilization of primary production through increased consumption and decreased losses to detritus as is reflected by the increased *EE* values for phytoplankton and detritus compartments. The overall ratio of herbivory to detritivory feeding decreased slightly during 1998 (6.54 and 5.22 for 1996 and 1998, respectively). Ratios between pelagic and benthic biomass and production were similar for both 1996 and 1998 states with the benthic system dominating in terms of biomass (pelagic/benthic biomass ratios equal 0.13 and 0.14 for 1996 and 1998, respectively) while the pelagic components accounted for most of the production (pelagic/benthic production ratios equal 8.46 and 7.79 for 1996 and 1998, respectively). Besides major changes in primary production between the two periods, which greatly impacted *T*, the overall biomasses of trophic levels II and above are virtually unchanged despite significant changes to several individual functional groups.

3.2. Community energetics

Several statistics on community energetics point to EN conditions as being of a higher 'maturity' than normal conditions. The primary production to total respiration ratio (*PP*/*R*) came closer to the proposed value of 1.0 for mature systems (Odum, 1969) (2.979 in 1996; 1.302 in 1998). Total primary production to biomass (*PP*/*B*) and biomass to total throughput (*B*/*T*) ratios indicated

Table 6
System statistics, cycling indices, and informational indices for the two modeled periods of Independence Bay. Changes in values from the 1996 state to the 1998 state are given as a percent; values in brackets are in percent of total system throughput.

Summary statistics	1996	1998	% Change
Sum of all consumption (t km^{-2} yr^{-1})	8389 (24.5%)	11,919 (48.0%)	42.1
Sum of all exports (t km^{-2} yr^{-1})	9444 (27.6%)	2145 (8.6%)	−77.3
Sum of all respiratory flows (t km^{-2} yr^{-1})	4772 (14.0%)	7097 (28.6%)	48.7
Sum of all flows into detritus (t km^{-2} yr^{-1})	11603 (33.9%)	3666 (14.8%)	−68.4
Total system throughput (t km^{-2} yr^{-1})	34208	24827	−27.4
Sum of all production (t km^{-2} yr^{-1})	16133	11610	−28.0
Calculated total net primary production (t km^{-2} yr^{-1})	14214	9242	−35.0
Net system production (t km^{-2} yr^{-1})	9442	2146	−77.3
Total biomass (excluding detritus) (t km^{-2})	754	674	−10.6
Pelagic/benthic biomass	0.13	0.14	15.6
Pelagic/benthic production	8.46	7.79	−8.0
Connectance index	0.222	0.224	0.9
System omnivory index	0.169	0.122	−27.8
Herbivory/detritivory	6.54	5.22	−20.2
Fishing			
Total catches (t km^{-2} yr^{-1})	12.605	248.930	1874.9
Mean trophic level of the catch	2.73	2.05	−24.9
Gross efficiency (catch/net PP)	0.001	0.027	2936.5
PP required/catch	29.39	9.26	−68.5
PP required/total PP (%)	1.43	17.85	1148.3
Community energetics			
Total primary production/total respiration	2.979	1.302	−56.3
Total primary production/total biomass	18.861	13.715	−27.3
Total biomass/total throughput	0.022	0.027	22.7
Cycling indices			
Finn's cycling index (% of total throughput)	5.11	8.88	73.8
Predatory cycling index (% of throughput w/o detritus)	9.07	5.14	−43.3
System development			
System overhead/capacity (%)	67.0	72.5	−1.2
Ascendancy/capacity (%)	33.0	27.5	−16.7

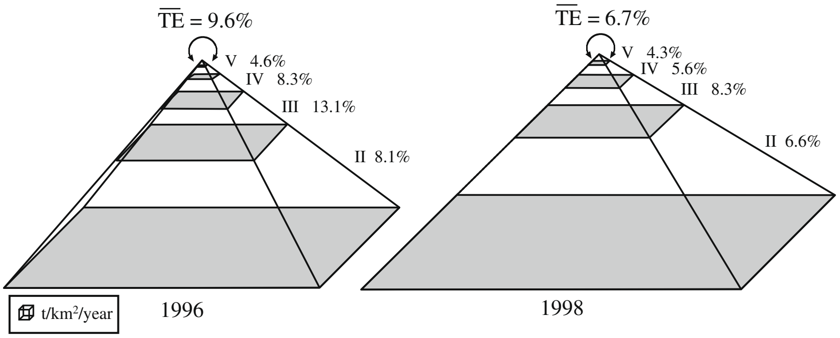

Fig. 3. Modified Lindeman pyramids of flows for steady-state models of Independence Bay. Transfer efficiencies are given for discrete trophic levels. Mean transfer efficiency is the geometric mean of trophic levels II–IV.

that the 1998 state could support a higher relative biomass per unit of primary production and total throughput. On the contrary, mean transfer efficiency (*TE*) was higher for the 1996 state (Fig. 3) due in part to a high utilization of herbivore and detritivore production by predatory invertebrates, as well as higher cannibalism, and can be observed in the high *EE* values for these groups (groups 5–14, Table 3). This 'bottleneck' of flows did not occur in 1998 due both to a decrease in predator biomass and an increase in primary consumer biomass due to the proliferation of scallops. As *TE* can only be calculated for consumer groups, and Ecopath does not quantify solar energy input to producer compartments, mean *TE* reflects the geometric mean of trophic levels II–IV only. Thus, the decrease in *TE* occurred despite an overall improvement in other holistic community energetic indices in 1998; specifically, a higher utilization of primary production and detritus.

3.3. Cycling indices

A higher degree of cycling, as indicated by the Finn's cycling index, was calculated for the EN period (5.11% for 1996; 8.88% for 1998). Again, the higher utilization of primary production and detritus was mainly responsible for this result. Removing this influence is possible with the related Predator cycling index, which showed that the 1996 state had more cycling at the higher trophic levels (9.07% for 1996; 5.14% for 1998).

3.4. Growth and development indices

The ascendancy to development capacity ratio (*A/C*) was slightly higher during normal upwelling conditions in 1996 (33.0% for 1996; 27.5% for 1998) and indicates that this state shows more maturity (i.e. higher total flows and predictability of flows).

3.5. Fishery

The boom of *A. purpuratus* during EN was mostly responsible for the more than 18-fold increase in total catches for the model area, to 248.9 t km^{-2} yr^{-1}. Pelagic predatory fish catches also increased about 7-fold, and as a result the model back-calculated a higher small pelagic fish biomass for 1998. The gross efficiency (catch/net *PP*) of the fishery increased 25-fold and the primary production required per unit of catch decreased, due mainly to the lower trophic level of the scallop (mean *TL* of catch – 2.74 and 2.05 for 1996 and 1998, respectively). The variable nature of the diving effort in response to changing resource abundances also played an important role. As the catch of scallops mainly drove the changes in effort, scallops show fairly similar fishing mortality (*F*) values for the two periods, while other groups that were reduced in biomass during 1998 show higher *F* values (misc. filter-feeders and predatory gastropods) (Table 3). Overall, the expansion of the fishery, combined with the decreased primary productivity, resulted in a value of 18% of total primary production needed to sustain the fishery – an 11-fold increase from 1996.

3.6. Functional group responses to forcing scenarios

The results of the forcing of trophic driver biomasses on the dynamics of remaining functional groups are presented for four scenarios in the following paragraphs.

3.6.1. Scenario 1 (S1): Decrease in primary production during EN (due to lack of nutrient upwelling)

As shown by Fig. 4, a decrease in phytoplankton and macroalgae biomass during EN (1997/98) resulted in decreases in polychaetes, misc. filter-feeders and herbivorous gastropods. A slightly lagged response is also seen in predatory gastropods, which decreased in biomass. While the single addition of the macroalgae driver decreased SS more than did that of the phytoplankton driver (−8.1% for macroalgae; −2.7% for phytoplankton), the average change in combination with other drivers was greater from the phytoplankton driver at −2.8% (Fig. 5).

3.6.2. Scenario 2 (S2): Decrease in predatory crab biomass during EN (due to temperature stress causing mortality and migration to deeper waters)

The application of this driver resulted in a small increase in biomass of the groups sea stars and small carnivores as a result of the reduced crab biomass (Fig. 4). The application of the predatory crab driver resulted in an average change of −4.8% in SS (Fig. 5).

3.6.3. Scenario 3 (S3): Increase in scallop biomass during EN (due to increased recruitment and growth)

Fig. 4 shows the functional group responses to the increased Scallop biomass during the EN warming, which included: (1) abundance increases in predatory gastropods, small carnivores, octopus, sea stars, and (2) abundance decreases in the groups polychaetes, herb. gastropods, benthic detritivores, and misc. filter-feeders. The model also predicts an increase in predatory crab biomass, which is contrary to the observed decrease, supporting the observation that EN warming likely induced a non-trophically mediated mass mortality and emigration of crabs to deeper, cooler waters (Arntz and Fahrbach, 1991). Despite some improvements, the average change from the application of the scallop driver was an increase of 1.8% in SS (Fig. 5), indicating a decrease in fit.

3.6.4. Scenario 4 (S4): Combined forcing of all four drivers (scallops, phytoplankton, macroalgae, and predatory crabs)

The previously mentioned improvements from each driver sum upto explain the dynamics in the majority of groups (Fig. 4). In most cases, the forced dynamics are similar to a dominating individually

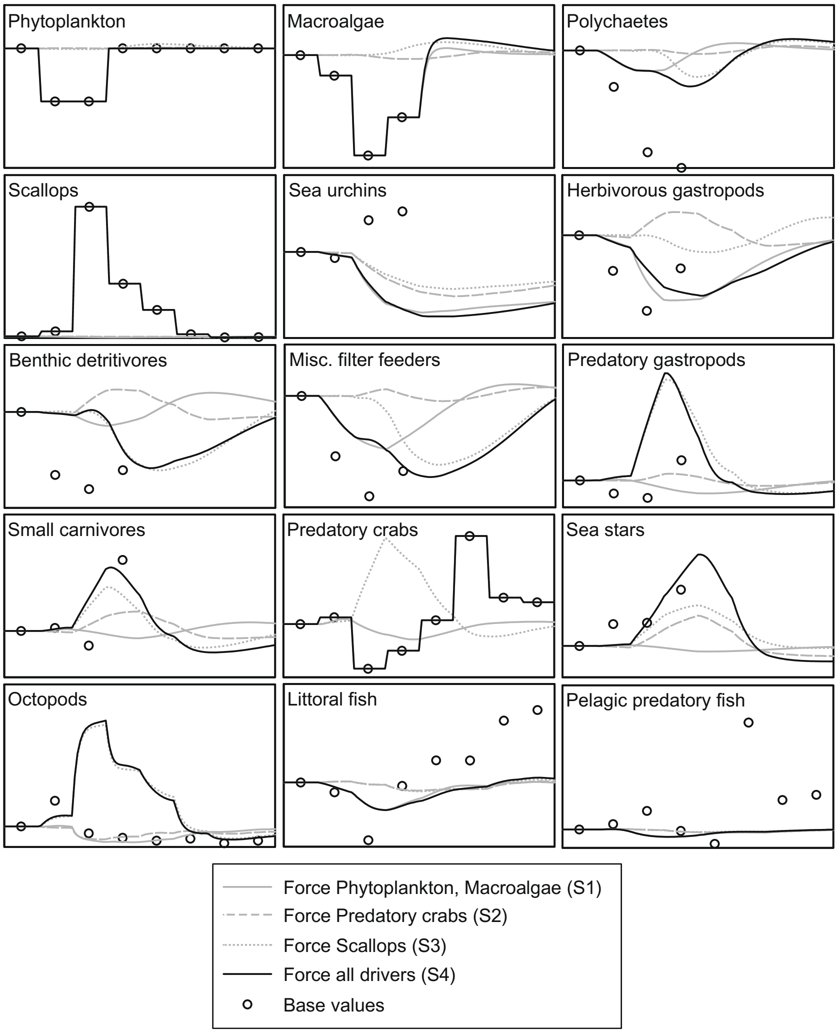

Fig. 4. Simulated versus observed biomass changes. All simulations consider changes in fishing effort (fishing and diving). Simulation trajectories are shown for each of the three scenarios (S1, bottom-up effect of reduced primary production – "Force Phytoplankton, Macroalgae"; S2, top-down effect of reduced benthic predation – "Force predatory crabs"; and S3, effect of scallop proliferation – "Force scallops") plus a combination of all four drivers applied together (S4, "Force all drivers").

forced driver; however, the dynamics of small carnivores and sea stars are improved by the combined application of all four drivers.

3.7. Vulnerability estimates

Table 7 summarizes the vulnerabilities computed for Scenario 4. v-values <1.2 were considered bottom-up control (BU), between 1.2 and 2 (mixed control, MX) and above 2 top-down control (TD).

Accordingly, top-down control is suggested for: (i) predatory gastropods on polychaetes, benthic detritivores and misc. filter-feeders; (ii) predatory crabs on scallops; and (iii) sea stars on predatory gastropods.

Bottom-up control configurations are more dominant and are suggested for: (i) polychaetes to predatory crabs; (ii) scallops to predatory gastropods and octopus; (iii) primary producers and zooplankton prey to fish groups; and (iv) littoral fish and small pelagic fish to marine mammals and seabirds.

4. Discussion

4.1. Summary statistics, flow structure and maturity

The total energy throughput of the Independence Bay ecosystem under normal upwelling conditions (1996 model; T = 34,208 t km^{-2} yr^{-1}) is higher than has been observed for other coastal zones along the Pacific coast, specifically, Gulfo Dulce, Costa Rica (T = 1404) and Tongoy Bay, Chile (T = 20,835 t km^{-2} yr^{-1}) (Wolff, 1994; Wolff et al., 1996), due mainly to its high primary production. When our results are compared to models of specific habitats in Tongoy Bay as constructed by Ortiz and Wolff (2002), the sand-gravel habitat is most similar in terms of total throughput (T = 33,579 t km^{-2} yr^{-1}). This type of substrate is typical of Independence Bay and is associated with strong currents where oxygen concentrations are increased through mixing and circulation and permit higher macrofaunal biomass. Similar values of production, energy flows to detritus, respiration, and exports are also observed between this habitat in Tongoy Bay and the model of Independence Bay under upwelling conditions.

While our estimate of Total throughput is not directly comparable to models that use differing units to describe flows (e.g. dry weight or carbon units), we can compare the proportions of different types of flows. Flow to detritus in Independence Bay during 1996 (33.9%) is similar to that of Tongoy (29%) as well as several US bay systems; e.g. Narragansett Bay (33%), Delaware Bay (30%), and Chesapeake Bay (27%) (Monaco and Ulanowicz, 1997). However, only the models of the South American bays calculated high proportions of exports as well (29–34% vs. 7–10% for US bays). Part of the difference may be attributable to higher exchange rates/low

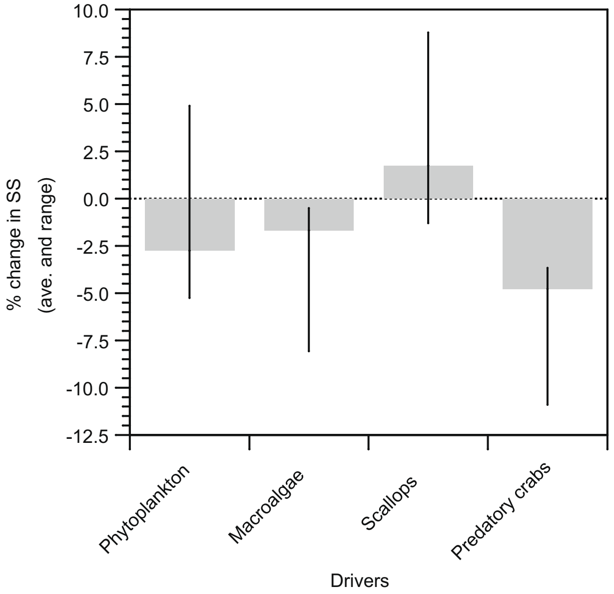

Fig. 5. Percent changes to sum of squares, *SS*, of the 1996–2003 simulation after the forcing of biomass changes of several functional groups 'drivers'. Drivers were applied in all possible sequences and combinations and *SS* was corrected for artificial improvements caused by the fitting of the driver's dynamics. Average change (bar) and range (line) are displayed. Negative values (i.e. decrease in *SS*) indicate an improvement in fit.

residency time of water in relatively open bays like Independence and Tongoy, resulting in more export of production (Rybarczyk et al., 2003); however, the high degree of primary production going unutilized and remaining in the sediments may be more typical of upwelling systems.

The dynamic nature of the artisanal fishery in response to changes in resources helps maintain the ecosystem's efficiency in the face of reduced predation pressure. In response to the scallop boom during EN, fishers migrated to Independence Bay. A main proportion of these migrant fishers were from Sechura Bay in the north of Peru (6 °S), where the largest fishery for scallops is normally found. These fishers were mainly involved in the diving fishery, which increased in effort by 170% in 1998 compared to the previous year. Peak diving effort reached 4932 boat trips per month (October 1998) compared to normal levels of around 750. Fishers also shifted effort to almost exclusively target scallops, yet other soft-bottom species were also taken. Octopus (*Octopus mimus*) is a particularly favored resource due to high price, and also increases in biomass during EN (Arntz et al., 1988). *O. mimus* growth and reproduction have been shown to increase under warmer conditions (Cortez et al., 1999) and embryonic development time is also greatly accelerated under EN-like conditions in the laboratory (Warnke, 1999). The increased catch of octopus is thus likely supported by increased production. Catch of pelagic predatory fish also increased, which may be explained through the overall shrinkage of the upwelling zone during EN and the subsequent intrusion of oceanic waters, which several predatory fish species are associated with (e.g. *Scomber japanicus, Sarda chilensis*, and *Scomberomerus sierra*). This movement may be further related to the pursuit of prey, as anchovy stocks were observed to both concentrate near the coast and then retreat southward to the latitudes near Independence Bay as recorded by acoustic surveys (Ñiquen and Bouchon, 2004).

The expansion of the diving fishery during EN is also observed through much higher indices of gross efficiency (catch/net PP) such that 18% of total primary production required to sustain the fishery. This value is lower than the value (25.1%) calculated by Pauly and Christensen (1995) for upwelling systems, and may reflect low mean trophic level of the fishery (2.05). Nevertheless, for an artisanal fishery, it shows a remarkable efficiency of harvest during EN. On the contrary, the value for normal conditions is extremely low at 1.4%, and illustrates the low level of exploitation of the fishery during normal upwelling periods, likely due to the low abundance of higher priced species like scallops and octopus. As a result, Independence Bay fishers are moving towards a combination of fishing and culture of scallops to maintain income levels between EN "boom times".

Nixon (1982) showed that there is a highly positive correlation between primary production and fishery yield in coastal lagoons, yet Independence Bay catches are highest during the low primary production characteristic of EN. While the fish catches also increased during EN mainly due to immigrations of fish towards the coast, the catch of benthic resources increased the most. Increased oxygen concentration during EN has been suggested as important in the proliferation of benthic species (Arntz and Fahrbach, 1991). Overall consumption of primary production by several primary consumers (i.e. scallops, herbivorous gastropods, and ben-

Table 7
Vulnerabilities calculated by EwE with the application of all four drivers (phytoplankton, macroalgae, scallops, predatory crabs). BU = Bottom-up control (vulnerability ≪ 2.0), TD = top-down control (vulnerability ≫ 2.0), MX = mixed/intermediate control (vulnerability values between 1.2 and 2.0).

	Prey/predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	Phytoplankton	BU	MX	MX				MX							BU			
2	Macroalgae				MX	MX	MX							BU				
3	Zooplankton	TD	MX					MX		MX				BU	BU	BU		
4	Polychaetes				MX				TD	MX	BU	MX		BU				
5	Scallops								BU	MX	TD	MX	BU					
6	Sea urchins									MX		MX						
7	Herbivorous gastropods								MX	MX	MX	MX	MX					
8	Benthic detritivores								TD	MX	MX	MX	BU	MX				
9	Misc. filter-feeders								TD	MX	BU	MX	BU					
10	Predatory gastropods										BU	TD	BU	MX				
11	Small carnivores								MX	MX	MX	MX	MX	MX				
12	Predatory crabs										MX			MX				
13	Sea stars										MX			MX				
14	Octopus												TD					
15	Littoral fish													MX			BU	BU
16	Small pelagic fish													MX		BU	BU	BU
17	Pelagic predatory fish																MX	
18	Marine mammals																	
19	Seabirds																	
20	Detritus	MX	BU	MX	MX	MX	MX	MX	BU	MX	MX	MX		BU				

thic detritivores) increased in order to sustain their increased biomasses – as calculated from *in situ* or empirically-based estimates. As a result, primary production during EN appears to be almost completely consumed in Independence Bay, although several assumptions were made concerning the levels of primary production. However, near-complete use of primary production during EN may be indicated by the clear, tropical-like water and decreases in benthic detrital material observed during EN. Based on the model, recruitment and production increases of scallops account for this result, as scallops consume 58% of phytoplankton production during EN. Wolff et al. (2007) found that the increase in scallops was likely a non-trophic effect resulting from increased larval survival in warmer temperatures. This recruitment success combined with increased oxygen concentrations is likely the main cause of the increase in fisheries yield.

Indicators of system maturity show some contradictions – some suggest normal conditions are more mature and developed while others for the EN state (1998). From a community energetics point of view, the EN state is able to support a similar biomass compared to 1996 despite lower primary production (*PP*/*B* ratio) and total throughput (*B*/*T* ratio), and thus the system's primary production to respiration ratio is closer to the value of 1.0 predicted for mature and efficient systems (Odum, 1969). Similarly, an increased Finn's cycling index is observed during EN due to a better utilization of primary production and detritus by the primary consumers (mainly scallops). These larger energy flows at lower trophic levels offset the negative impacts of EN at the higher trophic levels. During EN the transfer efficiencies (*TE*) of higher trophic levels are decreased and contribute to an overall lower mean *TE*, due to the negative impact of EN on benthic predatory groups (predatory gastropods, small carnivores, and especially predatory crabs). These impacts are also observed through a decreased predatory cycling index and Finn's mean path length during EN, indicating poorer cycling and transfer of energy in the higher trophic levels of the food web.

Relative ascendancy (*A*/*C*) indicates slightly more ecosystem development and maturity during 1996 (33.0% in 1996; 27.5% in EN). Related is the percent overhead (Φ/C), which indicates that the less mature EN state may be better able to withstand perturbation. Baird et al. (1991) found a similar discrepancy when comparing *A*/*C* to *FCI* in several marine ecosystems, where a negative correlation between indices was observed even though both should have increased with system maturity. They suggested that the discrepancy may lie in the fact that stress frequently impacts higher-level species more than lower-level species. As a result, the release of standing biomass of higher trophic levels can be taken up through increased recycling via "short intense loops".

It does appear that the higher trophic levels were more severely impacted by EN in Independence Bay. Furthermore, the most significant short intense loop would be the cycle through detritus, which increases during EN and results in the higher Finn's cycling index (*FCI*). As phytoplankton and macroalgae production were reduced during EN (9247 t m^{-2} y^{-1} during EN; 14,214 t m^{-2} y^{-1} during normal conditions), and consumption of detritus by scallops actually increased, the proportion of recycled detritus is significantly higher in 1998.

This result depends on the decreased primary production during EN. To illustrate, we can increase the primary production in the EN model to the levels of 1996 in order to observe a less-biased comparison (Fig. 6). The EN Finn's cycling index (*FCI*) decreased to a slightly lower value than 1996. However, the relative Ascendancy (*A*/*C*) and Overhead (Φ/C) increase and decrease, respectively, but not to the levels of 1996. Ascendancy is both a function of total throughput (*T*) and system development (i.e. average mutual information, *I*), and while the increase in primary production brings *T* to a similar level as 1996, the EN state still shows lower development, *I*. Under this scenario, EN would appear as of lower maturity despite increased overall community energetics.

Our models do not include information on the microbial loop, which is undoubtedly an important component of ecosystem functioning in Independence Bay. Energy flow through bacteria is likely enhanced during the warm, oxygen-rich conditions of EN. While bacterial functional groups are often removed in other models because their high flows overshadow other groups (Christensen, 1995), they may be of particular importance in our understanding of benthic processes in the Peruvian upwelling system. Thus, future research plans to investigate these important energy pathways for use in future models.

A community analysis for Independence Bay conducted by Wolff and Mendo (2002) indicated that benthic diversity and evenness increased during EN. An initial attempt to model the trophic changes also showed maintenance of flow structure during EN. The authors proposed that this adjustment to abiotic changes might indicate that EN is a condition to which the benthic community has adapted during evolution. This hypothesis is supported by the present study's results, yet may best apply to lower trophic levels that responded quicker to the perturbation. High trophic level benthic predatory groups have been observed to recover quite quickly (e.g. predatory crabs) after EN, but this is likely due to temporary emigrations to deeper waters rather than system adjustment. In this respect we wonder if the post-EN ecosystem, with higher primary production, higher residual scallop biomass, and a return of predatory groups, might not show higher flows or more maturity than the pre-EN state. If so, there may be some long-term

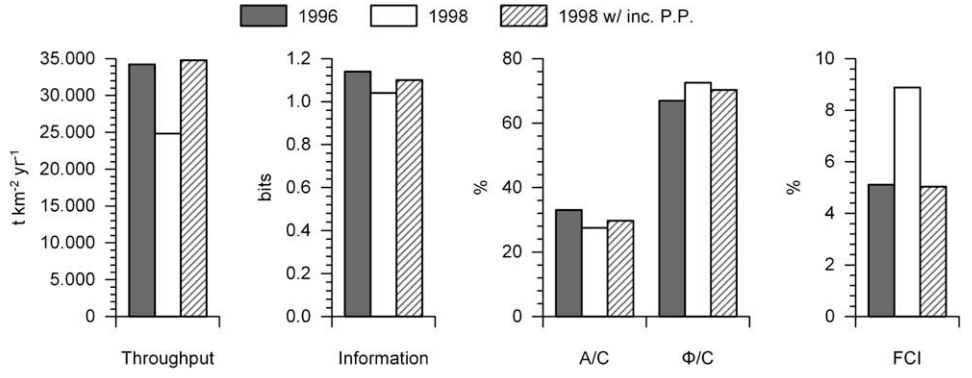

Fig. 6. Simulation of increasing primary production in the 1998 model to normal upwelling levels (1996 model values for macroalgae and phytoplankton) on indices of Ascendancy (*A*/*C*), overhead (Φ/C), mutual information (*I*), and Finn's cycling (*FCI*). Reference values for the 1996 model's indices are given for comparison.

positive impact from EN that may foster the idea that it is an integral part of HCS dynamics (Arntz and Valdivia, 1985b).

4.2. Bottom-up and top-down effects

When the model for normal conditions was forced from below with a reduction in primary producer biomass (phytoplankton and macroalgae to EN levels) the response confirms some of the EN-associated changes observed in functional group biomasses: misc. filter-feeders and herbivorous gastropods strongly decrease, and polychaetes benthic detritivores which also decrease somewhat. Oddly, macroalgae, when used as a single model driver, better explain the observed ecosystem changes (lowering SS) than phytoplankton.

Forcing a reduction in predatory crab biomass (release of top-down control), favors sea stars and small carnivores (competing predators), yet the modeled responses of other groups of the system is insignificant.

Neither EN triggered changes in the bottom-up (phytoplankton and macroalgae), nor the top-down (predatory crabs) forcing improve the fit of scallop dynamics, suggesting that trophic linkages of scallops to their food and predators do not cause proliferation of the scallop stock—an important if negative finding, especially since predatory crabs are well known scallop predators and their biomass reduction during the EN warming has been previously related to the scallop proliferation (Wolff and Alarcon, 1993; Wolff and Mendo, 2000).

While the scallop outburst during EN changed the entire character of the ecosystem, its inclusion as a model driver did not improve the overall fit of the simulation considerably. This may in part be due to lags in the population responses of several functional groups as compared to the reference data; however, the simulation correctly predicts the direction of response for a number of functional groups (positive: predatory gastropods, small carnivores, octopus, sea stars; Negative: polychaetes, herb. gastropods, and misc. filter-feeders), supporting the central role of the scallop in the Independence Bay ecosystem as prey for several consumer groups and as a competitor for other filter-feeders. It is likely that the more immediate decreases in several competing primary consumer groups may be due to the negative effects of competition for space, as the scallop banks became so thick in parts as to obscure the sea floor with several layers of scallops.

The scallop outburst apparently is caused by non-trophic effects (i.e. temperature mediated recruitment). However, once the scallops proliferated, the model suggests great changes to energy flow within the system. During EN scallops proliferated and the biomass of primary producers and predatory crabs decreased, affecting other groups in our simulations (scenario 4) (Fig. 4).

When forcing by the diving and finfish fishery is removed in our simulations, the simulated biomass trajectories of the functional groups were almost identical to those of scenario 4, suggesting that fishing plays a very limited role in the dynamics of the system. This may be explained by the fact that the diving fishery targeted mainly scallops and its increase in catch rate was about proportional to the scallop biomass increase; and the changes in finfish fishing rate were small over the whole period.

4.3. Vulnerabilities

It is important to emphasize that the manipulation of the 'drivers' did not improve the fit of the simulation without first allowing for a fitting of vulnerabilities. This is contrary to the findings of a similar exploration of the larger Peruvian Upwelling system (Taylor et al., 2008) whereby even default vulnerability values reproduced many important dynamics. This may be due to higher data quality in steady-state model (Tam et al., 2008) (as reflected in the Ecopath Pedigree Index, Peru system, 0.638; IB, 0.597; scales between 0 and 1 with highest values for direct measurements of the same system). Furthermore, the less-mobile nature of the benthic organisms in Independence Bay may prevent avoidance of deleterious conditions, thus making the effects of perturbations more pronounced. While the computed vulnerabilities for Independence Bay seem plausible, they should nevertheless be considered with caution since the time series available for the present study was quite short. In future years we will be able to extend the data set over longer periods and may be able to confirm some of the estimated vulnerabilities.

Generally, bottom-up control dominated the fit for the pelagic components such as energetic flow from plankton to small pelagic fish to the higher predators marine mammals and seabirds. Littoral fish also provided an important bottom-up link between benthic production (both macroalgae and invertebrate) to marine mammals. Top-down control was more important in the benthic components of the system. This may be expected given the high Ecological efficiencies calculated for many benthic primary consumers during the normal upwelling year of 1996, due to their high utilization by higher trophic levels. In addition, the fact that only 0.75% of the Ecoranger runs for 1996 resulted in a balanced model (as compared to 2.20% in the 1998 model) illustrates the tightly coupled flows to the benthic predatory groups, which restricted the parameter possibilities for the starting 1996 steady-state model.

A top-down configuration was fit for the predatory crab to scallop interaction. This is possible during normal upwelling periods as the crabs *Cancer setosus* and *Cancer porteri* are the dominant consumers of benthic production; however, the crab decrease during EN is not evidently responsible for the scallop outburst. Furthermore, this vulnerability setting must be taken with caution as the biomass fluctuations of both groups were forced through time and thus the result is likely an artifact. Top-down configurations between predatory snails and several of its prey (polychaetes, benthic detritivores and misc. filter-feeders) help to explain these prey decreases after the EN period. But this result too must be taken with caution as competitive interactions with scallops for space may have also attributed to their declines.

The finding that the abundance of scallop and other Independence Bay filter-feeders exerts bottom-up control on predators' abundance appears plausible and the finding is not new (Wolff and Alarcon, 1993). Despite the negative effects of EN on several higher-level benthic predators, the increased scallop biomass after EN apparently supported the recovery of predatory gastropods, small carnivores, predatory crabs, and sea stars, all of which show higher post-EN biomasses than in 1996. Furthermore, the (possibly normal) bottom-up control of scallops and other filter-feeders by phytoplankton under upwelling conditions may indeed be inverted during EN, when scallops are estimated to have consumed 58% of phytoplankton production alone. A similar role has been identified for the introduced Manila clam *Tapes philippinarum* in the Venice Lagoon system (Pranovi et al., 2003). Furthermore, it was suggested that this strong top-down control of phytoplankton by *T. philippinarum* may be responsible for the system not returning to a phytoplankton-based trophic web (Libralato et al., 2004), although this seems unlikely in Independence Bay given the constant refreshment of productive waters that enter from outside the bay.

4.4. Conclusions

Overall, it appears that the energy flow structure in Independence Bay is more or less maintained during El Niño despite negative impacts at higher benthic trophic levels. In particular, the proliferation of the scallop *A. purpuratus* apparently maintains the energy flow within Independence Bay despite the reduction in primary production. While some alleviation of top-down predation pressure may be felt by benthic primary consumers through the temperature–mediated decreases of crabs, the overall bottom-up affects of reduced primary production (macroalgae and phytoplankton) appears to have reduced the biomass of several functional groups. As seen for many areas along the Peruvian coast, Independence Bay becomes more tropical during EN. Under these conditions the system utilizes most of the (reduced) phytoplankton production so that exports of primary production to detritus are greatly reduced. While the El Niño state appears to show some higher efficiency in overall energetics, the structure and development appears impacted.

The rapid response and adaptation of the artisanal fishery to EN also increases the system's efficiency; however, this increased fishing pressure may have added stress to negatively impacted functional groups through higher fishing mortality. A management plan that allows for the newly recruited *A. purpuratus* population to fully grow and develop may not only reap higher monetary gains as suggested by Wolff and Mendo (2000), but may also enhance post-El Niño system through facilitation of the recovery of benthic predatory groups.

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