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Trophic and environmental drivers of the Sechura Bay Ecosystem (Peru) over an ENSO cycle

Marc H. Taylor · Matthias Wolff · Flora Vadas · Carmen Yamashiro

Abstract Interannual environmental variability in Peru is dominated by the El Niño Southern Oscillation (ENSO). The most dramatic changes are associated with the warm El Niño (EN) phase (opposite the cold La Niña phase), which disrupts the normal coastal upwelling and affects the dynamics of many coastal marine and terrestrial resources. This study presents a trophic model for Sechura Bay, located at the northern extension of the Peruvian upwelling system, where ENSO-induced environmental variability is most extreme. Using an initial steady-state model for the year 1996, we explore the dynamics of the ecosystem through the year 2003 (including the strong EN of 1997/98 and the weaker EN of 2002/03). Based on support from literature, we force biomass of several non-trophically-mediated 'drivers' (e.g. *Scallops*, *Benthic detritivores*, *Octopus*, and *Littoral fish*) to observe whether the fit between historical and simulated changes (by the trophic model) is improved. The results indicate that the Sechura Bay Ecosystem is a relatively inefficient system from a community energetics point of view, likely due to the periodic perturbations of ENSO. A combination of high system productivity and low trophic level target species of invertebrates (i.e. scallops) and fish (i.e. anchoveta) results in high catches and an efficient fishery. The importance of environmental drivers is suggested, given the relatively small improvements in the fit of the simulation with the addition of trophic drivers on remaining functional groups' dynamics. An additional multivariate regression model is presented for the scallop *Argopecten purpuratus*, which demonstrates a significant correlation between both spawning stock size and riverine discharge-mediated mortality on catch levels. These results are discussed in the context of the appropriateness of trophodynamic modeling in relatively open systems, and how management strategies may be focused given the highly environmentally influenced marine resources of the region.

Keywords El Niño · Scallop fisheries · Trophic relationships · Trophodynamic model · Humboldt Current · Peru

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Introduction

Sechura Bay (5.6°S, 80.9°W) (Fig. 1) is located in northern Peru and is considered within the zone of transition between cold water transported from the south by the Humboldt Current and warm water of the tropical equatorial region. Under normal upwelling conditions, this transition is found north of the bay; however, during the warm phase of the El Niño Southern Oscillation (ENSO), El Niño (EN), this transition zone is shifted southward by reflected Kelvin waves upon arrival to the coast. The bay is relatively shallow with depths of less than 30 m extending to 10 km from the shore.

Under upwelling conditions, the bay shows high primary productivity due to high nutrient availability and relatively warm water conditions when compared to higher latitudes (average temperature ca. 20°C). This productivity supports
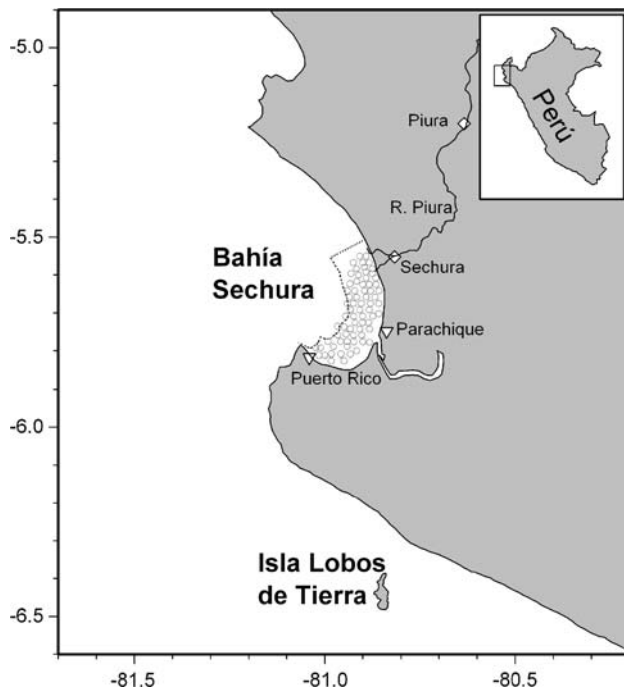
Fig. 1 Map of Sechura Bay. Macrobenthic fauna sampling stations from September 1996 are indicated by *gray circles* (*n* = 71). The area considered in the trophic model is from the mouth of the River Piura southward and extending offshore to the 30 m depth isocline (indicated by the *dashed line*). Main cities (*diamonds*) and ports (*triangles*) are shown

a large artisanal fishery in the bay of ca. 4,300 registered fishers and 970 boats (DIREPRO 2006). Additionally, migrant fisher communities may also come to the bay during non-EN periods to take advantage of the abundant fish and invertebrate resources. One example is that of the scallop *Argopecten purpuratus*, which maintains large populations in the bay and is a main target species due to a profitable export market. As a result, the state of Piura accounts for about 30% of total Peruvian landings of *A. purpuratus* (Ministry of Fisheries 2004).

Due to the bay's position near the transition zone of the Humboldt Current Large Marine Ecosystem, even EN events of smaller magnitude such as in 1991/92 and 2002/03, which may not be felt at higher latitudes, can be observed in Sechura Bay through higher sea surface temperature (SST). Extreme EN events, such as those occurred in 1997/98, resulted in much higher SST as well as increased rainfall and subsequent river discharge into the bay (Fig. 2). This environmental variability associated with ENSO is likely to play an important role in the dynamics of the ecosystem.

The objective of this study is to explore the importance of trophic and environmental drivers of dynamics to historical changes in Sechura Bay (1996–2003) through the use of a trophic flow model and dynamic simulations. Specifically, we force both fishing effort and the production of several functional group 'drivers', whose dynamics are
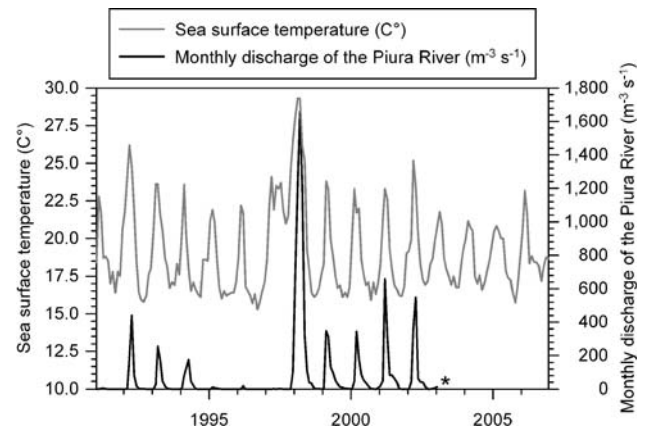

Fig. 2 Monthly averages of sea surface temperature (°C) of Sechura Bay and discharge of the Piura river (as measured at the Piura bridge; * series ends in 2003)

well cited in the literature as being non-trophically mediated, in order to measure their relative importance in the dynamics of the remaining functional groups of the model. An additional exploration of the influence of environmental factors on the economically important populations of *A. purpuratus* is also presented.

Materials and methods

Trophic model description

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 allows quantifying and balancing trophic flows among components (functional groups) of an ecosystem and also permits exploration of ecosystem dynamics under different scenarios of use or environmental change (http://www.ecopath.org). The Ecopath model links the production of each group with the consumption of all those groups trophically connected:

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

where P_i is the total production rate of (i), Y_i is the total fishery catch rate of (i), $M2_i$ is the total predation rate for group (i), B_i the biomass of the group, E_i the net migration rate (emigration–immigration), BA_i is the biomass accumulation rate for (i), while $M0_i = P_i \cdot (1-EE_i)$ is the 'other mortality' rate for (i) (Christensen et al. 2000). In order to ensure mass balance between the groups, a second master equation is used:

Consumption = Production + Respiration
                    + Unassimilated food

A steady-state model of Sechura Bay was constructed based on the year 1996 and includes the area south of

Table 1 Functional groups and representative species for the steady-state model of Sechura Bay in 1996

Functional group	Species
2. Macroalgae	*Caulerpa* sp. (99.4%), *Rhodymenia* sp. (0.6%)
4. Polychaetes	*Lumbrineris* sp., *Magelona phyllisae*
5. Scallops	*Argopecten purpuratus*
6. Sea urchins	*Arbacia* sp. (98.3%), *Tetrapigus niger* (1.7%)
7. Herbivorous gastropods	*Aplysia* sp. (51.2%), *Littorina* sp. (21.3%), *Scurria* sp. (10.7%), *Astraea buschii* (8.4%), *Tegula atra* (5.0%), *Tegula verrucosa* (1.1%), *Chiton* sp. (0.6%),
	Tegula sp. (0.6%), *Anachis* sp. (0.5%), *Mitrella* sp. (0.3%), *Columbella* sp. (0.2%)
8. Benthic detrivores	*Clypeasteroida* (35.8%), *Pagurus* sp. (21.5%), *Cycloxanthops* sp. (18.9%), *Brandtothuria* sp. (7.7%), *Turritella broderipiana* (4.7%), *Ophiuroidea* (3.5%),
	Majidae (3.3%), *Eurypanopeus* sp. (1.7%), *Dissodactylus* sp. (1.2%), *Litopenaeus* sp., *Farfantepenaeus californiensis*, *Penaeus* sp.
9. Misc. filter feeders	*Actinia* sp. (61.6%), *Tagelus* sp. (26.7%), *Chione* sp. (5.8%), *Halodakra subtrigona* (3.4%), *Glycimeris* sp. (2.2%), *Terebra purdyae* (0.3%)
10. Predatory gastropods	*Sinum cymba* (45.8%), *Thais chocolata* (26.2%), *Bursa sp.* (9.6%), *Priene* (7.8%), *Thais kiosquiformis* (3.7%), *Hexaplex brassica* (3.5%), *Thais haemastoma* (1.6%), *Bursa ventricosa* (1.3%), *Bursa nana* (0.5%)
11. Small carnivores	*Crassilabrum* sp. (54.4%), *Polinices uber* (26.4%), *Solenosteria fusiformes* (8.9%), *Triumphis distorta* (5.5%), *Natica unifasciata* (1.4%),
	Nassarius sp. (1.2%), *Prunum* sp. (1.1%), *Oliva* sp. (1.0%)
12. Predatory crabs	*Cancer porteri* (94.2%), *Callinectes arcuatus* (4.2%), *Callinectes toxotes* (1.6%)
13. Sea stars	*Luidia magallanica*
14. Octopods	*Octopus mimus*
15. Littoral fish	*Cynoscion analis* (58.3%), *Sciaena deliciosa* (10.4%), *Peprilus medius* (6.4%), *Stellifer minor* (6.4%), *Paralabrax humeralis* (5.3%), *Paralonchurus peruanus* (4.2%), *Anisotremus scapularis* (2.9%), *Isacia conceptionis* (2.8%), *Labrisomus philippii* (1.0%), *Gerres cinereus* (0.8%),
	Cheilodactylus variegatus (0.6%), *Larimus* sp. (0.5%), *Calamus brachysomus* (0.4%)
16. Small pelagic fish	*Engraulis ringens* (87.8%), *Anchoa nasus* (11.3%), *Mugil cephalus* (0.6%), *Sardinops sagax sagax* (0.3%), *Odontesthes regia regia* (0.1%)
17. Pelagic predatory fish	*Mustelus* sp., *Triakis* sp. (92.4%), *Scomber japonicus* (5.9%), *Mustelus whitneyi* (1.7%)
18. Marine mammals	*Otaria byronia*, *Arctocephalus australis*
19. Sea birds	*Leucocarbo bougainvillii*, *Sula variegata*, Pelecanus thagus
20. Cephalopods	*Loligo gahi*, *Dosidicus gigas*

Species listed are not exhaustive (small benthos groups show the most important species, representing >95% of biomass and/or species averaging >1 g m²)

the Piura River of <30 m depth (total area of ca. 400 km²) (Fig. 1), which incorporates the main area of the artisanal fishery (Gonzales and Yépez 2007). The model contained 21 functional groups including *Detritus*, two producer groups (*Phytoplankton* and *Macroalgae*), *Zooplankton*, six benthic primary consumer groups (*Polychaetes*, *Scallops*, *Sea urchins*, *Herbivorous gastropods*, *Benthic detritivores*, and *Miscellaneous filter feeders*), five benthic carnivore groups (*Predatory gastropods*, *Small carnivores*, *Predatory crabs*, *Sea stars*, and *Octopods*), three fish groups (*Littoral fish*, *Small pelagic fish*, and *Pelagic predatory fish*), *Cephalopods*,

and two top-predator groups (*Marine mammals* and *Sea birds*). Functional groups were designated according to similar diets, predators, productivities, and individual body size (Table 1).

Data sources

Input parameters are derived from various sources: local and regional estimates, empirical relationships, other models and assumed estimates (Table 2). Final values are shown in Tables 3 and 4.

Table 2 Sources of input data for the steady-state model of Sechura Bay in 1996

Functional group/parameter	B_i (t km^{-2})	P_i/B_i (year^{-1})	Q_i/B_i (year^{-1})	GE_i	EE_i	Y_i (t km^{-2} year^{-1})	DC
1. Phytoplankton	Converted chl *a* estimates from SeaWifs (Feldman and McClain 2007)	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	IMARPE cruise averages 1995–1999 for the area 5°–6°S and within 82°W	GU based on Mendoza (1993), Hutchings et al. (1995)	GU adapted from Polovina and Ow (1985)	EO	GE	–	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)	Wolff (1994)	EO	EO	IS	GU based on Rouillon et al. (2002)
6. Sea urchins	IE	EM	EO	GU	EO	–	GU
7. Herbivorous gastropods	IE	EM	EO	GU 0.3 based on Mann (1982)	EO	–	GU
8. Benthic detritivores	IE	EM	EO	GU	EO	IS	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	IS	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	–	GU based on Leon and Stotz (2004), IC
13. Sea stars	IE	Ortiz and Wolff (2002)	EO	GU	EO	–	GU, IC
14. Octopods	GU based on catch data	EO	Wolff and Perez (1992), Vega and Mendo (2002)	Wolff and Perez (1992), Vega and Mendo (2002)	EO	IS	Cortez et al. (1999), IC
15. Littoral fish	GU based on catch data	GU based on Wolff (1994)	EO	GU	EO	IS	GU based on FISHBASE (2006)
16. Small pelagic fish	GU based on catch data	GU	EO	GU 0,1 based on Moloney (2005)	GU	IS	GU based on FISHBASE (2006)
17. Pelagic predatory fish	GU based on catch data	GU based on Jarre et al. (1991)	EO	GU 0,1 based on Moloney (2005)	EO	IS	GU based on FISHBASE (2006)

Table 2 continued

Functional group/ parameter	B_i (t km^{-2})	P_i/B_i (year^{-1})	Q_i/B_i (year^{-1})	GE_i	EE_i	Y_i (t km^{-2} year^{-1})	DC
18. Marine mammals	GU	GU based on Jarre, Muck, and Pauly (1991)	EO	GU	EO	–	DC
19. Sea birds	GU	GU based on Moloney (200)	EO	GU based on Moloney (200)	EO	–	GU
20. Cephalopods	GU based on catch data	Z derived from VPA (IMARPE) (J. Argüelles, pers. comm.) for *Loligo gahi*	EO	Neira and Arancibia (2004)	EO	IS	Cardoso et al. (1998), Villegas (2001)
21. Detritus	EO	–	–	–	–	–	–

Abbreviations: *GC* gut content, *IE* IMARPE benthic macrofauna evaluation, *EM* empirical model (Brey 2001), *EO* ecopath output, *GU* guess estimate, *IC* iterative consumption routine (described herein), *IS* IMARPE landings statistics

Biomass Benthic macrofauna biomass was obtained from a survey conducted by IMARPE in September 1996. Epifauna and infauna of the upper sediment layer (approx. <5 cm depth) were collected from 71 quadrants of 1 m^2 each, and abundance and weight were recorded for each species (for further information on sampling, see Samamé et al. 1985; Yamashiro et al. 1990) (Fig. 1). 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, as much of this group's biomass is found deeper than 5 cm.

Estimates of *Phytoplankton* biomass were based on SeaWifs (Feldman and McClain 2007) remote sensing estimates of sea surface chlorophyll *a* (chl *a*) concentrations (mg m^{-3}) for the immediate region (4.9–6.6°S, 80.2–81.7°W) from December 1997 to April 2007, excluding EN values. Conversion factors used for chl *a* to wet weight were as follows: chl *a*:Carbon (40:1) (Brush et al. 2002), and Carbon:wet weight (14.25:1) (Brown et al. 1991). Finally, sea surface biomass was multiplied by a mean depth of 15 m, assuming a well-mixed water column, to arrive at units on a per m^2 basis.

Information on the *Zooplankton* in Sechura Bay is limited, and thus we used average values from IMARPE cruise samplings between 1995 and 1999, excluding EN values, for the immediate region (5°–6°S, <82°W; n = 60). Biomass of highly mobile species such as octopus, cephalopods, and fish species were estimated from catch data by assuming that the fishery takes 50% of yearly produced biomass (Table 3).

Catches Estimates of catch were derived from IMARPE catch statistics for the artisanal fishery from the two main landing sites for Sechura Bay—Parachique and Puerto Rico (Fig. 1). Catches were summed according to species' functional groups (Fig. 3) for use in the steady-state model and for the measuring of performance of the simulations (see Simulations of temporal dynamics).

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 Polychates and Misc. filter-feeders were increased to 1.0 based on other estimates from the literature (Table 3).

Table 3 Input–output parameters for the steady-state model of Sechura Bay in 1996 after application of the Ecoranger resampling routine

Functional group/parameter	Trophic level	B_i (t km^{-2})	P_i/B_i (year^{-1})	Q_i/B_i (year^{-1})	EE_i	GE_i	UA_i/Q_i	P/R	R/A	Catch (year^{-1})	F_i	$M0_i$	$M2_i$
1. Phytoplankton	1.00	21.335	343.886	–	0.685	–	–	–	–	–	–	108.454	235.432
2. Macroalgae	1.00	284.607	16.092	–	0.042	–	–	–	–	–	–	15.412	0.680
3. Zooplankton	2.18	27.874	40.059	157.883	0.780	0.254	0.20	0.464	0.683	–	–	8.813	31.246
4. Polychates	2.06	45.897	1.091	4.474	0.825	0.244	0.20	0.438	0.695	–	–	0.191	0.900
5. Scallops	2.00	23.689	1.364	10.556	0.884	0.129	0.20	0.193	0.838	2.340	0.099	0.158	1.108
6. Sea urchins	2.11	22.798	0.597	2.786	0.666	0.214	0.20	0.366	0.732	–	–	0.199	0.398
7. Herbivorous gastropods	2.00	25.258	1.235	4.116	0.665	0.300	0.20	0.600	0.625	–	–	0.414	0.821
8. Benthic detritivores	2.00	36.795	1.302	6.806	0.910	0.191	0.20	0.314	0.761	0.144	0.004	0.117	1.181
9. Misc. filter feeders	2.24	22.064	1.094	5.044	0.736	0.217	0.20	0.372	0.729	0.001	–	0.289	0.805
10. Predatory gastropods	3.07	37.297	1.511	3.881	0.747	0.389	0.20	0.948	0.513	0.379	0.010	0.383	1.118
11. Small carnivores	2.87	14.669	0.537	2.677	0.673	0.201	0.20	0.335	0.749	0.001	–	0.176	0.361
12. Predatory crabs	3.20	7.379	2.002	8.703	0.684	0.230	0.20	0.404	0.712	–	–	0.633	1.369
13. Sea stars	3.15	1.033	0.731	3.670	0.741	0.199	0.20	0.332	0.751	–	–	0.189	0.542
14. Octopods	3.74	0.015	4.911	12.799	0.899	0.384	0.20	0.922	0.520	0.033	2.247	0.496	2.168
15. Littoral fish	2.81	2.613	1.195	14.300	0.694	0.084	0.20	0.117	0.896	1.795	0.687	0.366	0.142
16. Small pelagic fish	2.12	82.134	1.727	18.706	0.639	0.092	0.35	0.166	0.858	81.409	0.991	0.623	0.113
17. Pelagic predatory fish	3.15	1.161	0.869	8.123	0.464	0.107	0.30	0.181	0.847	0.425	0.367	0.466	0.037
18. Marine mammals	3.34	0.019	0.103	46.179	0.000	0.002	0.20	0.003	0.997	–	–	0.103	0.000
19. Sea birds	3.19	0.020	0.037	60.156	0.000	0.001	0.26	0.001	0.999	–	–	0.037	0.000
20. Cephalopods	3.14	0.371	4.249	11.125	0.522	0.382	0.20	0.477	1.001	0.822	2.218	2.031	0.000
21. Detritus	1.00	–	–	–	0.105	–	–	–	–	–	–	0.000	0.000

B biomass, P_i/B_i production rate, Q_i/B_i consumption rate, EE_i ecotrophic efficiency, GE_i conversion efficiency, UA_i/Q_i unassimilated portion of consumption, P/R production/respiration ratio, R/A respiration/assimilation ratio, F_i fishing mortality, $M0_i$ non-predatory natural mortality, $M2_i$ predation mortality

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

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

where G = realized daily growth rate (day^{-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 demonstrated 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):

$$G_{max} = 0.97 \times e^{0.0633 \times T}$$

Where T = water temperature (°C). The 'normal' upwelling phytoplankton production of 1996 assumed a mean temperature of 20°C with 50% light (from self-shading) and 0% nutrient limitation factors. P/B values for other groups are taken from the literature (Table 2)

Consumption (Q)/conversion efficiency (GE) Direct estimates of consumption rates (Q/B) were available for a few of the benthic invertebrate groups, (Octopods, 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, 3).

Diet matrices Direct diet studies for Sechura Bay are limited, and thus general knowledge from literature was

Table 4 Diet matrix for the steady-state model of Sechura Bay in 1996 after application of the Ecoranger resampling routine

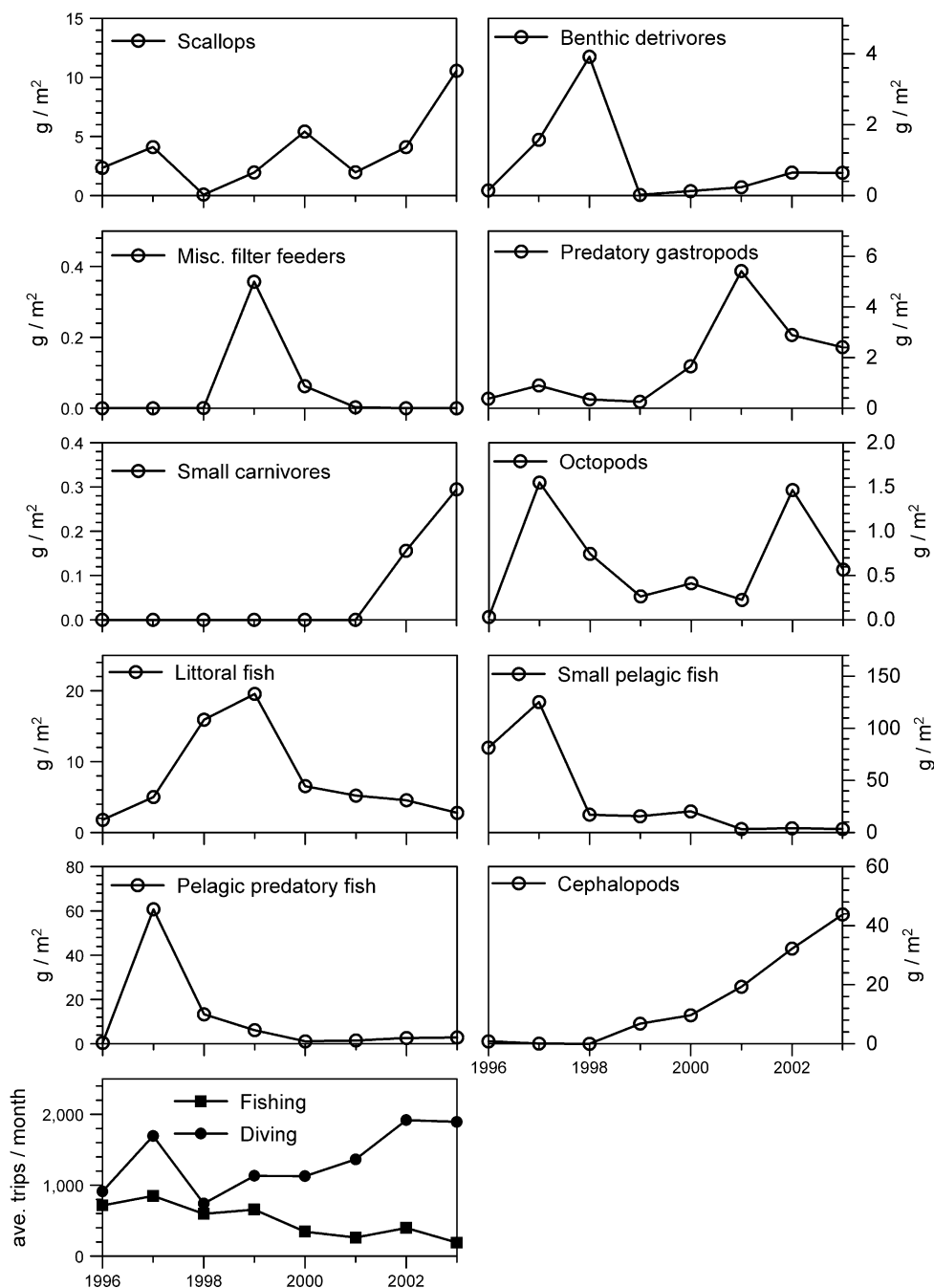| Prey\predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. Phytoplankton	0.764	0.327	0.788				0.701							0.901				
2. Macroalgae				0.800	0.808	0.198							0.259					
3. Zooplankton	0.149	0.052					0.197		0.000				0.502	0.099	0.483			0.300
4. Polychates				0.102				0.108	0.125	0.097	0.103		0.189					
5. Scallops								0.098	0.105	0.085	0.106	0.109						
6. Sea urchins									0.206		0.173							
7. Herbivorous gastropods								0.083	0.073	0.079	0.090	0.092						
8. Benthic detritivores								0.171	0.178	0.157	0.174	0.171	0.003					
9. Misc. filter feeders								0.070	0.084	0.061	0.078	0.084						
10. Predatory gastropods								0.235		0.140	0.153	0.168	0.001					
11. Small carnivores								0.021	0.023	0.018	0.022	0.025	0.000					
12. Predatory crabs									0.159			0.176	0.001					
13. Sea stars									0.008				0.000					
14. Octopods												0.175						
15. Littoral fish													0.001			0.252	0.105	
16. Small pelagic fish													0.001		0.517	0.699	0.895	0.700
17. Pelagic predatory fish																0.048		
18. Marine mammals																		
19. Sea birds																		
20. Cephalopods																		
21. Detritus	0.087	0.622	0.212	0.097	0.192	0.802	0.101	0.215	0.206	0.196	0.099		0.043					

Values of 0.000 indicates a proportion of <0.0005

used in the construction of diet matrices (Table 2). Macroinvertebrate predator groups are described to be rather unselective and opportunistic feeders, limited more by their modes of feeding (Wilson and Parkes 1998). Therefore, diet proportions were adjusted to reflect predatory groups' consumption rates as well as the available production of prey groups. Specifically, the diets of carnivorous benthic invertebrate groups (*Predatory gastropods, Small carnivores*, *Predatory crabs, Sea stars*, and *Octopods*) assumed a base percentage of detritus feeding (10–20%), and then production of their prey was iteratively distributed based on the consumption rates of the aforementioned benthic predators. 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 (Table 4).

Addressing parameter uncertainty

The balanced steady-state model for 1996 was subjected to the resampling routine *Ecoranger* 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 (Table 5). However, the initial results often gave parameter values 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

Fig. 3 Yearly captures from
Sechura Bay by functional
group as used for fitting the
simulations from 1996 to 2003.
Landings data provided by
IMARPE were converted to the
same unit values as the model
(g m^{-2} y^{-1}) through division
by the model area (400 km^2).
Bottom graph shows yearly
average fishing effort for the
two fleets, *Fishing* and *Diving*
(effort units = average
trips·month^{-1})

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 informa-
tion, see Christensen et al. 2000).

System statistics and indices

The Ecopath with Ecosim package allowed for the calcu-
lation of several statistics of the steady-state model

concerning flow structure and community energetics.
These allowed for the comparison of Sechura Bay to
published models of other coastal systems.

General descriptive statistics include: (1) Total
throughput (*T*)—measure of the total sum of flows within
the system and indicates the 'size' or activity of the system;
and (2) Contributions to *T* from different types of flows—
Consumption, Export, Respiration and Flows to detritus.

Several indices of community energetics are presented
that allow for the interpretation of system's development
according to Odum (1969). More developed systems are

Table 5 Pedigree index values assigned to model parameters for the steady-state model of Sechura Bay in 1996

Functional group	B	P/B	Q/B	Diet	C
Phytoplankton	0	0.2			
Macroalgae	1	0.6			
Zooplankton	0	0.6	0.1	0	
Polychates	1	0.5	0	0	
Scallops	1	1	1	0.7	1
Sea urchins	1	0.5	0	0	
Herbivorous gastropods	1	0.5	0	0	
Benthic detrivores	1	0.5	0	0	1
Misc. filter feeders	1	0.5	0	0	1
Predatory gastropods	1	0.5	0	0	1
Small carnivores	1	0.5	0	0	
Predatory crabs	1	1	1	1	
Sea stars	1	0.5	0	0	
Octopods	1	1	1	0.2	1
Littoral fish	0.4	0.1	0	0.2	1
Small pelagic fish	0	0.1	0	0.2	1
Pelagic predatory fish	0.4	0.1	0	0.2	1
Marine mammals	0	0.2	0.2	0.2	
Sea birds	0	0.2	0.2	0.2	
Cephalopods	0.4	1	0.6	0.5	

Lower pedigree index values correspond to guesstimates or other models, whereas higher pedigree index values correspond to high precision estimates locally based. Pedigree = 0.462 (t^* = 2.21)

B Biomass, *P* production, *Q* consumption, *C* diet and catch

hypothesized to be highly efficient in terms of energy transfer to higher trophic levels and, thus, able to sustain a higher biomass in proportion to primary production. The following indices of community energetics are calculated: (1) Total primary production (*PP*) to Total respiration (*R*) ratio (*PP/R*); (2) Biomass (*B*) supported by Total primary production (*PP/B*); (3) Biomass supported by Total throughput (*B/T*), and (4) Energy Transfer efficiency (*TE*) between discrete trophic levels. Calculated ratios of production to respiration (*P/R*) and respiration to assimilation (*R/A*) were compared with independent estimates of similar taxa from the literature in order to gauge biological consistency.

Statistics concerning the fishery and its efficiency were also presented, including: (1) gross efficiency (catch/net *PP*); (2) mean trophic level of the catch; and (3) primary production needed to sustain the fishery.

Simulations of temporal dynamics

Using the 'best' steady-state model for 1996 as a starting point (as defined by the Ecoranger routine described earlier), we explored the temporal dynamics of the ecosystem

from 1996 to 2003 using the Ecosim routine of the EwE package. Following the forcing of the yearly fishing effort for the two fishing fleets, *Fishing* and *Diving*, we applied several functional group 'drivers' to the model in order to measure their impact on the fit of the model. Drivers included the relative biomass changes of four trophically important and highly dynamic functional groups (*Scallops*, *Benthic detritivores*, *Octopods*, and *Littoral fish*) as calculated from catch per unit effort (CPUE). These drivers are well cited in the literature as having significant environmental influences on their dynamics. Populations of the scallop *A. purpuratus* in Independence Bay have been shown to fluctuate more in response to temperature-mediated larval development time and subsequent mortality changes rather than from purely trophic changes (Wolff et al. 2007; Taylor et al. 2007d). Penaeid shrimp dynamics in the region have been correlated to shifts in carrying capacity as a result of variable SST and river discharge (Mendo and Tam 1993). As the catches of the *Benthic detritivore* group are dominated by shrimp, we have included this group as a non-trophic mediated driver. *Octopus* was included due to the observed temperature-mediated growth and reproduction for *Octopus mimus* (Cortez et al. 1999), helping explain the large booms of octopus during EN periods (Arntz et al. 1988). Additionally, *O. mimus* embryonic development time has also been shown to be greatly accelerated under EN-like conditions in the laboratory (Warnke 1999), which may also contribute to increased production rates. Finally, the immigration of subtropical fish species southward is linked to the intrusion of subtropical equatorial waters during EN (Arntz and Tarazona 1990) contributing to the *Littoral fish* dynamics.

Drivers' biomasses were then fixed through time in all possible sequences and combinations (*n* = 64). The performance of each simulation was measured against the time-series of observed relative biomass changes (CPUE) for the remaining unforced groups through the calculation of the sum of squares (SS):

$$SS = \sum \left[Log(B_{obs.}) - Log(B_{pred.}) \right]^2$$

where $B_{obs.}$ = observed biomass (g m^{-2}), and $B_{pred.}$ = predicted biomass (g m^{-2}).

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

$$dB_i/dt = g_i \left[\sum_k Q_{ki}(t) \right] - \sum_j Q_{ij}(t) - M0_i B_i - \sum F_{if}(t) B_i$$

for species or functional groups *i* = 1, . . ., *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 modeled predation. The final sum represents the instantaneous fishing mortality rate, F, as a sum of fishing components caused by fishing fleets f (for further information, see Walters and Martell 2004).

Exploration of environmental drivers to scallop production

A multiple regression analysis was conducted to explore the influence of environmental factors on the dynamics of the economically important scallop (A. purpuratus) population in Sechura Bay. Using the methods employed by Wolff et al. (2007) for the scallop stocks in Independence Bay, Peru (16°S), the model attempts to forecast scallop catch as a function of the environmental conditions during the previous spawning period. Specifically, the dependent variable was defined as the scallop 'catch' (kg), versus the independent variables 'spawning stock' (kg) and the temperature-dependent 'settlement factor' (arbitrary units) for scallop recruitment. Settlement factor is based on a day-degree larval development time, whereby higher temperatures shorten the development time and consequently the pre-settlement mortality. In addition, we added the independent factor of 'river discharge' ($m^3 \ s^{-1}$) as Sechura Bay experiences highly variable input of freshwater from the Piura River depending on rainfall associated with ENSO, which affects the salinity of the bay.

The variables were defined as follows: Catch is calculated as the average monthly catch from September to August. Spawning stock is calculated as the average catch during the 6-month main spawning season (January–June) preceding the catch. River discharge is the average river discharge recorded during the catch period (September–August). Settlement factor is calculated from the average temperature 6-month main spawning season (January–June).

Data-series and their sources: Monthly catches (IMARPE); Sea surface temperature (SST) collected in Sechura Bay (IMARPE); and Piura River discharge (Sanchez Cerro Bridge, Piura—Sistema de Alerta Temprana 'SIAT').

Assumptions of the model

1. Scallop landings reflect the size of the scallop stock in the bay. If the stock increases or decreases, the fishery grows or shrinks accordingly, so that the relative fishing rate remains relatively constant, and the catch is proportional to stock size.

2. Scallop landings during the post-recruitment period, which starts in late winter (August/September) each year largely depend on the recruits spawned during the preceding summer/autumn period [January–June, note: this period is slightly later than that of Independence Bay as determined by histological analysis of gametogenesis (IMARPE, Huayurá, personal communication)], typical for annual "pulse fisheries".

3. Spawning stock is assumed proportional to scallop landings during spawning (January–June).

4. Larval survival in the natural environment (from egg release to settlement) is significantly lower than the observed 0.1% in the hatchery (Wolff et al. 1991).

5. Day degrees (dd) for larval development including successful settlement were considered to be approx. 400 for the temperature range 14–25°C, based on hatchery data by DiSalvo et al. (1984), Uriarte et al. (1996) and Wolff et al. (1991). During cold water conditions (14°C) larvae would need more than 28 days to settle, whereas only about 16 days are needed at the high EN temperatures of 25°C.

6. Piura River discharge is a good proxy for hydrological changes in Sechura Bay (e.g. change in salinity or sedimentation rate), which may impact the adult stock production.

Results

Trophic model

Initial parameters of the balanced model can be found on the Pangea website (Taylor et al. 2007a, b). Ecoranger resampling resulted in balanced models in 2.62% of the runs with the 'best' fitting model parameters shown in Table 3. The analysis of trophic flows in Sechura Bay for 1996 indicated an intermediate level of consumption of phytoplankton production by higher trophic levels (EE = 0.69) and low recycling of detritus (EE = 0.10). This inefficiency explains the high proportions of Total throughput (T) (27820 t km^{-2} $year^{-1}$) allocated to Exports (28%) and Flows to detritus (31%). Inefficient transfer of energy to higher trophic levels is reflected by the mean transfer efficiency value of 6.6% (geometric mean of trophic levels II–IV). Furthermore, the relatively high PP/R ratio (2.97) indicated that the system may be considered developing and immature (Table 6).

Respiration rates and conversion efficiencies can vary widely, especially depending on the population structure—whereby younger individuals will generally invest more energy in production, whereas older individuals will respire

Table 6 System statistics and flow indices for the steady-state model of Sechura Bay in 1996

Summary statistics	Sechura Bay—1996
Sum of all consumption (t km^{-2} year^{-1})	7227 (26%)
Sum of all exports (t km^{-2} year^{-1})	7908 (28%)
Sum of all respiratory flows (t km^{-2} year^{-1})	4008 (14%)
Sum of all flows into detritus (t km^{-2} year^{-1})	8676 (31%)
Total system throughput (t km^{-2} year^{-1})	27820
Fishing	
Total catches (t km^{-2} year^{-1})	87.349
Mean trophic level of the catch	2.15
Gross efficiency (catch/net PP)	0.007
PP required/catch.	15.66
PP required/total PP (%)	6.64
Community energetics	
Total primary production/total respiration	2.973
Total primary production/total biomass	18.137
Total biomass/total throughput	0.024

most of their assimilated consumption. Nevertheless, the model estimates of respiration fell within acceptable ranges as described in the literature for taxonomic groups. *P/R* ratios of fish groups ranged between 0.117 and 0.181, which is slightly higher than the mean value of 0.11 presented by Humphreys (1979). Benthic invertebrate *P/R* ratios had a wide range (0.193–0.948), but the average value of 0.475 is also very close to mean values of 0.482 and 0.439 for aquatic invertebrates as described by Humphreys (1979) and Schwinghamer et al. (1986), respectively. All but one (Scallops—0.838) of our *R/A* estimates for benthic invertebrates fell within the expected range of 0.5–0.75 given by Mann (1982). The average *R/A* ratio was 0.693, which is similar to the average value of 0.7 given by Davis and Wilson (1985) for macroinvertebrates.

The total fishery catches were high (87 t km^{-2} year^{-1}). Due to the targeting of low trophic level primary consumer species (e.g. *Engraulis ringens*, *Anchoa nasus*, and *Argopecten subnodosus*) the mean trophic level of the catch was close to 2.0 (2.15). As a result, the fishery had a high gross efficiency (catch/net PP; 0.01) and low PP required per unit of catch (15.66). Overall, the fishery required 6.6% of the total PP to sustain it (Table 6).

Simulations

The initial application of fishing effort changes for the two fleets slightly improved the fit between the observed and the simulated catches (ca. −6.4% in SS), indicating some effect to overall dynamics. The application of the functional group drivers had little improvement on the fit of the simulation (−1.7 to 11.1% average change in SS for all drivers, Fig. 4).
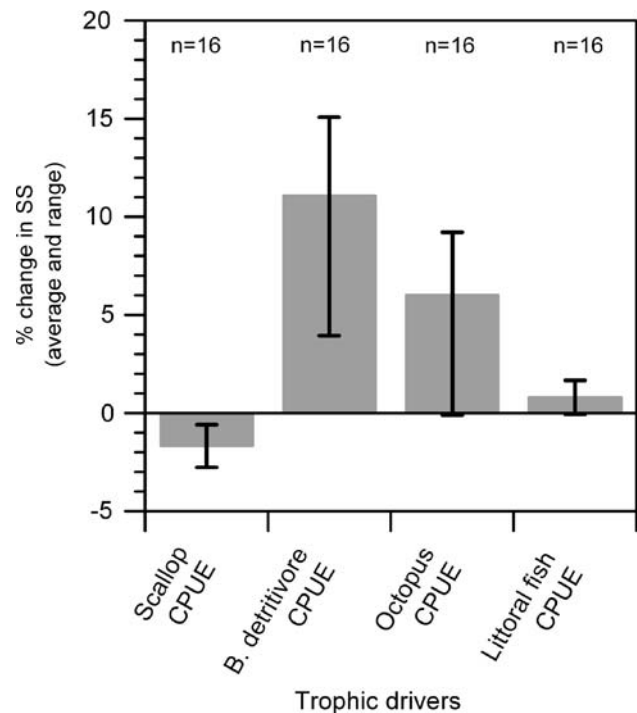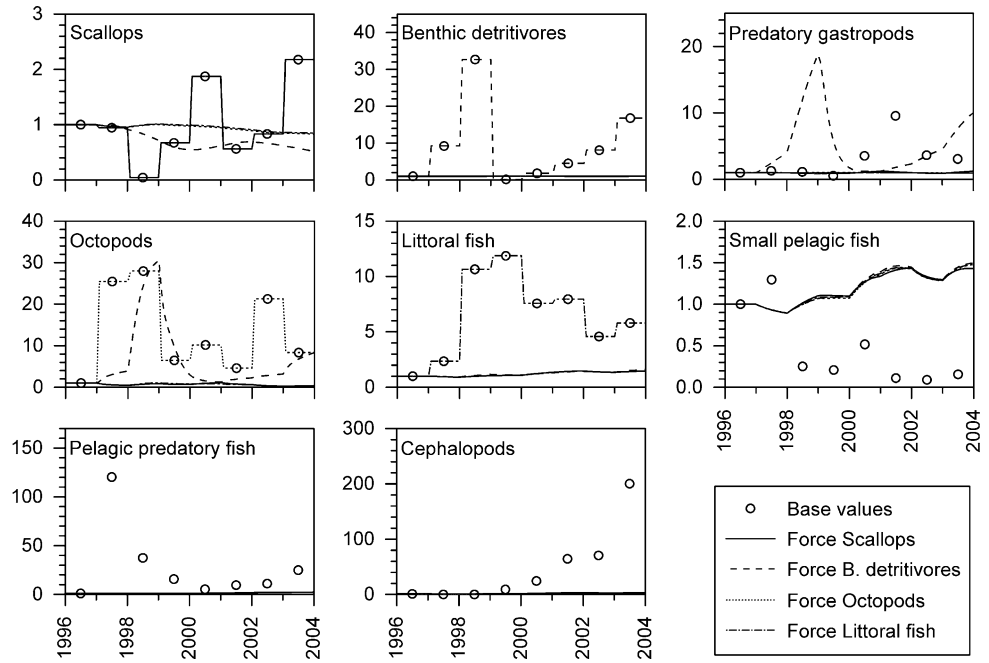

Fig. 4 Percent changes to sum of squares, *SS*, of the 1996–2003 simulation after the forcing of relative biomass (CPUE) changes of several functional groups 'drivers'. Average change (*bar*) and range (*line*) are displayed. Drivers were applied in all possible sequences and combinations, and *SS* was corrected for artificial improvements caused by the fitting of the driver's dynamics. Negative values (i.e. decrease in *SS*) indicate an improvement in fit

Scallop CPUE was the only driver that improved fit on average (−1.7% in SS, respectively), although the improvement was minimal. The impact of each individually applied driver on simulated dynamics can be seen in Fig. 5.

Multiple regression

None of the independent variables were significant predictors of catch when applied alone [Spawning stock (SS) $P = 0.347$; Settlement factor (SF) $P = 0.215$; River discharge (RD) $P = 0.236$]. When SS and SF were applied together, as done by Wolff et al. (2007) for Independence Bay, the regression was not significant ($R^2 = 0.362$; $P = 0.509$). The addition of the independent variable RD increased the fit dramatically ($R^2 = 0.959$; $P = 0.060$); however, a significant regression was achieved only from the combination of the independent variables SS and RD (without SF) ($R^2 = 0.916$; $P = 0.024*$). Predicted versus observed values of scallop catch can be seen in Fig. 6 along with the statistics of the multiple regression. The relationship reveals that spawning stock size and river discharge influence catch levels positively and negatively, respectively.

Fig. 5 Simulated versus observed (catch per unit effort) relative biomass changes. All simulations consider changes in fishing effort (fishing and diving). Simulation trajectories are shown for each of the four 'drivers' (*Scallops*, *Benthic detritivores*, *Octopods*, *Littoral fish*) as applied individually
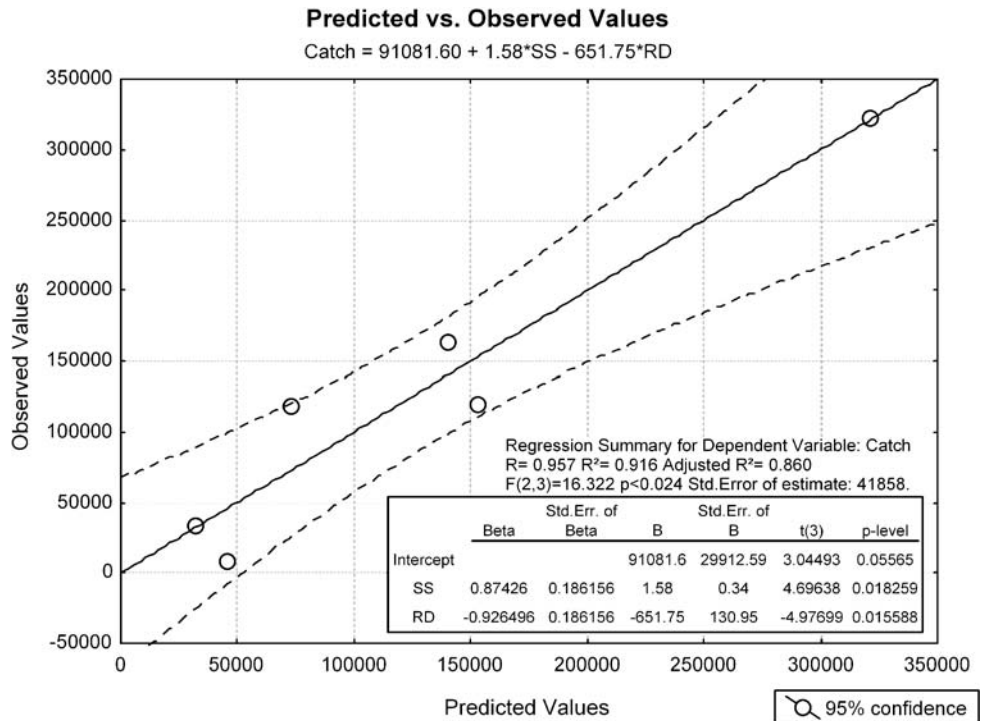

Discussion

General system configuration

Sechura Bay is located near the northernmost extension of the Peruvian coastal upwelling where, due to its proximity to the equator and resulting large Rossby radius, strong upwelling occurs even under relatively low wind-forcing

conditions. Estimates of chl *a*, as derived from remote sensing during non-EN years, showed relatively typical values of the coastal Peruvian upwelling system (3.00 mg chl *a* m^{-3}), and production rates under upwelling conditions are assumed to be at the higher end due to a higher mean sea surface temperature. For example, when compared to the southern extension of the main upwelling zone near Independence Bay (16°S), mean temperatures in

Fig. 6 Predicted versus observed values of annual catches (kg; ave mo. catch Sep–Aug) for the scallop *Argopecten purpuratus* as calculated by the multiple regression analysis. Independent variables include: Spawning stock (*SS*) (kg; average monthly catch of previous Jan–June) and River discharge (*RD*) (m^3 s^{-1}; Sep–Aug)

Sechura Bay are approximately 4°C higher (20° vs. 16°C), resulting in a 29% increase in phytoplankton production rates according to the modified Eppley curve presented by Brush et al. (2002). In part due to this high primary production, the Total throughput in Sechura Bay was estimated at 27820 t km^{-2} year^{-1}, which is of a similar magnitude to other coastal bays along the coast of South America (Tongoy Bay, Chile (20594), Ortiz and Wolff 2002; Independence Bay, Peru (34208), Taylor et al. 2007d).

Despite the advantages of a combined upwelling and higher mean SST for high primary production, the lower subtropical latitudes of the western coast of South America are subject to the highest interannual SST variability associated with ENSO (Lluch-Cota et al. 2001; Montecinos et al. 2003). This variability is caused by oscillations in the zone of transition between the cold waters of the Humboldt Current and the warm waters of the tropical equatorial region, and may act as a periodic perturbation to "reset" the system and prevent the development of a high trophic efficiency. Under the negative SST anomalies of 1996, the system is functioning as a typical upwelling region with exports and flows to detritus equaling 28 and 31%, respectively, due to inefficient consumption of primary production. 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 are able to compare the proportions of types of flows. The proportion of flows to detritus in Sechura Bay is similar to those estimated for several US bay systems (Narragansett Bay (33%), Delaware Bay (30%), and Chesapeake Bay (27%) by Monaco and Ulanowicz 1997) and other bay systems along the coast of South America (Tongoy Bay (29%) by Ortiz and Wolff 2002; Independence Bay (34%) by Taylor et al. 2007d). However, only the models of the South American bays calculated high proportions of exports as well (29–34% vs. 7–10% for US bays). Rybarczyk et al. (2003) found a similarly high proportion of export flows (26%) for Somme Bay, France, which they in part attribute to high exchange rates/low residency time of water in the system. Sechura Bay is in fact a very open bay and losses of primary production may occur; however, the benthic evaluations conducted in 1996 observed standing detrital material at about one-third of the sample locations, which may be evidence of primary production going unutilized and remaining in the sediments under strong upwelling conditions.

Indices of community energetics show a similar degree of development when compared to the bays of Independence and Tongoy (*PP/R*, *PP/B*, and *T/B* ratios); however, the mean transfer efficiency of trophic levels II–IV is lowest in Sechura Bay (6.6%) as compared to the other South American bay systems (9.6 and 11.4% for Independence and Tongoy, respectively) probably due to the fact that perturbations frequently impact higher-level species to a greater extent than the lower trophic components (Baird et al. 1991). This is likely due to the fact that higher trophic levels have lower production ratios and thus slower biomass recovery times. As transfer efficiency indicates the development of higher trophic connections, the latitudinal trend of increasing transfer efficiencies at higher latitudes may be related to decreasing ENSO-related variability and impact to the coast of the Humboldt Current ecosystem.

Role of fishing

The fishery is highly productive with catches equaling 87 t km^{-2} year^{-1} for 1996. The catch is dominated by small pelagic fish; specifically, Peruvian anchoveta, *Engraulis ringens* (84.6% of total catch), and Longnose anchovy, *Anchoa nasus* (10.9% of total catch). Due to the low trophic level of these groups, the efficiency of the fishery is high, which is sustained by a smaller fraction of the total primary production (6.6%) when compared to average estimates of upwelling systems (25.1%) (Pauly and Christensen 1995).

Sechura is one of the largest bays of the western South American coast, measuring 89 km from north to south with oxygenated bottom depths <30 m extending about 10 km offshore. Below 30 m benthic biomass drops off significantly due to decreased oxygen concentrations. For this reason, the diving fishery operates almost exclusively in shallow depths (<30 m). Despite such an expansive area for exploitation, the diving fishery in Sechura is a relatively recent development, spurred on in the early 1990s by a boom in the scallop fishery and by the introduction of diving techniques to the area of fishers from the south (i.e. hookah and air compressor systems). As a result, between 1994 and 1997 the diving fleet increased to include nearly 500 boats (Tafur et al. 2000). Nevertheless, the fishing mortality rates of the benthic target species are very low, even for the targeted scallops. For example, an exploitation ratio (*F/Z*) of 7% for scallops in Sechura Bay compares to 23–25% for Independence Bay (Taylor et al. 2007d). It is likely that both the young state of development of the diving fishery, and the higher associated costs of travel to the farther fishing grounds in the larger Sechura Bay, may limit to some extent the overall impact and help to explain the low fishing mortalities of the benthic resources (Table 3).

The addition of fishing effort dynamics did make some improvement to the fit of the simulations (−6.4% in SS), implying that changing fishing intensity may have some impact on the overall changes of catch through time. Given

the low fishing mortality rates associated with the targets of the *Diving* fleet (i.e. benthic invertebrate groups), this improvement is mainly attributable to slightly better fits in the targets of the *Fishing* fleet. In particular, the increases in relative biomass for *Littoral fish*, *Pelagic predatory fish*, and *Cephalopods* (Fig. 5) are slightly improved through the introduction of decreasing fishing effort in the *Fishing* fleet (Fig. 3).

Despite this improvement, the impact of the artisanal fishery in Sechura appears small and in stark contrast to what has been observed for the Peruvian upwelling system overall with respect to the industrial fishery. Taylor et al. (2007c) showed that the changes in industrial fishing rates in the upwelling region (4°–16°S, 110 km extension from the coast) helped to explain 27.1% of the biomass and catch variability during the same time period of 1996–2003. In contrast, the artisanal fishery seems to operate more in response to the fluctuating availability of resources and does not have the same problems of overcapacitation as has been shown for the industrial fishery (Fréon 2006).

Applicability of trophic modeling to the Sechura Bay Ecosystem

Through the modeling of trophic flows for Sechura Bay we have gained insight into the general system configuration during periods of normal upwelling (1996) and provide some of the first estimates of fishing mortality of the benthic resources, which appear to be very low. The application of Ecoranger has helped to add some weight to our input parameters due to the fact that locally derived estimates of production, consumption, and diet were scarce. Our assumptions regarding these values allowed for the initial balancing of the model, and confidence intervals of 20% give favorable results from the Ecoranger resampling routine whereby resulting energy budgets of functional groups are within acceptable ranges. Generally, highest respiration rates were found for the warm-blooded sea birds and marine mammals, and lower values for poikilotherms (fish and invertebrates), with less mobile benthic invertebrates having the lowest respiration ratios (R/A). Furthermore, within the invertebrate groups, lowest respiration rates are calculated for strongly carnivorous groups (predatory gastropods, octopods, and cephalopods). Higher assimilation efficiencies have been proposed for carnivorous organisms possibly due to the high nutrient value of their food (Welch 1968); however, this tendency is not supported for aquatic mollusks (Huebner and Edwards 1981), and thus our decision to leave unassimilation ratios for all benthic invertebrates at the Ecopath default of 20% may be reasonable. The lower R/A ratios calculated in the model are rather a result of higher conversion efficiencies

("gross efficiency", GE) (0.3–0.35) as is supported by Huebner and Edwards (1981) for carnivorous invertebrates as well as from local estimates of *Octopus mimus* (Wolff and Perez 1992; Vega and Mendo 2002) and the jumbo squid, *Dosidicus gigas* (Alegre et al. 2005).

We hypothesized that the fit of the simulations would be improved through the forcing of functional group 'drivers' whose changes in biomass and production were known to be a result of non-trophic environmentally mediated interactions (i.e. *Scallops*, *Benthic detritivores* (shrimp), *Octopus*, and *Littoral fish*). Overall, these drivers help little in explaining the remaining functional groups' dynamics. We propose three hypotheses for the poor performance of the dynamic simulation.

First, the Sechura Bay ecosystem is highly open to outside influences, and thus the scale of the model does not reproduce well the dynamics of functional groups whose life cycles are enclosed in a larger geographic area or whose distribution is linked to particular water masses. We have taken into account the southward migration of more tropical equatorial-associated fish species to Sechura Bay due to their possible impact on benthic resources; however, other groups also show important dynamics on a larger scale. *Small pelagic fish* catch dynamics in Sechura are mainly due to latitudinal migrations of the stocks in response to changing centers of upwelling and associated plankton variability. One example is the southward retreat of the Peruvian anchoveta during the strong EN of 1997/98 (Alheit and Ñiquen 2004), which helps in explaining the decreased catches in Sechura. *Cephalopod* catches have increased following the EN of 1997/98 to become an important target of the artisanal fishery. This is due almost exclusively to large-scale increases in population growth and range expansion of the Jumbo squid, *Dosidicus gigas*. Evidence suggests that its large-scale expansion is a bottom-up response to increases in its principle prey—mesopelagic fish (e.g. *Vinciguerria lucetia*) (Taylor et al. 2007c). Mesopelagic fish themselves are not found much within the shelf region of Peru, but adult Jumbo squid in their reproduction phase or nearing senescence can be found in coastal waters (Argüelles et al. 2007) where they are targeted by the artisanal fishery. It is also worthwhile to note that the model presented in Taylor et al. (2007c) for the Northern Humboldt Current system took care to define both offshore (∼110 km) and latitudinal (4°–16°) boundaries that enclosed the life cycles and spatial movements of main functional groups in response to ENSO variability. As a result, the model could explain more of the time series variability after the introduction of drivers (−33% in SS). However, even with this large scale, the forcing of the mesopelagic fish expansion into the model area proved to be an important factor in the dynamics of more coastally associated groups (−9% in SS). Thus, we believe that the

applicability of trophodynamic models depends on a certain degree of "closure" of trophic flows in order to be able to reproduce dynamics.

Secondly, other groups' dynamics, besides the forced drivers, may also be highly influenced by environmental variability. It is possible that given the dramatic changes in temperature and salinity in Sechura Bay, other less mobile benthic invertebrate species may also be affected by ENSO-related variability. Respiration rates of poikilotherms are sensitive to changes in temperature and thus, depending on the organism's tolerances, conversion efficiencies may also be affected. Several ongoing studies regarding these influences are being conducted within the CENSOR (http://www.censor.name) project, which will aid future modeling efforts.

Finally, the data availability and quality may have affected the accuracy of some parameters and time series data sets. We have constructed our model for the base year of 1996 for several reasons: (1) availability of benthic biomass estimates; (2) it marks beginning of constant monitoring of catch and effort data by IMARPE; and (3) it precedes the strong EN event of 1997/98, which offers insight into system dynamics resulting from extreme environmental variability. Our catch and effort data comes from the two main ports in the bay (Puerto Rico and Parachique). Biomass estimates were available for benthic groups based on evaluations conducted by IMARPE in 1996, but fish and cephalopod biomasses were approximated by assuming that the fishery takes about 50% of these groups' production. Such fishing rates are likely, given the operating capacity of the fishers, especially regarding the fleets geared toward anchovy and other pelagic fish. Furthermore, the artisanal fleet has traditionally focused on fishing, and thus we have more confidence in relative biomass changes as calculated by CPUE. On the other hand, the diving activities are less intensive as well as relatively young in development. Although these activities have continued to grow since the mid-1990s, relative changes as calculated by CPUE for our time series may be less indicative of the actual resource dynamics. Future simulations will be able to take advantage of improved time series as derived from more regularly conducted benthic evaluations by IMARPE since 2000.

Importance of environmental variability
and implications for management

Although Sechura Bay is a system relatively open to outside influences, the dynamics of some principle resources may still be largely influenced by local variability. We have explored one such example with the scallop *A. purpuratus* for which a simple two-factor multiple regression model is able to predict catches.

Scallop biomass has been shown to be enhanced in southern Peru and northern Chile during EN events (Wolff 1987; Stotz 2000). These events improve benthic oxygen concentrations through a lowering of the thermocline and also increased metabolic activity (respiration, somatic growth) in response to the increased temperature. New findings suggest that reduced mortality in the larval stage, due to faster development to settlement times, may be mainly responsible for population booms during EN periods (Wolff et al. 2007). Our exploration of the environmental influences on the scallop stock in Sechura Bay suggests a greater importance of riverine inputs to the bay. The importance of both spawning stock (positive) and river discharge (negative) suggests some degree of self-recruitment with the additional negative effect (i.e. mortality) of riverine discharge on the adult population.

Contrary to Independence Bay and many of the main scallop habitats in northern Chile that border the Atacama Desert (known as the most arid region on Earth), Sechura experiences seasonal rainfall and, additionally, flooding is common during EN events. For example, the most recent EN of 1997/98 increased the discharge volume of the Piura River more than four times the normal levels, causing massive flooding damage to the region. In addition, mean temperatures are consistently higher in Sechura as compared with the south, and thus scallop recruitment appears to be less limited by extreme cold conditions and, in fact, scallops may spawn multiple times in the year (IMARPE, personal communication). The importance of riverine input to the bay on scallop mortality has long been suggested by fishers, either through increased sediment load affecting their filtering capacity or through salinity changes. We believe that while sediment loads may increase in the bay, these changes are likely to be temporary and, furthermore, *A. purpuratus* appears to be well-adapted to periodic sedimentation events in other areas (e.g. wind-blown terrigenous material to Paracas Bay, Peru). On the other hand, physiological studies of *A. purpuratus* have shown that the scope for growth is greatly diminished by reduced salinity with negative values calculated for salinities below 27‰ (Navarro and Gonzalez 1998). Unfortunately, longer time series of salinity changes in the bay are not available; however, Aronés et al. (2007) have measured salinities of ca. 23‰ off Paita Bay during the EN of 1997/98 (immediately north of Sechura; average of a four station transect extending >25 km offshore). With the implementation of regular environmental sampling series within the CENSOR project, future EN events will provide a test to this hypothesis for Sechura Bay.

It is likely that similar explorations for other resources may also show an importance of environmental variability on resource dynamics in Sechura Bay. This information will have importance in the designation of management strategies in response to ENSO. Previously, artisanal fishers have operated in a highly mobile manner in response to changing resources (e.g. migration of fishers towards population increases of *A. purpuratus* in Independence Bay during EN periods); however, increasing regionalization may make this more difficult in the future.

Even if the responses of resources are successfully linked to environmental variability, the predictions of strong EN phenomena are presently only accurate for a few months to half a year, thus preventing longer-term strategies for fishers. Nevertheless, forecasts of even a few months could mean substantial benefits; in fact some Peruvian fishers and farmers have based their seeding or harvesting schedules (albeit erroneously at times) on the ENSO predictions of the NOAA website. As these predictions improve, as well as the known responses of resource availabilities, we may see an increased importance of ENSO forecasting to management strategies. For example, forecasting would allow culturists time for harvest or relocation of scallops to other areas, and fishers could make gear changes or other adjustments in preparation for switching to alternative resources.

Significant emphasis has been placed in recent years for developing an ecosystem-based approach to fisheries (for review, see Browman and Stergiou 2004). Trophic modeling tools, such as EwE, have no doubt shed new light on our understanding of ecosystem dynamics and continue to increase in importance for management. Additionally, the incorporation of environmental drivers on ecosystem dynamics is often needed to reproduce historical changes. This study confirms this, and furthermore indicates that systems which are both open to outside influences or bordering variable water masses may be less predictable from a trophic modeling perspective than that of more closed systems.

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