

Trophic role of small pelagic fishes in a tropical upwelling ecosystem

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Abstract

On the basis of an Ecopath model and Ecosim model simulations, the trophic role of small pelagic fish in the Gulf of Salamanca, a tropical upwelling ecosystem on the Caribbean coast of Colombia, was explored using a combination of fishing vulnerabilities and harvest scenarios. Dynamic simulated changes in the biomass of small pelagic fish caused reallocation of the biomass of higher trophic-level organisms but not of lower trophic-level organisms (plankton). This was attributed to bottom-up control exerted by small pelagic fish on pelagic predatory fish, the highest trophic-level predators with a diverse diet through which consequences of changes in small pelagic fish biomass propagate. Plankton biomass remained almost unchanged, although plankton is the main food of small pelagic fish. Overall, the results indicate that small pelagic fish play an important role in this ecosystem because perturbations of their biomass (brought about by fishing) propagate through the upper part of the system. However, they have little effect on the lower trophic-level groups. By extension, the postulated crucial “wasp-waist” role of intermediate trophic levels occupied by small pelagic fish in temperate and subtropical most productive upwelling regions may not have a full equivalent in tropical less productive upwelling areas.

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1. Introduction

Trophic interactions are one of the determinants of distribution and abundance of organisms. Debate as to whether community control is exerted by bottom-up forces, i.e. by resource availability or by top-down forces, i.e. by predation, seems to have reached a consensus, that in general, the two forces are dynamically linked inside food webs (Hunter and Price, 1992; Menge, 1992), implying that predation is as important as resource limitation (Verity, 1998). New studies have documented trophic cascades in unexpected sys-

tems such as the open ocean (Pace et al., 1999), and historical reconstructions suggest that long-term overfishing (a top-down force) set off a series of trophic cascades in coastal marine ecosystems (Jackson, 2001). Ecosystems in which there is unequivocal dominance of top-down forces tend to have low diversity (Strong, 1992). However, on a broader scale, primacy of bottom-up forces is postulated because the removal of primary producers plainly means the disappearance of the system (Hunter and Price, 1992). The challenge now is to describe the circumstances that modulate the effects of resource limitation and predation levels over time in a community.

In many marine ecosystems, particularly in upwelling regions, there are often a few small plankton-feeding pelagic fish species that occupy an

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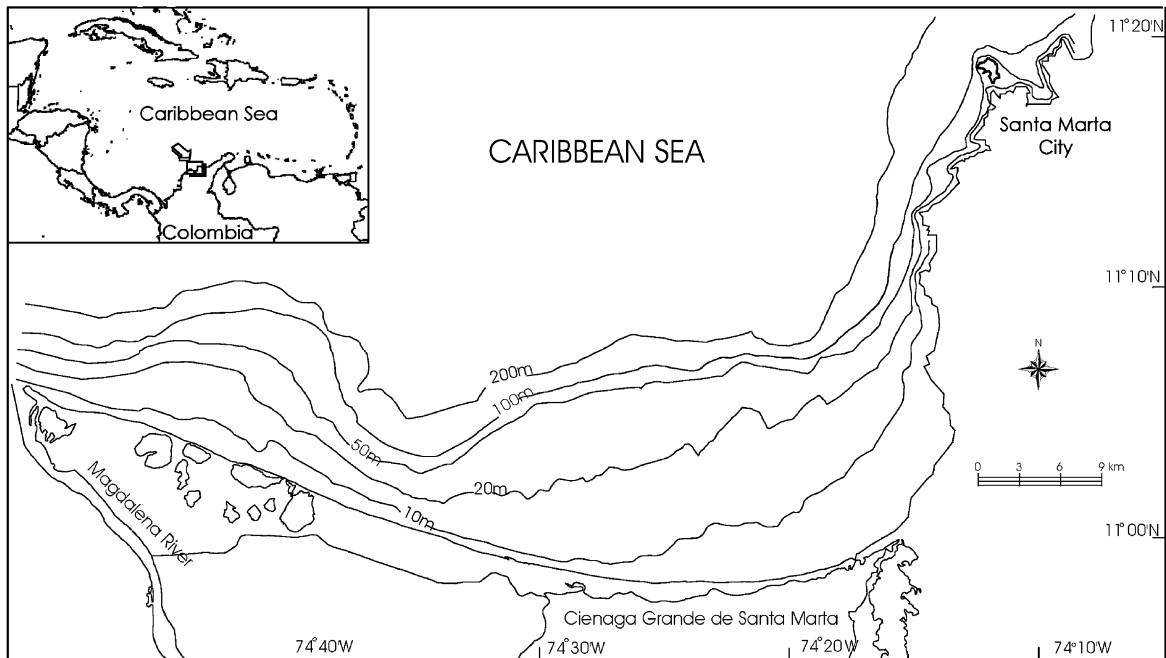


Fig. 1. Location of the Gulf of Salamanca ecosystem in Colombia, Caribbean Sea.

intermediate to low trophic level. Species diversity above and below this trophic level tends to be high (Cury et al., 2000). The small pelagic fish in such systems are called forage fish because very often they contribute substantially to fishery catches (Hall, 1999) and to diets of predators. Their intermediate trophic role has been postulated as crucial as small pelagic fish would exert top-down control on zooplankton and bottom-up control on pelagic predatory fish, i.e. “wasp-waist” type control *sensu* Rice (1995).

The above description applies to the marine ecosystem of the Gulf of Salamanca, a tropical region on the Caribbean coast of Colombia (Fig. 1). The Gulf of Salamanca hosts a rich marine fauna and flora. The artisanal fishery there captures more than 100 species, mostly fish and some invertebrates (García, 1999a). More than 120 fish species have been found in demersal trawl surveys (García et al., 1998). Also, more than 110 infauna families (polychaetes, amphipods, molluscs, etc.) have been reported (Vides, 1999), as well as more than 150 crustacean and molluscan species in the epifauna (Arango and Solano, 1999). The most important small pelagic fish in the Gulf of Salamanca is

the Atlantic anchovy (*Cetengraulis edentulus*), which represents more than 55% of total landings.

Coastal upwelling off the northernmost Colombian Caribbean coast, including the Gulf of Salamanca, has been documented since the earliest oceanographic studies (Gordon, 1967), but only recent studies have analysed the structure of this upwelling zone by means of satellite observations (Blanco, 1988; Muller-Karger et al., 1989; Andrade, 1995, 2000). Although the mouth of the Magdalena River is located in the western side of the Gulf of Salamanca, the River plume do not penetrate into the Gulf since it is deviated to the south by the interaction with the cyclonic Panama Colombian Gyre (Moore and Maul, 1998). Wind data have shown that in the Gulf of Salamanca during the dry season (December–April, average wind velocities about 5 m/s in contrast to wind velocities of about 1 m/s in the rainy season) NE trade winds drive a surface offshore Ekman drift and an associated nearshore upwelling (Ciales et al., 2002). This result corroborated previous biological observations (Bula, 1977; Blanco et al., 1994), and results of the analysis of sea surface temperature time

series data obtained from the satellite sensor AVHRR (Purca et al., 2001). The upwelling off the Colombian Coast stimulates phytoplankton growth but water is relatively nutrient-poor in comparison with the major eastern boundary currents (Corredor, 1979).

Here we describe and explore the trophic role of small pelagic fish (Atlantic anchovy) in the Gulf of Salamanca ecosystem by determining their status in the trophic network and assessing the ecosystem response to perturbations of their biomass brought about by simulated extreme fishing regimes. The potential “wasp-waist” control exerted by the Atlantic anchovy is tested using assumptions of various control mechanisms of small pelagic fish and zooplankton under the simulated fishing regimes and finally, our findings

are compared with the results of previous modelling studies in other upwelling regions.

2. Methods

A mass-balanced model for the Gulf of Salamanca (Duarte and García, 2000, 2002) was constructed using the Ecopath software (Christensen and Pauly, 1992). The model had 18 compartments as shown in Fig. 2. The input parameters (Table 1) were mostly obtained from data collected in three scientific cruises carried out in 1997 (February, July and November) on the continental shelf (10–200 m depth; García, 1999a). Biomass of fish and epifauna was estimated

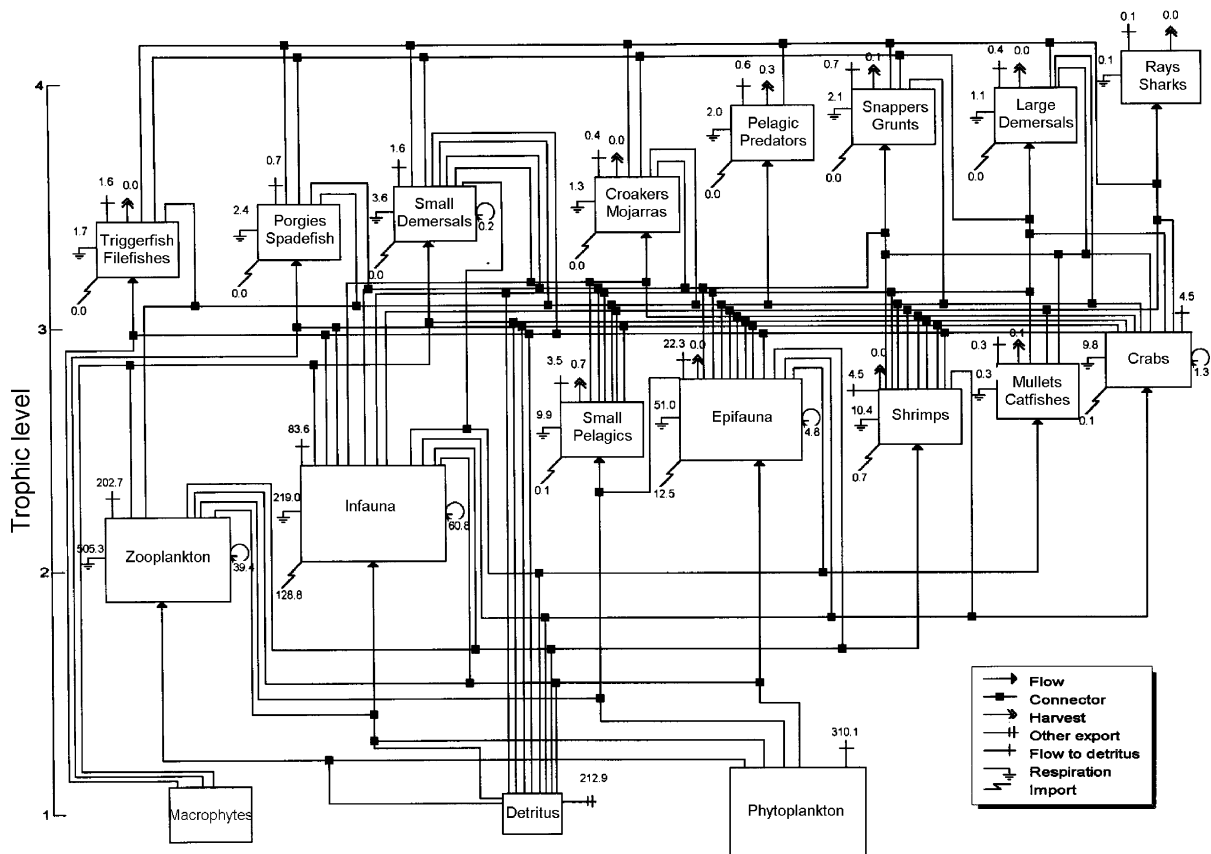


Fig. 2. A balanced trophic model of the Gulf of Salamanca ecosystem, Colombian Caribbean. Flows are in tonnes km⁻² per year. The surface area of the boxes is proportional to the logarithm of the biomass represented. The components of the system are structured along the vertical axis according to their trophic level defined as 1 for primary producers and detritus and as 1 plus the weighted average of the prey's trophic level for consumers.

Table 1

Input parameters for trophic modelling of the Gulf of Salamanca

No.	Group	Trophic level	Biomass (tonnes km ⁻²)	P/B (per year)	Q/B (per year)	EE
1	Phytoplankton	1.0	10.080	102.56 ^a	–	0.700
2	Macrophytes	1.0	0.053	11.00 ^b	–	0.700
3	Zooplankton	2.1	6.290	18.70 ^c	125.41 ^{a,d}	0.643
4	Infauna	2.2	15.000	7.00	27.00 ^a	0.975
5	Epifauna	2.6	5.000	5.00 ^{e,d}	19.00 ^a	0.868
6	Shrimps	2.6	0.704	7.57 ^a	28.00 ^d	0.900
7	Small pelagic fish	2.6	0.835	3.37 ^{f,g}	18.98	0.900
8	Mulletts/catfish	2.7	0.150	1.00 ^{h,i}	4.50	0.859
9	Crabs	2.9	1.300	3.80 ^e	14.16 ^a	0.836
10	Triggerfish/filefish	3.3	0.480	0.80	7.39	0.532
11	Porgies/spadefish	3.4	0.280	0.76	11.85	0.924
12	Croakers/mojarras	3.5	0.120	1.58	15.30	0.971
13	Small demersal fish	3.5	0.800	2.30	8.55	0.847
14	Pelagic predatory fish	3.8	0.330	0.91	8.80	0.956
15	Large demersal fish	3.9	0.270	0.60	6.00	0.744
16	Snappers/grunts	3.9	0.450	0.89	6.99	0.839
17	Rays/sharks	4.0	0.040	0.60 ^{e,d}	5.30 ^{a,d}	0.050
18	Detritus	1.0	–	–	–	0.666

Parameters calculated by Ecopath II are presented in bold. *P/B* is the production/biomass ratio, *Q/B* is the consumption/biomass ratio and EE is the ecotrophic efficiency. Parameters obtained from the literature are indicated.

^a Arregín-Sánchez et al. (1993).

^b Polovina (1984).

^c Chrisholm and Roff (1990).

^d Wolff et al. (1998).

^e Manickhand-Heileman et al. (1998).

^f Osorio (1997).

^g Manjarres et al. (1993).

^h Tijero et al. (1998).

ⁱ Sánchez et al. (1998).

by the swept-area method from captures with bottom trawl samples. Zooplankton and infauna biomass was derived from sampling by plankton nets and dredge, respectively. Production to biomass (*P/B*) ratios of fish were included as the equivalent of the total mortality (Allen, 1971). Consumption to biomass (*Q/B*) ratios of fish was computed by means of empirical models (García and Duarte, 2002). Based mainly from fish stomach content analysis of specimens collected in the Gulf of Salamanca during the study period. This trophic information was gathered in digital format (Duarte et al., 1999). Landings recorded by INPA and the INPA-VECEP/UE program (García et al., 1999). The model was mostly based on local data. A pedigree index of 0.743 was calculated identifying the origin and quality of the information employed to estimate the input parameters (see Christensen et al., 2000). The fished groups and their most important components included in the analysis were:

epifauna (*Panulirus argus* Latreille, 1804), shrimps (*Xiphopenaeus kroyeri* Heller, 1862), small pelagic fish (*C. edentulus* Cuvier, 1829), small demersal fish (*Bothus*, *Polydactylus*), large demersal fish (*Elops*, *Epinephelus*), pelagic predatory fish (*Sphyrnaena*, *Scomberomorus*, *Caranx*), croakers/mojarras (*Micro-pogonias*, *Menticirrhus*, *Diapterus*), porgies/spadefish (*Calamus*, *Chaetodipterus*), triggerfish/filefish (*Balistes*, *Aluterus*) and snappers/grunts (*Lutjanus*, *Conodon*). Diets (Table 2) were obtained from stomach content analysis and in some cases from the literature (Melo, 1998; Navajas, 1998; Duarte and García, 1999a,b; Duarte et al., 1999; Schiller and García, 2000).

Table 3 shows a list of the 10 most abundant species or species/groups in the landings and their relative importance between 1993 and 1998. An estimated 6400 tonnes of invertebrates and fishes were extracted from the Gulf of Salamanca during this period (García

Table 2

Diet composition matrix for trophic groups in the Gulf of Salamanca

No.	Prey/predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	Phytoplankton	0.850	0.100	0.050		0.500										
2	Macrophytes								0.009	0.010		0.050				
3	Zooplankton	0.050	0.050	0.100	0.250	0.400						0.039	0.037			
4	Infauna		0.150	0.350	0.100		0.344	0.200	0.334	0.110	0.289	0.040		0.029	0.027	0.048
5	Epifauna			0.050	0.150	0.100	0.162	0.200	0.297	0.646	0.121	0.495	0.150	0.342	0.251	0.179
6	Shrimps							0.100	0.004	0.079	0.160	0.172	0.194	0.138	0.124	0.160
7	Small pelagic fish									0.031	0.116		0.405	0.003	0.101	0.110
8	Mulletts/catfish													0.021	0.011	0.030
9	Crabs							0.070	0.213	0.021	0.037	0.129		0.151	0.260	0.032
10	Triggerfish/filefish												0.050	0.028		0.056
11	Porgies/spadefish												0.016	0.051	0.020	0.015
12	Croakers/mojarras												0.015	0.030	0.021	0.020
13	Small demersal fish						0.018		0.013		0.179	0.024	0.034	0.179	0.182	0.220
14	Pelagic predatory fish															0.070
15	Large demersal fish												0.030		0.003	0.010
16	Snappers/grunts												0.070	0.009		0.050
17	Rays/sharks															
18	Detritus	0.100	0.700	0.450	0.500		0.476	0.430	0.130	0.103	0.099	0.052		0.019		

et al., 1999). There was high diversity in the landings, which included more than 100 species. Ten groups represent more than 90% of the total landings, and the Atlantic anchovy represents more than 55% of total landings. The anchovy has low economic value, but its fishery has a key social importance (Duarte and Garcia, 2002) as it is used as food for farmed crocodiles. No discards are reported for the Gulf. The landings of each component for 1997 were used in

the balanced model and appear in Table 4. The highest proportion of landings was by beach seines; they accounted for almost all the small pelagic fish and a large fraction of the pelagic predatory fish, the second most abundant group in the landings.

The role and trophic status of small pelagic fishes in the ecosystem (mass-balance model) was explored in terms of: (a) their trophic level estimated from the model, (b) their fishing and predatory mortality rates

Table 3

The 10 components most frequently captured by artisanal fisheries in the Gulf of Salamanca between May 1993 and May 1998

Scientific name	Common name	Catch (tonnes)	Total catch (%)	Cumulative catch (%)
<i>Cetengraulis edentulus</i>	Atlantic anchovy	3548	55.4	55.4
<i>Sphyrna guachancho</i> , <i>S. picudilla</i> , <i>S. barracuda</i>	Barracuda	485	7.6	63.0
<i>Caranx bartholomei</i> , <i>C. crysus</i> , <i>C. ruber</i>	Jack	346	5.4	68.4
<i>Caranx hippos</i> , <i>C. latus</i>	Jack	337	5.3	73.7
<i>Scomberomorus brasiliensis</i> , <i>S. regalis</i>	Mackerel	310	4.8	78.5
<i>Conodon nobilis</i>	Barred grunt	291	4.5	83.0
<i>Lutjanus</i> spp. ^a , <i>R. aurorubens</i> , <i>O. chrysurus</i> , <i>P. aquilonaris</i> , <i>L. maximus</i>	Snapper	204	3.2	86.2
<i>Microgobias furnieri</i> , <i>Menthicirrhus americanus</i> , <i>Menthicirrhus littoralis</i>	Croaker	157	2.5	88.6
<i>Ariopsis bonillae</i> , <i>Arius proops</i> , <i>Bagre marinus</i> , <i>Cathorops spixi</i>	Sea catfish	152	2.4	91.0
<i>Mugil incilis</i>	Parassi mullet	145	2.3	93.3
Others (at least 97 species)		156	6.7	100.0

Common names are from Cervigón et al. (1992).

^a *L. synagris*, *L. griseus*, *L. cyanopterus*, *L. analis*, *L. bucanella*, *L. vivanus*, *L. jocu*, *L. purpureus*, *L. mahogoni*, *L. apodus*.

Table 4

Landings (tonnes km⁻², 1997) of the trophic groups included in the Ecopath model used for the simulation

No.	Group name	Beach seine	Gill net	Long line	Fishing line	Total
5	Epifauna	–	0.001	–	–	0.001
6	Shrimps	0.005	–	–	–	0.005
7	Small pelagic fish	0.690	0.005	–	–	0.695
8	Mulletts/catfish	0.002	0.025	0.009	0.018	0.054
10	Triggerfish/filefish	–	–	0.002	–	0.002
11	Porgies/spadefish	–	–	0.001	–	0.001
12	Croakers/mojarras	–	0.017	0.004	–	0.021
13	Small demersal fish	–	–	0.0002	–	0.0002
14	Pelagic predatory fish	0.081	0.118	0.001	0.073	0.273
15	Large demersal fish	0.001	0.011	0.007	0.003	0.022
16	Snappers/grunts	0.003	0.003	0.054	0.047	0.107
17	Rays/sharks	–	–	0.001	–	0.001
	Sum	0.782	0.18	0.079	0.141	1.182

and (c) their mixed trophic impacts on all other groups (see Ulanowicz and Puccia, 1990; Christensen et al., 2000).

On the basis of the balanced Ecopath model, dynamic simulations were performed using the Ecosim module developed by Walters et al. (1997), which re-expresses the linear equations that describe equilibrium conditions in Ecopath as differential equations, allowing the exploration of a variety of harvest regimes. Our questions pertain to the role of energy flow forces and the circumstances that modulate such forces as mediated by small pelagic fish. In Ecosim, each prey pool is viewed as a composite of biomass that is either available or unavailable to each consumer at any moment in time. The rate at which biomass changes state from unavailable to available to predators is a function of a vulnerability ratio (ranging from 0 to 1), which is controlled by the modeller (see Walters et al., 1997, for details). Setting a low value of the vulnerability ratio leads to bottom-up control of flow rates from prey to predators, while a high value leads to top-down control and trophic cascade effects.

Scenarios for small pelagic fish were constructed with vulnerability ratios of 0.1 (bottom-up control), 0.5 (mixed trophic control) and 0.9 (top-down control). Because small pelagic fish feed on zooplankton, the impact of changing zooplankton vulnerability to small pelagic fish (vulnerability ratios 0.5 and 0.9) was also explored. The vulnerabilities of all other groups were set at 0.5. Two extreme fishing regimes of small pelagic fish were imposed over the simulation period: (a) catch rates of zero, i.e. returning

all biomass lost to fishing to the ecosystem, and (b) infinity catch (three-fold sustained increase of base fishing mortality rate), i.e. causing the deletion of small pelagic fish from the ecosystem.

Time dynamic simulations were run for 5 years without a change of fishing in order to assure initial stable conditions, after which runs continued for an additional 30-year period (except for one case, see Section 3). Apart from manipulation of the vulnerability ratios above, the default settings of Ecosim (Ecopath with Ecosim 4.0 version) were left unchanged. The Ecopath with Ecosim program allows the inclusion of economic values. Thus, performance indicators of the simulations were calculated including the predicted economic value of the catch.

3. Results

3.1. Role of small pelagic fish in the mass-balance model

Small pelagic fish have a trophic level (TL) of 2.6 (TLs ranged from 1 to 4 in this model), with only primary producers (phytoplankton and macrophytes), detritus (by definition), zooplankton and infauna below them (Table 1). As prey, the small pelagic fish have direct trophic relations with pelagic predatory fish, croakers/mojarras, rays/sharks, snappers/grunts, porgies/spadefish and large demersal fish, in that order of importance in predator diet. As predators, small pelagic fish have a direct trophic relation with

Table 5
Mortality rates by trophic group in the Gulf of Salamanca

No.	Group name	P/B ($= Z$)	Fishing mortality rate	Predation mortality rate	Other mortality rate
1	Phytoplankton	102.560	0.000	71.792	30.768
2	Macrophytes	11.000	0.000	7.700	3.300
3	Zooplankton	18.700	0.000	12.851	5.849
4	Infauna	7.000	0.000	6.825	0.175
5	Epifauna	5.000	0.000	4.341	0.659
6	Shrimps	7.570	0.008	6.805	0.757
7	Small pelagic fish	3.370	0.833	2.200	0.337
8	Mulletts/catfish	1.000	0.360	0.500	0.140
9	Crabs	3.800	0.000	3.178	0.622
10	Triggerfishes/filefish	0.800	0.006	0.422	0.372
11	Porgies/spadefish	0.760	0.004	0.699	0.058
12	Croakers/mojarras	1.580	0.180	1.354	0.046
13	Small demersal fish	2.300	0.000	1.948	0.352
14	Pelagic predatory fish	0.910	0.827	0.045	0.038
15	Large demersal fish	0.600	0.079	0.365	0.155
16	Snappers/grunts	0.890	0.238	0.508	0.143
17	Rays/sharks	0.600	0.031	0.000	0.570

phytoplankton, zooplankton and epifauna in that order of importance (Table 2).

Table 5 shows the mortality rates of all groups and its partition into different causes. Small pelagic fish have an intermediate total mortality (3.37) in relation to the other groups, of which 0.833 (25%) is due to fishing, 2.2 (65%) is due to predation and 0.337 (10%) is due to other causes (**Table 5**). As many as 11 pathways extend from primary producers to small pelagic

fish and 30 pathways derive from small pelagic fish to the highest trophic-level (or top) predators in the balanced model. Table 6 shows mortality rates due to predation only. Pelagic predatory fish cause the highest predation mortality rate of small pelagic fish.

The mixed trophic impact of small pelagic fish on all other groups is shown in Fig. 3. The highest positive impact, either directly or indirectly, is exerted on beach seines, croakers/mojarras, pelagic predator

Table 6
Predation mortality rates of trophic groups in the Gulf of Salamanca ecosystem

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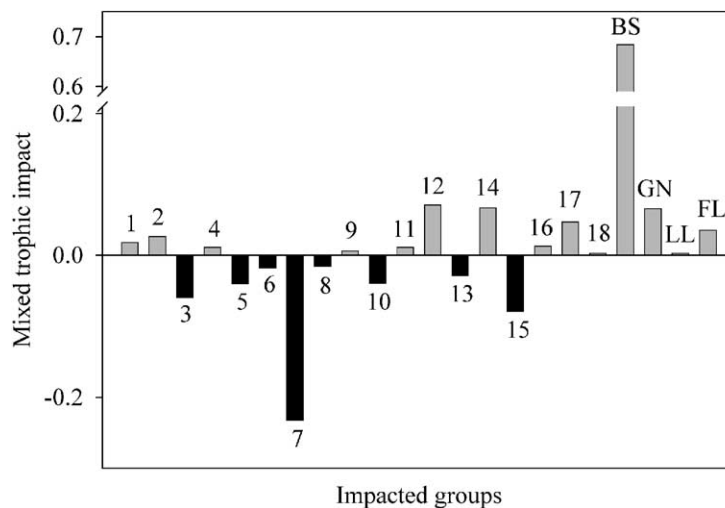


Fig. 3. Mixed trophic impact of small pelagic fish as the impacting group in the food web of the Gulf of Salamanca. The impacts are relative to a scale of -1 to $+1$, where 0 indicates no impact. Impacted groups are numbered as in Tables 1–6. BS, beach seine; GN, gill net; LL, long line; FL, fishing line.

Table 7

Relative importance of each impacting trophic group ranked according to their total mixed trophic impacts (addition of positive and negative mixed trophic impacts regardless of sign)

Total impact	Total positive impact	Total negative impact
Pelagic predatory fish	Detritus	Pelagic predatory fish
Detritus	Epifauna	Snappers/grunts
Snappers/grunts	Phytoplankton	Large demersal fish
Epifauna	Pelagic predatory fish	Small demersal fish
Small demersal fish	Small pelagic fish	Gill net
Phytoplankton	Snappers/grunts	Crabs
Gill net	Gill net	Fishing line
Large demersal fish	Shrimps	Zooplankton
Small pelagic fish	Crabs	Beach seine
Crabs	Beach seine	Long line
Beach seine	Mullets/catfish	Infauna
Fishing line	Infauna	Epifauna
Shrimps	Small demersal fish	Shrimps
Infauna	Fishing line	Croakers/mojarras
Zooplankton	Croakers/mojarras	Porgies/spadefish
Long line	Large demersal fish	Triggerfish/filefish
Croakers/mojarras	Long line	Small pelagic fish
Mullets/catfish	Triggerfish/filefish	Phytoplankton
Triggerfish/filefish	Zooplankton	Detritus
Porgies/spadefish	Macrophytes	Rays/sharks
Rays/sharks	Rays/sharks	Mullets/catfish
Macrophytes	Porgies/spadefish	Macrophytes

Impact on themselves was excluded.

fish and gill nets. The highest negative impact (except within-groups) is exerted on large demersal fish and epifauna (Fig. 3).

Table 7 shows a ranking of groups obtained by adding the relative mixed trophic impacts (relative but comparable values among groups; impact on themselves excluded) of each group (as impacting group) from the mixed trophic impact table produced by Ecopath. In terms of total impact (addition of mixed trophic impact values regardless of sign), small pelagic fish have an intermediary position, a rather high position in terms of positive impact and a rather low position in terms of negative impact (Table 7).

The fishery mediates 19.7% of total mixed trophic impact, 30.5% of total positive impact and 9.1% of total negative impact (excluding self-impact). In about 9% of all paired interactions, predation is beneficial on prey due to positive indirect impact.

3.2. Simulations

Figs. 4 and 5 show changes in biomass distribution for different flow control mechanisms (bottom-up, mixed, top-down) for small pelagic fish and zooplankton (mixed, top-down) under infinite catches of small pelagic fish, i.e. a fish mortality rate that drives small pelagic fish to extinction and under no catch of small pelagic fish, i.e. zero fishing mortality, respectively.

In the infinite catch scenario, the biomass of the different groups undergoes reallocation (Fig. 4). This reallocation occurs independently of the vulnerability ratios assayed because the extirpation of small pelagic fish from the system occurs so rapidly. Under the zero catch of small pelagic fish regime, vulnerability ratios of small pelagic fish and zooplankton do affect the biomass (Fig. 5). Three categories of groups emerge from these simulations: groups that do not change, groups whose biomass decrease and groups whose biomass increases (Figs. 4 and 5).

Groups that do not change under any circumstance (not even when zooplankton is made highly vulnerable to small pelagic fish) include phytoplankton and zooplankton, which, however, constitute 90% of the diet of small pelagic fish in the base model (Table 2). It is clear from the diet and mortality matrices (Tables 2 and 6) that all consumers of phytoplankton (infauna, epifauna and small pelagic fish) are also consumers of zooplankton, which in turn consumes phytoplankton.

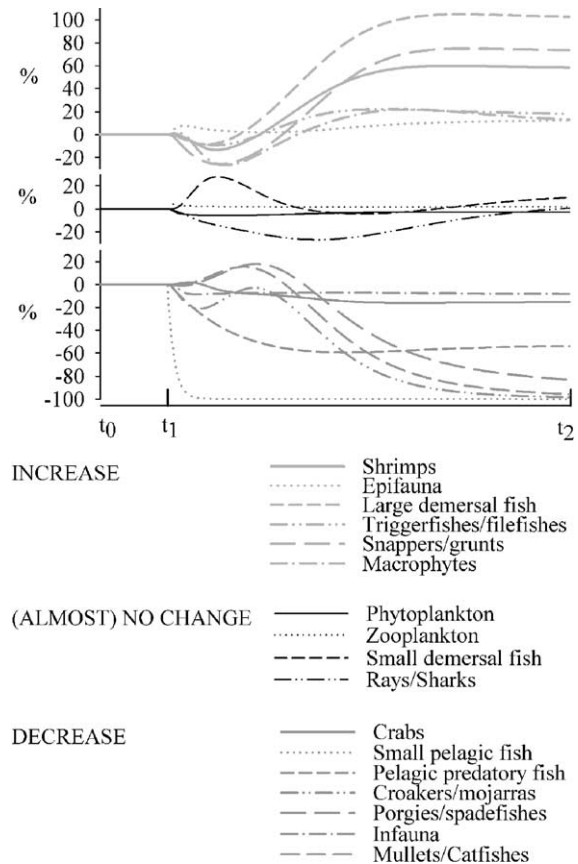


Fig. 4. Simulated relative change in biomass by group under an infinite catch on small pelagic fish. In the simulations, a 5-year period under the base fishing mortality rate begins at t_0 ; during the period t_1 – t_2 (30 years), a sustained three-fold increase of fishing mortality rate on small pelagic fish was imposed. Biomass curves were grouped in increasing (upper panel), almost no change (middle panel) and decreasing (lower panel). Changes of biomasses occur independently of the trophic control (vulnerability ratios) assayed.

That is, there is a double relationship with zooplankton: the latter is prey and competitor at the same time. The simulated vulnerabilities of small pelagic fish and zooplankton and fishing regimes of small pelagic fish were factors too weak to alter the comparatively low base predation mortality rates they inflict on phytoplankton and zooplankton (Table 6). Note also that the stronger mixed impact of small pelagic fish does not include phytoplankton or zooplankton (Fig. 3).

Of the groups whose biomass do change in the extreme simulated harvest regimes, most of those whose

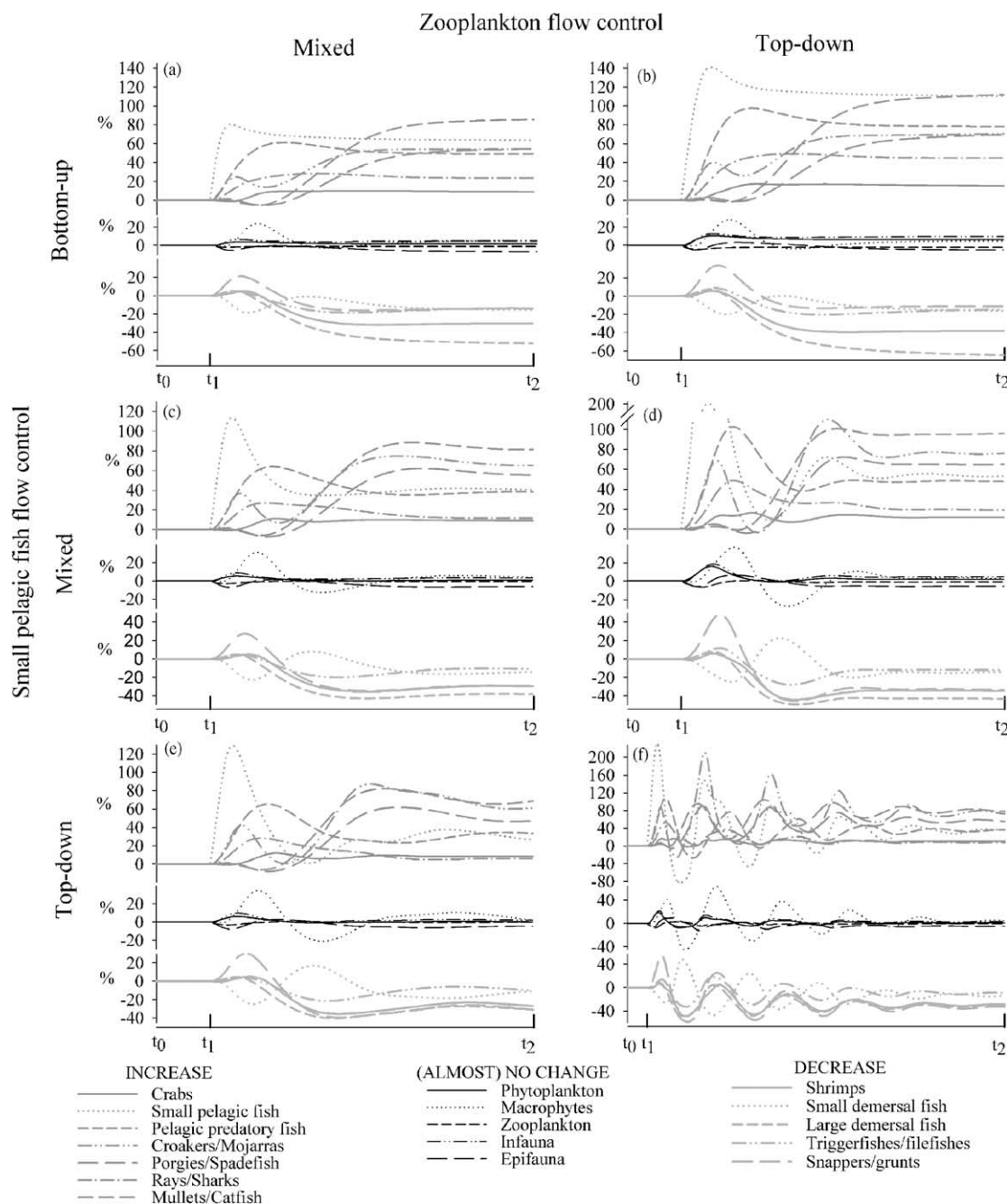


Fig. 5. Simulated relative change in biomass by group under a complete closure of fishery on small pelagic fish. In each simulation, a 5-year period under the base fishing mortality rate begins at t_0 ; during the period t_1 – t_2 (30 years), small pelagic fishes were subject to a catch rate of zero. Three flow mechanisms were assumed for small pelagic fish: bottom-up (a and b), mixed trophic (c and d), and top-down (e and f); two flow control mechanisms were assumed for zooplankton: mixed-trophic (a, c and e) and top-down (b, d and f). Biomass curves were grouped for each case as in Fig. 4. Scales are proportional between cases, except in panel (f) where simulation runs for 100 years and a strong oscillatory behaviour was observed.

biomass decrease in the scenario of infinite catch rate increase their biomass in the zero catch rate scenario (Figs. 4 and 5). This is because the impact on top predators of changes in small pelagic fish biomass is strong (bottom-up control; Fig. 3). Top predators in turn control (top-down control) snappers/grunts and large demersal fish. All these groups together control mullets/catfish, croakers/mojarras and porgies/spadefish (the two last-mentioned groups are also directly controlled in a bottom-up manner by small pelagic fish; Fig. 3).

The large demersal fish and snappers/grunts and mullets/catfish deserve further analysis. Large demersal fish feed on small pelagic fish (Table 2). However, their biomass decreases when no fishing is exerted on small pelagic fish, especially under bottom-up control by small pelagic fish (Fig. 5a and b) conversely, when infinite catch effort is exerted on small pelagic fish, large demersal fish double their biomass (Fig. 4). This occurs because (i) the mortality rate imposed by large demersal fish on small pelagic fish is the smallest of such rates (weak link; Table 6) and (ii) more importantly, the main predators of large demersal fish are pelagic predatory fish (strong link; Table 6) which, in turn, are controlled by small pelagic fish. Hence, the predatory force exerted on large demersal fish is stronger than the consumer force they exert on small pelagic fish. Note also that in the basic model, the strongest mixed trophic negative impact by small pelagic fish (excluding themselves) was on large demersal fish (Fig. 3).

Snappers/grunts, which also feed on small pelagic fish, have a biomass trajectory that resembles that of large demersal fish (Figs. 4 and 5) and for the same reasons. However, the consumption link between snappers/grunts and small pelagic fish is stronger (Table 6) than that with large demersal fish. Large demersal fish and snappers/grunts are the main predators of mullets/catfish (Tables 2 and 6); thus, their biomass follows an inverse trajectory, i.e. mullets/catfish have strong top-down control.

A direct explanation of the strong inverse impact of changes in small pelagic fish biomass on shrimp biomass is not apparent (Figs. 4 and 5). It may be a consequence of reduced (or increased) competition for zooplankton because both groups feed heavily on zooplankton (Tables 2 and 6), which is not the case for other competitors for zooplankton, i.e. infauna,

epifauna and small demersal fish, whose biomasses change little (Figs. 4 and 5).

Under the infinite catch scenarios for small pelagic fish, croakers/mojarras and mullets/catfishes are almost extirpated from the system (impacted by enhanced predation and/or lack of food; Tables 2 and 6), while other groups are substantially reduced (Fig. 4). Note that croakers/mojarras is the group most positively impacted by small pelagic fish (Fig. 3) in the basic model.

As expected, the predicted small pelagic fish biomass in the zero catch scenarios decreases with increasing vulnerability (Fig. 5). Bottom-up control of small pelagic fish on pelagic predatory fish (whose main prey are small pelagic fish; Table 2) is more evident when their vulnerability is low ($V = 0.1$; Fig. 5a and b). When there is time for small pelagic fish biomass to build up such that, although the rate of change from unavailable to available biomass is lower, the absolute amount made available after the suspension of fishing allows a 48–77% building up of biomass of pelagic predatory fish, depending on the vulnerability of zooplankton to small pelagic fish (Fig. 5a and b). When vulnerability of small pelagic fish is high ($V = 0.9$; Fig. 5e and f), there is no such strong build up of their biomass; consequently, the biomass of pelagic predatory fish increases only 33%, irrespective of zooplankton vulnerability.

When zooplankton vulnerability to small pelagic fish is high (Fig. 5b, d and f), small pelagic fish biomass increases more than when does zooplankton vulnerability is low (Fig. 5a, c and e), with all the associated consequences in the system of a high biomass of small pelagic fish (Fig. 5). With increasing vulnerability of both small pelagic fish and zooplankton, the system becomes unstable, in particular under top-down control ($V = 0.9$) for both small pelagic fish and zooplankton. In this case, simulations must be run for a 100-year period to reach stability in the biomass trajectories (Fig. 5f).

Table 8 shows performance indicators for the simulations. The disappearance of small pelagic fish from the ecosystem brings about a large reduction in total landings and economic value, reinforcing the view of small pelagic fish as forage fishes. Conversely, zero catch of small pelagic fish results in increased total landings and economic value of the fishery.

Table 8

Performance indicators calculated over the simulation periods for each control type

Control by small pelagic fish	All ^a	Bottom-up ^b		Mixed ^b		Top-down ^b	
Control by zooplankton	All	Mixed	Top-down	Mixed	Top-down	Mixed	Top-down
Predicted total biomass	0.98	1.02	1.05	1.01	1.02	1.00	1.01
Predicted total landings	0.39	1.35	1.66	1.20	1.27	1.11	1.14
Predicted economic value	0.38	1.35	1.68	1.20	1.27	1.12	1.15

Predicted values are relative to baseline simulation parameters. Time of simulations as in Figs. 4 and 5.

^a Results of simulations of an infinite catch of small pelagic fish (three-fold sustained increase of the base fishing mortality rate).^b Results of simulations of zero catch of small pelagic fish.

4. Discussion

The analysis of the modelled trophic network has shown that small pelagic fish have an important intermediary role in the trophic structure of the Gulf of Salamanca ecosystem, i.e. as a link between low and high trophic levels and as forage fish (high, positive, mixed trophic impact) in contrast to consumer fish (low, negative, mixed trophic impact); a property that appears to be a common characteristic of upwelling ecosystems (Jarre-Teichmann and Christensen, 1998). Thus, the trophic level of small pelagic fishes in the Gulf of Salamanca (TL = 2.6) is consistent with the calculated mean trophic level of small pelagic fishes in upwelling ecosystems (TL = 2.6, S.E. = 0.28, $n = 24$; Pauly and Christensen, 1995), which suggest a stronger trophic link of this group with plankton in upwelling systems than in non-tropical shelves and coastal/coral systems (TL = 3.0, S.E. = 0.15, $n = 3$ and TL = 3.2, S.E. = 0.20, $n = 9$, respectively; Pauly and Christensen, 1995).

However, our prior expectation that small pelagic fishes in the Gulf of Salamanca ecosystem exerted a “wasp-waist” type control (Rice, 1995; Cury et al., 2000), i.e. top-down control of zooplankton and bottom-up control of pelagic predators, was not fully confirmed. Indeed, dynamic perturbations of small pelagic fish biomass (brought about by simulated fishing levels) propagated through the upper part of the system. But the lower part remained relatively unchanged. Our results contrast with previous modelling predictions on Peru, Monterrey and Benguela upwelling ecosystems where the simulation of a sustained heavily exploitation of small pelagic fish caused increments in the zooplankton biomass (Mackinson et al., 1997; Shannon et al., 2000). But simulations

of Venezuela and Southern Brazil upwelling ecosystems showed that the lower trophic groups biomass were only marginally disturbed by the change of small pelagic fish biomass (Mackinson et al., 1997; Vasconcellos and Gasalla, 2000). Thus, the postulated crucial “wasp-waist” role of intermediate trophic levels occupied by small pelagic fish in temperate and subtropical most productive upwelling regions may not have a full equivalent in tropical less productive upwelling systems.

Tropical analogues of temperate “wasp-waist” ecosystems have been proposed, which tend to be dominated by analogous tropical species, such as sardinellas, anchovellas, thread herrings and juvenile triggerfish (Bakun, 1996). This indicates that the “wasp-waist” species richness is a general feature in the configuration of the biological structure of many marine ecosystems, also observed in the Gulf of Salamanca, but the “wasp-waist” control appears to be a characteristic only of the most productive upwelling systems.

The simulated fishing regimes have indicated that the impact of predation by small pelagic fish on planktonic groups must be strongly buffered in the system (as it is configured in the base model), such that extreme situations like no fishing (which increases small pelagic fish biomass by 6–74%; Fig. 5) and extirpation by overfishing of small pelagic fish leave phytoplankton and zooplankton biomasses almost unchanged, even in scenarios where zooplankton was highly vulnerable to predation by small pelagic fish. The fact that zooplankton has many predators in this system might explain its insensitivity to both vulnerability to and different levels of biomass of small pelagic fish. Furthermore, the zooplankton group of the modelled food web takes part in numerous

“intraguild predation” structures (wherein a predator feeds on two components, one of which is prey of the other; Polis and Holt, 1992) constructed by both weak and strong interactions. The net result of all these feeding interactions may be the stability of both zooplankton and phytoplankton biomass. Weak to intermediate strength links in the food webs has been proposed as important mechanism in promoting community stability (McCann et al., 1998).

In the upper part of the food web, “intraguild predation” structures must also occur where top and intermediary predators have a diverse diet. In this case, however, the potential for extreme situations is present. Walters et al. (1997) noted that these feeding triangles would cause erroneous prediction of extinction of planktivorous fish by a piscivore (after reducing its fishing mortality) in a simple pelagic food web.

Under the infinite catch scenario, croakers/mojarras and mullets/catfishes are almost extirpated from the system (less than 10% of the original biomass; Fig. 4). This suggest a trophic cascade starting with decreasing pelagic predatory fish biomass (as a consequence of the collapse of small pelagic fish) that leads to increase in large demersal fish and snappers/grunts biomasses, which, in turn, leads to reduction in croakers/mojarras and mullet/catfish biomasses. Simulations in the Venezuela upwelling ecosystem also predicted that croakers were the most disrupted group in that system when the fishing mortality of small pelagic fish was increased (Vasconcellos et al., 1997). Thus, it seems that the key feature for small pelagic fish to affect the upper part of the food web is having bottom-up control of at least one top predator group that has a diverse diet.

It is difficult to assess the likelihood of the cascade of deletions caused by the disappearance by fishing of small pelagic fish (Fig. 4). The triangular feeding structures can be an artefact of construction of the food web due to aggregation of species and stages of species into single “boxes” or groups. It is, therefore, advisable to search for more natural (functional) criteria in the construction of food webs and to follow Walters et al. (1997) advice to divide each group, particularly top predators, into two sub-groups representing the juvenile planktivore/benthivore stage and the adult stage, respectively. In addition, possible compensatory mechanisms that can eliminate the predatory effects were not considered in the predictions. The

pelagic predatory fish can switch to another type of prey (Hughes and Croy, 1993) or can migrate to other feeding ground. Although marine ecosystems show a considerable resilience, drastic responses have been observed several times (Cury et al., 2001), and a severe perturbation, such as a species deletion, might have deep consequences in the structure and stability of the system (Pimm, 1980).

Assumptions on the type of control of different trophic components have been found important in predicting the effects of fishing in other upwelling ecosystem (Mackinson et al., 1997; Shannon et al., 2000; Vasconcellos and Gasalla, 2000), as was the case here. There is clearly a need for conducting experimental manipulations in order to (1) estimate vulnerability ratios and (2) compare predictions with field data. Such manipulations would allow sounder conclusions on the interaction of assumed type of flow control under different harvest regimes (Walters et al., 1997). The instability of the system found here under high vulnerability of both small pelagic fish and zooplankton suggests that in nature, low or intermediate vulnerabilities are more likely to be the rule than otherwise.

Although small pelagic fish make the greatest contribution to the fishery (more than 50%; Table 3), their contribution as food for predators in the system is 2.64 times higher. Predation appears to be more important than fishery in removing biomass in upwelling systems (Cury et al., 2000) as well as in other ecosystems including intensively fished ecosystems (Bax, 1998). On the other hand, the fishery mediates almost 20% of total mixed trophic impacts and more than 30% of total positive impacts. Furthermore in 9% of paired interactions predation is beneficial to prey due to positive indirect impacts. In exploited high-diversity ecosystems, like the Gulf of Salamanca, actual diversity must also respond to this type of top-down control.

One of the main difficulties in tropical fisheries management is to predict general trends in fish communities and in the catches there from (García, 1999b), because these trends depend upon the myriad of ecological interactions that take place in such diverse settings. The Ecopath with Ecosim approach allows the assessment of community biomass trajectories under varying conditions and has proved to be coherent and versatile enough to cope with diverse ecosystems like the Gulf of Salamanca both in terms of exploration of ecological hypotheses and

in formulation of management options. For instance, the Gulf of Salamanca fishing authorities might now have a rationale for promoting a reduction in fishing pressure on small pelagic fish, as this would increase the yield of high-price fish, thus, in the medium run, fishers would be better off.

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