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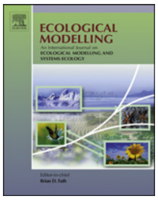

Highlights

Ecological Modelling xx (2012) xxx–xxx

Trophic structure and energy fluxes around a Mediterranean fish farm

Just T. Bayle-Sempere*, Francisco Arreguín-Sánchez, Pablo Sánchez-Jerez, Luis A. Salcido-Guevara,
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▶We model a fish farm trophic structure by means of a mass-balance model. ▶Wild aggregated fishes mediate positively the final impact of fish farming. ▶The connectance and system omnivory define an immature ecosystem. ▶The artificial food pellets provide resources enough to meet future perturbations. ▶The system was heavily forced sustained by high input of artificial food pellets.

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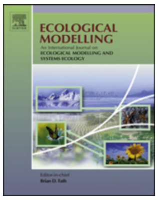

Trophic structure and energy fluxes around a Mediterranean fish farm

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ABSTRACT

A fish farm in Southeastern Spain was described using an Ecopath mass-balanced model, aimed at characterising its structure, the interactions among ecological groups and the impact of fish farms and fisheries. The model comprised 41 functional groups (including the artificial food input). Comparing consumption and respiration to total system throughput suggests lower energy use in the fish farm, resulting in an accumulation of detritus. The production to total system throughput ratio was low due to the low efficiency of the modelled ecosystem. The connectance and system omnivory indexes were low, typical of a simple or immature food web in terms of structure and dynamics. Artificial food pellets provided energy and nutrients to sustain system function and generate a considerable reserve from which it can draw to meet unexpected perturbations. The study shows the substantial effect the artificial food pellets have on the wild aggregated fishes, which could act to buffer the ecosystem and hence prevent environmental degradation.

1. Introduction

Coastal intensive fish farming is widespread and a growing activity throughout the world, producing about 20.1 million tonnes of fish per year (FAO, 2010). In temperate and tropical warm water areas, a wide variety of species are cultured and significant sea-cage industries exist around the world (Tacon and Halwart, 2007). In the Mediterranean Sea, the number of fish farms has increased dramatically from early '80 in coastal waters (Ferlin and LaCroix, 2005), mostly in Greece and Spain (Theodorou, 1999; Sánchez-Mata and Mora, 2000), rearing mainly seabass (*Dicentrarchus labrax*) and seabream (*Sparus aurata*). While there is a clear need for the continued worldwide expansion of aquaculture, this development needs to be promoted and managed in a responsible manner that minimises negative environmental impacts. That decision making and marine management should be based on the ecosystem-based approach, integrating the interactions among economic, environmental, social and equity considerations.

The substantial amount of nutrients (in both forms of organic and artificial pellets) released into the marine environment contribute to the over-accumulation of organic matter beneath cages (Karakassis et al., 1998; Heilskov and Holmer, 2001), degrading benthic communities (Karakassis and Hatziyanni, 2000; Delgado et al., 1999; Karakassis et al., 2000; Aguado and Ruiz, 2011), as well as increasing nutrient inputs in the water column (Tovar et al., 2000). As a direct ecological effect, fish farming also favours the aggregation of wild fish around the cages (Dempster et al., 2002) due to the artificial structures attaching the cages and the great amount of uneaten artificial food (Sánchez-Jerez et al., 2011). The high abundance and biomass of farm-associated wild fish appear as an important component mediating the final impact of aquaculture in both negative and positive direction: e.g., they can add an important amount of NH_4^+ and DOC to the water column by leaching during faeces sinking, enlarging potentially the spatial dispersion patterns of wastes from the fish farm (Fernández Jover et al., 2007b); or can reduce the over-sedimentation of uneaten food pellets due to their ingestion and, hence, minimize the final negative impacts on the benthic communities. These issues are not considered in the usual models to predict the impact of fish farming (see Cromey and Black, 2005, for a review) despite the ecological importance of the farm-associated wild fish (Dempster et al., 2002) and the fact that the phenomenon of aggregation of wild fish occurs globally (Dempster et al., 2004, 2009). Additionally, the study of the aggregated wild fish assemblage is as much important, as some managers are promoting the exploitation of these aggregations or asking about the effects on exploited wild fish populations by fisheries (IUCN, 2007).

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Despite controversy over the conflict between fish farming and management of coastal areas around the world, a few true ecosystem approaches exist on the impact of this activity on the environment. Most are focused on some generic ecological groups (e.g., Tsagaraki et al., 2011; Petihakis et al., 2012) or on marine mammals (e.g., Díaz-López et al., 2008; Piroddi et al., 2011), but any considering the interactions of fish farming with other ecological components or human activities as proposed for the ecosystem-based management approach. Ecopath is useful to investigate the direct ecological effects of fish farming, but, as a novelty in respect to other used mass-balanced models on fish farming, it allows a true ecosystemic approach by analysing too indirect effects induced by external disturbances such as fishing or alterations in the food web due to cascade processes. The assessment of indirect effects of fish farming is the unique way to balance diverse societal objectives within ecologically and operationally meaningful boundaries and can also be considered as a form of ordinary sensitivity analysis about how each ecological group vary with respect to the others. The understanding of these fish farming interactions with other anthropogenic stressors is the basis for developing strategies for sustainable aquaculture and integrated coastal zone management. Moreover, Ecopath is a common framework and well balanced between simplicity and the complexity of other ecosystem models, which provides a methodology to standardise model outputs, thereby making it easy to compare across other ecosystems without requiring advanced computer programming skills to operate (Christensen et al., 2005). The application of an Ecopath food web mass-balanced model, such as included in this paper, is of primary interest for both scientific and management purposes, since it allows the combination of an extensive set of diverse ecological data in order to interpret the ecosystem functioning around fish farms and design a more suitable ecosystem approach management.

In this study, we present a trophic model focused on biomass flows among components and species associated to sea-cage fish farms, and especially on those wild fish species aggregated around these man-made structures. The purposes of this study are to obtain a steady-state mass-balanced representation for a certain period of the energy flows and trophic relationships among species from which to derive ecosystem indicators based on the network structure of the food web (using thermodynamic concepts, information theory, trophic level index and network analysis; Müller, 1997), in order to assess the environmental deviation created by the fish farm compared with other modelled ecosystems.

2. Methods and materials

2.1. Study site

We considered a fish farm located in the Santa Pola Bay, Southwestern Mediterranean Sea (38°05.743′N, 000°36.341′W; Fig. 1) operating from July 2000. The installation is 3704 m from the shore, with a maximum water column depth of 21 m at the study site, covering a total area of 140,000 m^2 on soft muddy bottoms. The water temperature undergoes yearly variation, with surface values ranging between 13 °C (February) and 28 °C (August). Water clarity (Secchi disk depth) varied between 8 m and 20 m from winter to summer. The fish farm consists of 24 floating cages, each with an approximate volume of 449 m^3, rearing a total fish biomass of 775 tonnes, with gilthead seabream *S. aurata*, European seabass *D. labrax* and meagre *Argyrosomus regius*. Food pellets were aquafeed extruders formulated with 36% fishmeal, 16% wheat meal, 12% corn gluten feed, 12% soybean meal, 10% wheat gluten meal, 10% fish oil, 4% soybean oil and other additives such as vitamins and antioxidants. Fish are fed by on demand, either manually or by using a manually operated air compressor type feeder, once a day during the cold season (October–April) or twice in the warm season (May–October). The trophic level of the food pellets by definition is 1 because it does not consume living biomass from the modelled fish farm ecosystem.

2.2. The model

Trophic interactions and energy flux were modelled by means of Ecopath with Ecosim model (EwE; Christensen et al., 2005) that provides a static description of an ecosystem at a precise period in time. It can describe principal species, autotrophs and heterotrophs, individually or by aggregating them into functional groups (e.g., species with a similar ecotrophic role). The model is based on the premise that the considered system is balanced in the given time period (Polovina, 1984); that is, production is equal to consumption following the equation:

$$B_i\left(\frac{P}{B}\right)_i \mathrm{EE}_i - \Sigma_j B_j\left(\frac{Q}{B}\right)_j DC_{ji} - Y_i - \mathrm{BA}_i - E_i = 0$$

where for an i group, P_i is production, B_i is biomass ($\mathrm{t\,km^{-2}}$) in tonnes wet weight and EE_i is ecotrophic efficiency. Q_j is the consumption for predators, BA_i is the biomass accumulation rate for i and E_i is the net migration rate of the group. Because material transfers among groups is through trophic relationships, this equation is re-expressed including the biomass of predators and the instantaneous rate of total mortality (Z) at equilibrium (Allen, 1971) in the form of P/B rate, describing the biomass flow balance between inputs and outputs for each group (see Christensen et al., 2005, for a complete explanation). A system of linear equations was established in which three parameters were introduced: biomass (B); total biological production rate (P/B); total food consumption rate (Q/B), and only one, EE, was estimated by the model. Diet composition is expressed as a fraction of prey in the average diet of a predator. Fishing activities are also included by adding data on landings ($\mathrm{t\,km^{-2}}$).

2.3. Field data

We used an annual base average on the information gathered between 2001 and 2007 on the study ecosystem. Most species were included in functional groups sharing similar trophic roles. Only those of particular interest were kept as individual groups: wild fish species aggregated around the fish farm (Mediterranean horse mackerel *Trachurus mediterraneus*, mullets, pompano *Trachinotus ovatus*, sparids, bogue *Boops boops*, round sardinella *Sardinella aurita*, planktivorous fishes, bluefish *Pomatomus saltatrix*, striped barracuda *Sphyraena sphyraena*, greater amberjack *Seriola dumerilii*, common eagle ray *Myliobatis aquila*, grey triggerfish *Balistes capriscus*), commercially important species such as striped red mullet *Mullus surmulletus*, red scorpionfish *Scorpaena scrofa* and cephalopods; several groups of invertebrates, juvenile fish species aggregated around sea-cages, the reared species (gilthead seabream, European seabass and maegre) and the artificial food pellets used to nourish the caged fish considered just like detritus. The microbial food web was not directly considered in the model, but it was indirectly considered within the zooplankton diet composition and detritus dynamics (Calbet et al., 2002).

Biomass was compiled from own studies and from published studies (Annex 1), and was calculated with the swept area method (Pauly, 1984) that is based on the densities of organisms (i.e., the weight of the fish caught per unit area covered by an experimental sampling method), from which the potential yield can be obtained. For commercial groups, P/B corresponded to the instantaneous rate of natural mortality (M), and was estimated from data in FishBase

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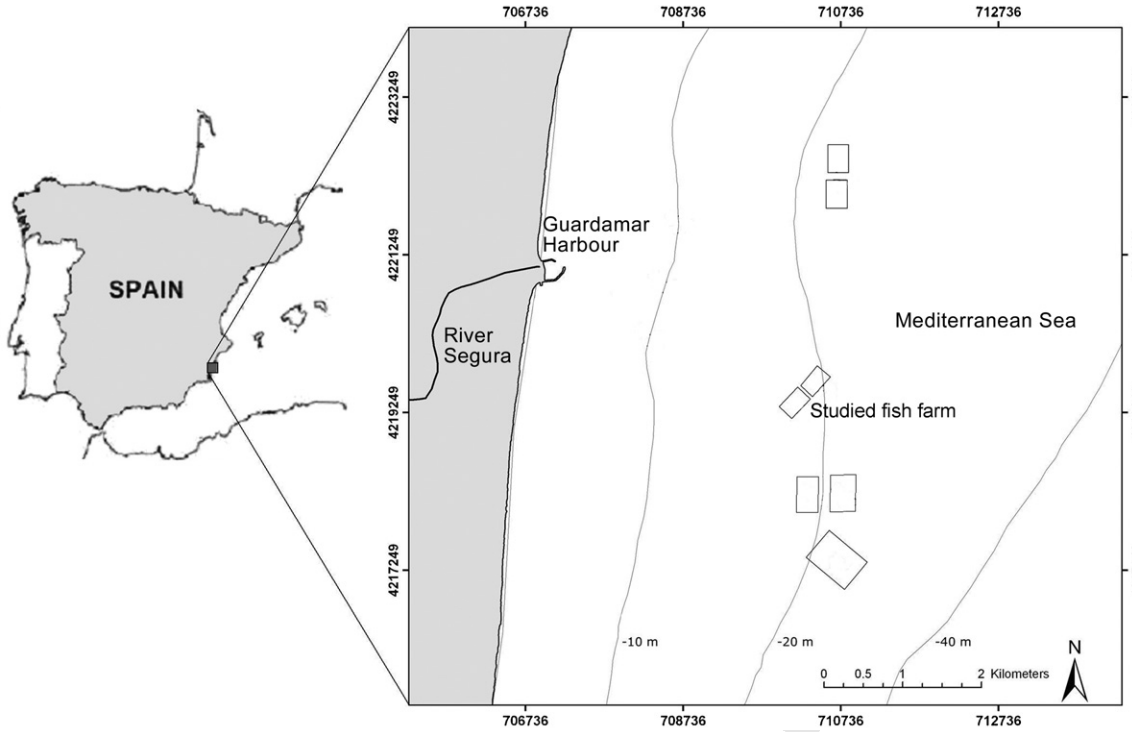

Fig. 1.

Q4 (Froese and Pauly, 2003) for fish species, using the empirical equation of Pauly (1980). We used mortality values reported in the literature for the remaining functional groups. Q/B values for fish groups were computed following Palomares and Pauly (1989), which considers environmental temperature, fish weight and size, and caudal fin morphology. For the rest of the functional groups, Q/B was taken from the literature (Annex 1).

A predator–prey matrix was developed from own data and reports of stomach contents for the different functional groups, using reports for similar species or groups when no data were available. On the other hand, fishing fleets and catches (Y_i) of important species were included in the model for both small scale commercial (García-Rodríguez et al., 2006) and recreational fishing (Sánchez-Jerez et al., 2007), impacting on cephalopods, gastropods, striped red mullet, striped barracuda, sparids, bogue, greater amberjack, red scorpionfish and comber *Serranus* spp. Catch data were corrected by considering discard information drawn from the literature (Sánchez et al., 2004; Tudela, 2004; Forcada et al., 2009).

2.4. Data analysis

We used EE < 1 as the primary criterion to balance the model, obtaining it by modifying the initial diet consumption values for each prey and producing small changes (±5% max.). We selected this approach because proportions for each prey in the diet of predators is the source of greatest uncertainty, avoiding large modifications (e.g., adding or removing prey items) of the feeding patterns of functional groups. Consistency of the model was mainly verified by checking that respiration to assimilation and production to respiration ratios were less than 1, and comparing trends in the respiration to biomass ratio (R/B), which must be higher for active species than for sedentary groups. Once the model was balanced and consistent, we minimised residuals of each parameter with the Ecoranger routine (Kavanagh et al., 2004), which allows entry of a coefficient of variation (in this case, we used 5%) and a previous probabilistic distribution (we assumed normal frequency) for every input data. Random input variables were then drawn in a Monte Carlo procedure included in the routine. At each step, the resulting model, defined by simulated input data, was then evaluated using physiological and mass-balanced constraints. This process was repeated until we got 9000 suitable models, and then the best fitting one was chosen with the least square criterion. Mixed trophic impacts of each group were computed in order to evidence the direct and indirect impacts (positive or negative) that a group has on each of the others.

Several flow indices were estimated, such as total system ascendancy, overhead and the ratio overhead: ascendancy (as a measure of ecosystem resiliency; Pérez-España and Arreguín-Sánchez, 2001), total system throughput (Ulanowicz and Norden, 1990), some ecological key descriptors (Odum, 1971) such as total consumption, sum of all respiratory flows, sum of all flows into detritus, sum of all production, total primary production, mean trophic level of the catch, system omnivory index and connectance index to define the system maturity and stability level. Consumption vs. biomass of consumers, and primary production required to sustain both the consumption of each group and the harvest vs. trophic level, were plotted in order to evidence the role of the artificial food pellets in the system. Some ratios were calculated from these estimates in order to compare values from other models in similar ecological conditions or existing in the same regional context (Palomares et al., 1993; Sánchez and Olaso, 2004; Coll et al., 2006; Díaz-López et al., 2008) in order to define the ecological status generated by aquaculture in the considered system.

3. Results

3.1. Steady-state representation of the modelled ecosystem

Input data estimated values are listed in Table 1; main data sources are compiled in Annex 1. The model included 41 functional groups, spanning the main trophic components of the ecosystem and including commercial targeted and non-targeted fish and

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Table 1
Q9 Inputs and estimated values (in bold) for the fish farm model.

	Group name	Trophic level	Omnivory index	Biomass in hab. area (tonnes/km^2)	P/B (year^{-1})	Q/B (year^{-1})	EE	Detr. import (tonnes/km^2/year)
1	Red scorpionfish	**3.89**	**0.069**	0.103	1.537	5.603	**0.099**	0
2	Striped barracuda	**3.77**	**0.163**	0.029	2.679	9.444	**0.347**	0
3	Great amberjack	**3.73**	**0.278**	0.098	2.505	7.799	**0.008**	0
4	Bluefish	**3.44**	**0.957**	14.453	2.669	10.082	**0.000**	0
5	Cephalopods	**3.21**	**0.077**	0.205	1.676	4.536	**0.789**	0
6	Grey triggerfish	**3.17**	**0.558**	0.023	1.495	5.221	**0.164**	0
7	Buccichi's goby	**3.16**	**0.055**	0.018	2.979	9.989	**0.420**	0
8	Juveniles gilthead seabream	**3.09**	**0.002**	0.429	6.184	16.868	**0.563**	0
9	Common eagleray	**3.07**	**0.001**	0.341	2.438	8.455	**0.000**	0
10	Juveniles pelagic planktivorous fishes	**3.04**	**0.003**	6.432	5.295	14.566	**0.589**	0
11	Juveniles sparids	**3.04**	**0.003**	0.221	5.700	15.089	**0.562**	0
12	Juveniles. pompano	**3.02**	**0.002**	0.958	4.902	12.745	**0.542**	0
13	Juveniles bogue	**3.01**	**0.001**	1.849	6.63	19.383	**0.521**	0
14	Juveniles mullet	**3.00**	**0.000**	0.587	8.908	24.112	**0.479**	0
15	Juveniles med. horse mackerel	**3.00**	**0.000**	0.490	7.49	20.370	**0.445**	0
16	Sparids	**2.92**	**0.375**	0.435	2.403	8.200	**0.248**	0
17	Striped red mullet	**2.70**	**0.291**	2.066	1.187	4.848	**0.282**	0
18	Medit. horse mackerel	**2.68**	**0.708**	11.788	2.49	7.924	**0.120**	0
19	Comber	**2.54**	**0.356**	0.020	1.878	6.997	**0.676**	0
20	Pelagic planktivorous fishes	**2.45**	**0.386**	0.319	2.691	8.898	**0.259**	0
21	Crabs	**2.41**	**0.367**	0.020	2.257	10.988	**0.821**	0
22	Shrimps	**2.30**	**0.235**	0.011	3.315	15.590	**0.681**	0
23	Echinoderms	**2.18**	**0.158**	6.93	0.549	3.193	**0.478**	0
24	Mysids	**2.12**	**0.112**	2.331	5.122	25.522	**0.630**	0
25	Anphipods	**2.12**	**0.12**	70.385	4.682	22.628	**0.656**	0
26	Bogue	**2.12**	**0.155**	0.388	2.640	8.936	**0.080**	0
27	Polychaetes	**2.07**	**0.070**	3.887	4.200	10.810	**0.565**	0
28	Pompano	**2.07**	**0.107**	60.056	2.737	9.392	**0.050**	0
29	Wild gilthead seabream	**2.06**	**0.130**	0.588	0.571	1.779	**0.284**	0
30	Gastropods	**2.00**	**0.000**	0.011	1.851	11.566	**0.760**	0
31	Bivalves	**2.00**	**0.000**	0.010	1.635	10.636	**0.784**	0
32	Reared gilthead seabream	**2.00**	**0.000**	6353.633	1.290	3.313	**0.567**	0
33	Reared meagre	**2.00**	**0.000**	728.88	1.257	3.473	**0.588**	0
34	Reared european seabass	**2.00**	**0.000**	384.595	1.273	3.548	**0.731**	0
35	Mullets	**2.00**	**0.000**	180.422	2.993	11.464	**0.016**	0
36	Round sardinella	**2.00**	**0.000**	6.117	4.015	13.906	**0.135**	0
37	Planktonic copepods	**2.00**	**0.000**	3.980	51.137	310.533	**0.914**	0
38	Phytoplankton	**1.00**	**0.000**	11.549	136.653	–	**0.700**	0
39	Algae	**1.00**	**0.000**	9.893	2.707	–	**0.518**	0
40	Artificial food pellets	**1.00**	**0.000**	31,200	–	–	**0.897**	31,200
41	Detritus	**1.00**	**0.297**	631.73	–	–	**0.061**	4680

invertebrate groups, a detritus group and the artificial food pellets, which were considered also as a second detritus group since it is not a living and consumer group, but support food web as an energy source. The pedigree index (0.664) measures the quality of the model with respect to the input data, and ranked within the highest values when compared with another 393 previously constructed models, for which pedigree values ranged between 0.164 and 0.676 (Morissette, 2007). Results of the model showed that functional groups were organised within three integer trophic levels (TLs), with the highest values corresponding to red scorpionfish, striped barracuda, greater amberjack, bluefish, cephalopods and grey triggerfish. The remaining functional groups were classified between 3.16 and 2.0 for most of the fish species and invertebrates, and 1.0 match for phytoplankton, algae, artificial food pellets and detritus. All fish groups obtained a TL slightly lower than those reported in the FishBase database (Froese and Pauly, 2003). Low EE values were obtained for some groups (e.g., greater amberjack, pompano, bogue, mullets, detritus). High EE resulted for pelagic copepods, artificial food pellets and crabs. High values of omnivory corresponded to bluefish and Mediterranean horse mackerel, evidencing a wide trophic range of these predators in this ecosystem; some fish groups were equal to zero because they fed exclusively on artificial food pellets.

Direct and indirect trophic impacts in the ecosystem occurred among some groups (Fig. 2). Bluefish impacted negatively on most of the adults and juvenile fish species aggregated around the fish farm. Conversely, this species positively affected some groups of invertebrates, greater amberjack, comber and juvenile mullets. On the other hand, artificial food pellets impacted positively on the adult fish species aggregated around the cages, as well as slightly on the trammel net and recreational fisheries (and, oddly enough, this effect is greater than that on the reared species). These groups, together with juveniles of some species, will have an indirect positive effect by trammel net fisheries because it controls their predators, predicting a cascade effect. Detritus will have a slight positive impact on most of the juveniles groups, evidencing the use of this resource by these early stages.

3.2. Network structure of the food web

Nutritional conversion efficiency (gi) ranged from 0.154 to 0.389 tonnes per year (Table 2), with a positive relationship to trophic level. The R/B ratio was consistent with other authors (Jarre-Teichmann, 1992; Arreguín-Sánchez et al., 1993; Olivieri et al., 1993; Pauly and Christensen, 1996; Vega-Cendejas, 1998; Zetina-Rejón, 1999). Respiration to assimilation ratio ranged from 0.519 to 0.808, with the highest values corresponding to medium and high trophic levels. Table 3 shows the adjusted predator–prey matrix, and Table 4 exhibits the ecological indicators of the system. The total system throughput was 119,601 tonnes/km^2/year, where internal consumption accounts for 26% of total flows, respiration 11.55%, detritus 42.47% and export out of the system (fishing and fish farming) 20.01%. Detritus exhibited a very low ecotrophic efficiency (0.061), evidencing an accumulation pattern of biomass in this functional group. The connectance index reached 0.191, reflecting a low level of theoretical possible trophic connections, in accordance with the low value of the system omnivory index. For each living group, the total consumption (expressed as $\log_{10} Q$) exhibited a significant ($p < 0.01$) relationship with total $\log_{10}$ biomass, being greater for such species showing higher biomasses (i.e., the reared species, mullets and pompanos); all of the groups' values, except planktonic copepods, remained close to the average tendency (Fig. 3). Artificial food pellets contributed with 90.1% of the total internal consumption, corresponding to

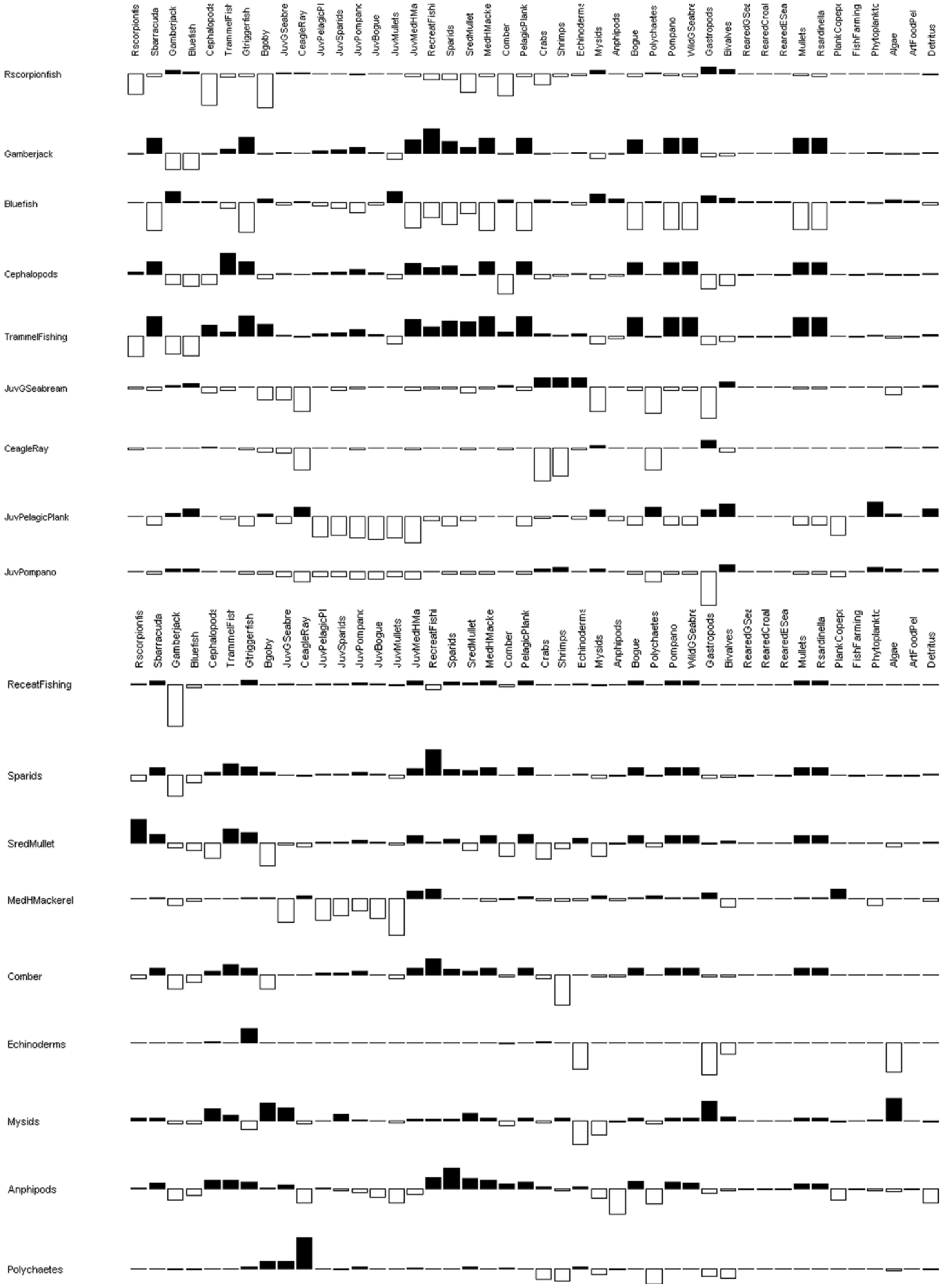

Fig. 2.

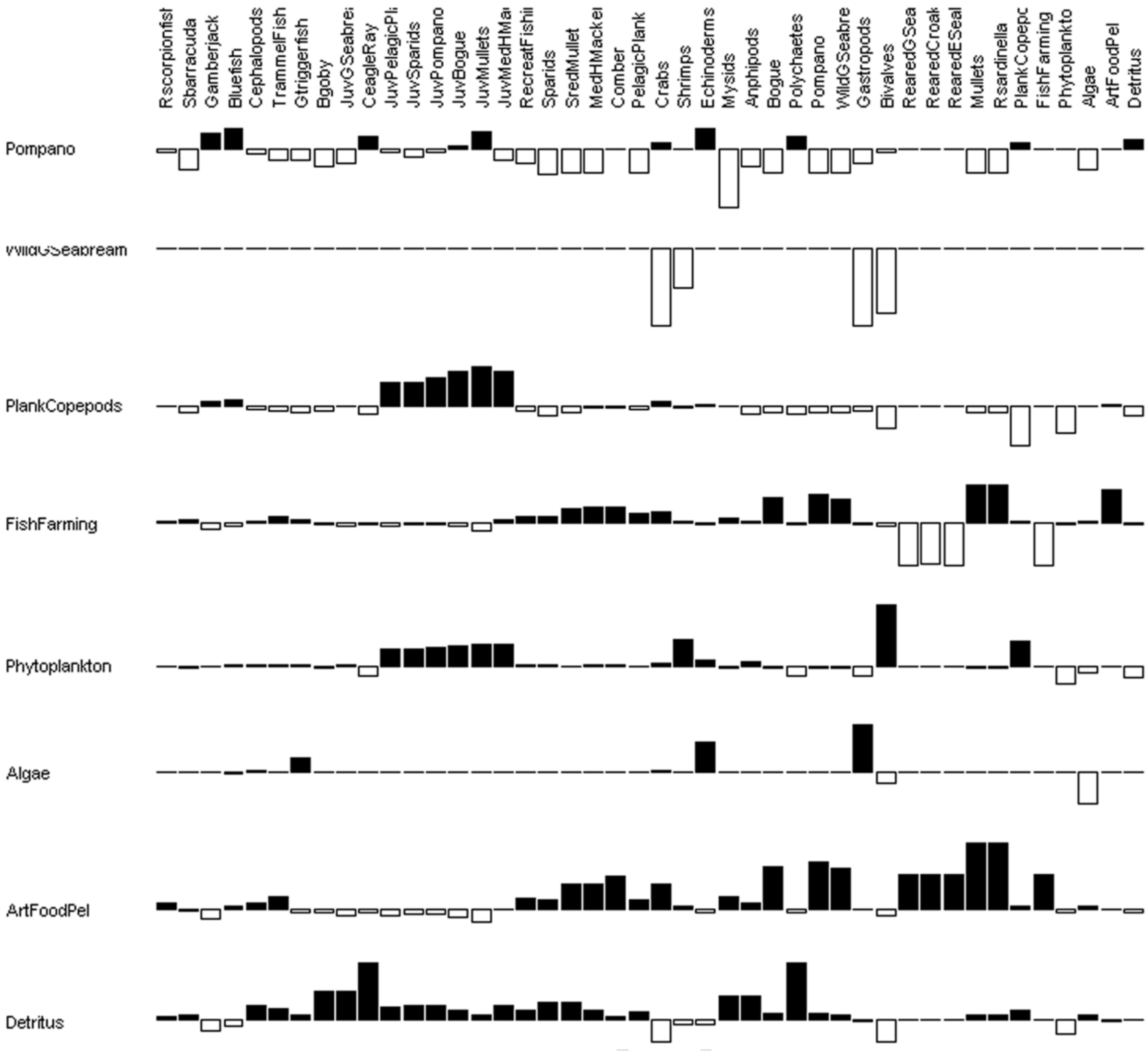

Fig. 2. (*Continued*)

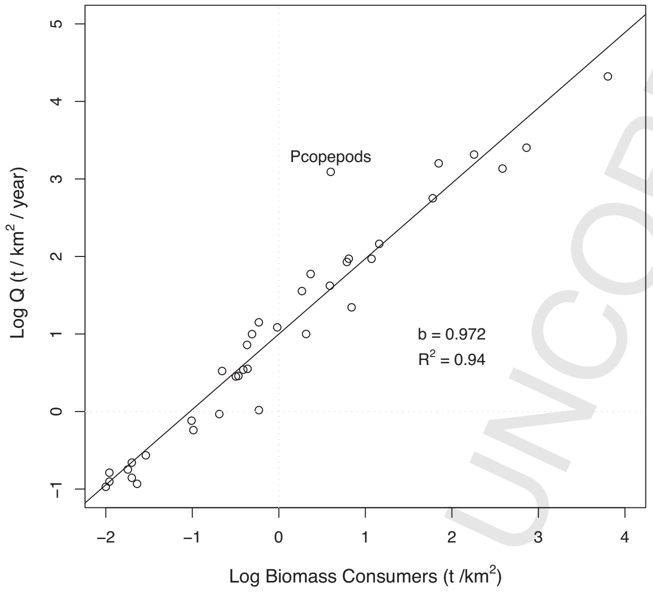

Fig. 3.

8.4% for aggregated wild fishes, 80.3% for reared fishes, 1.4% for other groups and 9.9% flowed to detritus. With respect to the total consumption of aggregated wild fishes, artificial food pellets represented 82.3% of their whole diet, being the main inflow for most of these species (Fig. 4). The rate total primary production to total respiration (TPP/TR) was 0.116, indicating that TR is 8.61-fold greater than primary production; for this reason, net system production is negative. The total primary production to biomass ratio was 0.204 year^{-1}, suggesting a false mature state of the system, since this accounts for pellets as primary producer. The total primary production (PPR) required to sustain the consumption of the living groups, considering both that from primary producers and detritus (Fig. 5A) and only from detritus (that included artificial food pellets too; Fig. 5B), increased as the TLs increased, although the statistical relationship was not significant. On the other hand, the PPR required to sustain the fisheries exhibited negative slopes due to an oversupply of primary production created by the artificial food pellets which is not effectively integrated along the food chain. Both plots were very similar, evidencing the main role of the artificial food pellets over the natural primary producers (Table 5). Q5

3.3. Environmental situation created by the fish farm

Comparing this model with five models of marine and littoral ecosystems around the Iberian Peninsula, we observed that ratios of

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Table 2
Ecological attributes for the fish farm model.

	Group name	P/Q	R/B (year^{-1})	Assimilation (tonnes/km^2/year)	R/A	Production (tonnes/km^2/year)	Flow to detrit. (tonnes/km^2/year)
1	Red scorpionfish	0.274	2.946	0.462	0.657	0.158	0.258
2	Striped barracuda	0.284	4.876	0.218	0.645	0.077	0.105
3	Great amberjack	0.321	3.734	0.610	0.599	0.245	0.396
4	Bluefish	0.265	5.397	116.577	0.669	38.575	67.715
5	Cephalopods	0.369	1.953	0.743	0.538	0.344	0.258
6	Grey triggerfish	0.286	2.682	0.094	0.642	0.034	0.052
7	Buccichi's goby	0.298	5.013	0.143	0.627	0.053	0.067
8	Juveniles gilthead seabream	0.367	7.311	5.795	0.542	2.653	2.608
9	Common eagleray	0.288	4.325	2.307	0.639	0.831	1.408
10	Juveniles pelagic planktivorous fishes	0.364	6.358	74.952	0.546	34.057	32.726
11	Juveniles sparids	0.378	6.371	2.670	0.528	1.260	1.220
12	Juveniles. pompano	0.385	5.294	9.769	0.519	4.696	4.592
13	Juveniles bogue	0.342	8.876	28.67	0.572	12.259	13.034
14	Juveniles mullet	0.369	10.382	11.329	0.538	5.229	5.556
15	Juveniles med. horse mackerel	0.368	8.807	7.990	0.540	3.670	4.037
16	Sparids	0.293	4.157	2.850	0.634	1.045	1.497
17	Striped red mullet	0.245	2.691	8.011	0.694	2.452	3.764
18	Medit. horse mackerel	0.314	3.85	74.729	0.607	29.352	44.501
19	Comber	0.268	3.719	0.112	0.665	0.038	0.040
20	Pelagic planktivorous fishes	0.302	4.427	2.268	0.622	0.858	1.202
21	Crabs	0.205	6.534	0.176	0.743	0.045	0.052
22	Shrimps	0.213	9.156	0.131	0.734	0.035	0.044
23	Echinoderms	0.172	2.005	17.699	0.785	3.805	6.410
24	Mysids	0.201	15.295	47.585	0.749	11.939	16.309
25	Anphipods	0.207	13.42	1274.143	0.741	329.543	431.819
26	Bogue	0.295	4.509	2.772	0.631	1.024	1.635
27	Polychaetes	0.389	4.448	33.61	0.514	16.325	15.501
28	Pompano	0.291	4.777	451.253	0.636	164.373	268.989
29	Wild gilthead seabream	0.321	0.852	0.836	0.598	0.336	0.450
30	Gastropods	0.160	7.402	0.100	0.800	0.020	0.030
31	Bivalves	0.154	6.873	0.086	0.808	0.017	0.025
32	Reared gilthead seabream	0.389	1.361	16,840.920	0.513	8196.187	7756.17
33	Reared meagre	0.362	1.521	2025.325	0.548	916.202	884.233
34	Reared european seabass	0.359	1.565	1091.498	0.551	489.589	404.418
35	Mullets	0.261	6.178	1654.652	0.674	540.003	945.304
36	Round sardinella	0.289	7.110	68.050	0.639	24.560	38.256
37	Planktonic copepods	0.165	197.289	988.728	0.794	203.525	264.768
38	Phytoplankton	–	–	–	–	1578.205	472.732
39	Algae	–	–	–	–	26.780	12.918
40	Artificial food pellets	–	–	–	–	–	3210.400
41	Detritus	–	–	–	–	–	0.000

total consumption and total respiration to total system throughput suggest lower natural system energy usage in the fish farm, close to that reported for the Cantabrian Sea. Similarly, the total production to total system throughput ratio resulted very low compared with the other ecosystems, suggesting the low efficiency of the fish farming activity. The very high accumulation of heterotrophic biomass causes the lower values for total primary production to total respiration and total biomass ratios, reflected in the greater value for the total biomass to total system throughput quotient. The connectance index resulted lower for the fish farm, although comparable with the value given for the South Catalan Sea, suggesting a simpler food web in terms of structure and dynamics, being

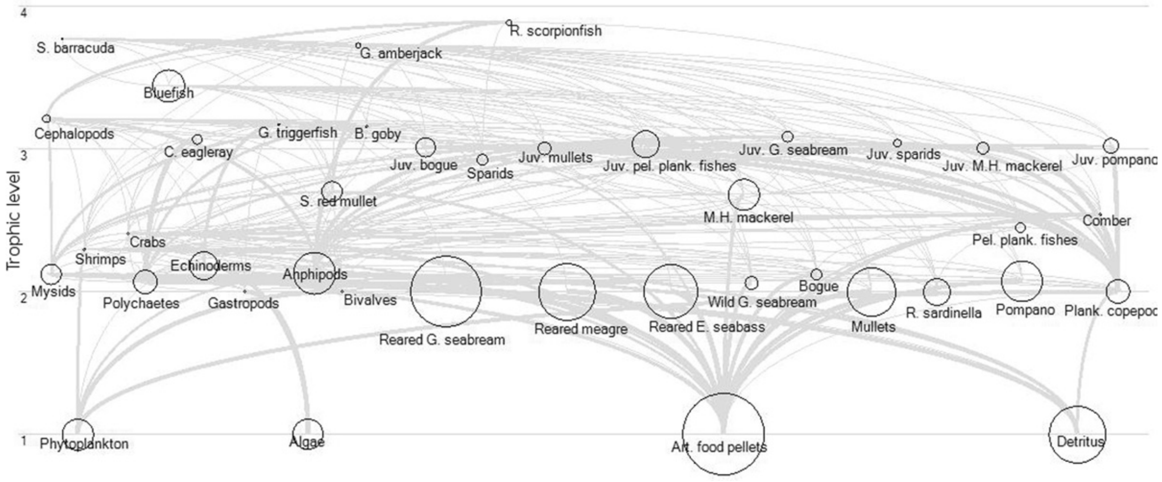

Fig. 4.

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Table 3
Adjusted diet matrix for the fish farm model.

	Prey	Predator							
		1	2	3	4	5	6	7	8
1	Red scorpionfish								
2	Striped barracuda				1.8E−4				
3	Great amberjack								
4	Bluefish		4.7E−5	1.1E−4					
5	Cephalopods	3.6E−1		3.0E−3		3.9E−2		4.7E−2	
6	Grey triggerfish				3.8E−5				
7	Bucchichi's goby	3.2E−2	9.9E−6			2.0E−3			
8	Juveniles gilthead seabream		1.2E−4	3.0E−3	6.0E−3	5.0E−3			
9	Common eagleray								
10	Juv. pelagic plank. fishes		9.0E−3	8.0E−3	7.9E−2	1.0E−2			
11	Juveniles sparids		2.0E−3	1.4E−4	3.0E−3	6.0E−3			
12	Juveniles. pompano		2.0E−3	2.0E−3	1.2E−2				
13	Juveniles bogue		9.9E−4	3.0E−3	2.4E−2	3.2E−7			
14	Juveniles mullets		4.8E−4	6.5E−4	5.0E−3	3.2E−7			
15	Juv. med. horse mackerel		9.9E−4	2.0E−3	1.1E−2				
16	Sparids	3.7E−2	5.1E−5	3.4E−4	2.0E−3	2.0E−5			
17	Striped red mullet	5.2E−1	1.2E−4	4.0E−3	2.0E−3	4.7E−2			
18	Medit. horse mackerel		6.4E−4	3.0E−3	2.4E−2	2.0E−7			
19	Comber	2.7E−2	2.5E−8		1.2E−6	6.0E−3			
20	Pelagic planktivorous fishes		9.9E−5	8.2E−4	2.0E−3	2.0E−7			
21	Crabs	2.1E−2				2.0E−3	5.7E−4		1.7E−7
22	Shrimps	9.0E−3				2.0E−3	5.7E−4	2.0E−3	
23	Echinoderms					4.6E−2	4.9E−1		
24	Mysids					2.6E−1		3.3E−1	2.0E−1
25	Anphipods					4.3E−1		3.3E−1	3.7E−1
26	Bogue		1.8E−4	3.4E−4	5.5E−4	2.0E−5			
27	Polychaetes					5.5E−2	2.1E−2	3.0E−1	2.7E−1
28	Pompano		6.5E−4		5.6E−2	4.2E−2			
29	Wild gilthead seabream		4.7E−4	2.0E−4	6.5E−4	2.3E−5			
30	Gastropods					3.0E−3	4.0E−3		3.2E−4
31	Bivalves					2.0E−3	1.4E−2		
32	Reared gilthead seabream				5.1E−2				
33	Reared meagre				1.9E−2				
34	Reared european seabass				6.0E−3				
35	Mullets		2.0E−3	3.0E−3	5.7E−2	4.5E−2			
36	Round sardinella		2.0E−3	6.0E−3	2.3E−2	1.8E−5			
37	Planktonic copepods								1.7E−1
38	Phytoplankton								
39	Algae								
40	Artificial food pellets								
41	Detritus								
42	Import		9.8E−1	9.6E−1	6.2E−1	0.0E+0	4.8E−1		

	Prey	Predator							
		9	10	11	12	13	14	15	16
1	Red scorpionfish								
2	Striped barracuda								
3	Great amberjack								
4	Bluefish								
5	Cephalopods				2.6E−7			1.1E−7	
6	Grey triggerfish								
7	Bucchichi's goby								
8	Juveniles gilthead seabream		2.6E−7		2.6E−5			9.8E−6	
9	Common eagleray								
10	Juv. pelagic plank. fishes		2.8E−6		3.1E−5			1.1E−5	
11	Juveniles sparids		2.5E−7		2.5E−7			1.0E−7	
12	Juveniles. pompano		3.0E−6		1.5E−6			2.0E−5	
13	Juveniles bogue		3.2E−7		5.3E−6			2.3E−6	
14	Juveniles mullets		3.1E−6		3.1E−5			1.2E−5	
15	Juv. med. horse mackerel		3.3E−6		2.5E−5			2.2E−5	
16	Sparids								
17	Striped red mullet								
18	Medit. horse mackerel								
19	Comber								
20	Pelagic planktivorous fishes								
21	Crabs	5.0E−3							
22	Shrimps	3.0E−3							
23	Echinoderms								
24	Mysids			9.8E−2					
25	Anphipods		3.0E−1	2.0E−1	1.5E−1	8.0E−2	3.0E−2		5.5E−1
26	Bogue								
27	Polychaetes	9.9E−1			5.3E−2			2.2E−2	1.3E−2
28	Pompano								

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Table 3 (*Continued*)

	Prey	Predator 9	10	11	12	13	14	15	16
29	Wild gilthead seabream								
30	Gastropods				2.0E−4				
31	Bivalves	5.1E−4							
32	Reared gilthead seabream								
33	Reared meagre								
34	Reared european seabass								
35	Mullets								
36	Round sardinella								
37	Planktonic copepods		7.1E−1	7.0E−1	8.0E−1	9.2E−1	9.7E−1	9.8E−1	
38	Phytoplankton								
39	Algae								
40	Artificial food pellets								1.2E−1
41	Detritus								

	Prey	Predator 17	18	19	20	21	22	23	24
1	Red scorpionfish								
2	Striped barracuda								
3	Great amberjack								
4	Bluefish								
5	Cephalopods								
6	Grey triggerfish								
7	Buccichi's goby			1.5E−2		6.7E−8	1.0E−7		
8	Juveniles gilthead seabream		6.0E−3						
9	Common eagleray								
10	Juv. pelagic plank. fishes		9.2E−2			7.0E−3	1.2E−5		
11	Juveniles sparids		3.0E−3			3.0E−3			
12	Juveniles. pompano		8.0E−3						
13	Juveniles bogue		3.1E−2			1.2E−7			
14	Juveniles mullets		1.9E−2			1.3E−7			
15	Juv. med. horse mackerel		9.3E−4						
16	Sparids					8.2E−8	1.0E−7		
17	Striped red mullet					1.4E−2	7.0E−3		
18	Medit. horse mackerel					7.5E−8	1.1E−7		
19	Comber					9.2E−7			
20	Pelagic planktivorous fishes			5.0E−3		7.7E−8	1.0E−7		
21	Crabs	5.6E−4		6.0E−3		6.6E−4	1.1E−7	1.0E−7	9.9E−8
22	Shrimps	2.0E−4		2.9E−2		3.0E−3	5.7E−5		
23	Echinoderms					4.4E−2		2.3E−2	2.0E−2
24	Mysids	1.4E−1		8.0E−3		2.2E−2	6.8E−2		1.8E−2
25	Anphipods	3.9E−1	1.1E−1	3.4E−1	5.8E−2	2.2E−2	6.6E−2	3.4E−2	2.1E−2
26	Bogue			1.1E−4		8.2E−8	1.0E−7		
27	Polychaetes	9.0E−2		5.0E−2		8.0E−2	1.0E−6	1.1E−5	9.2E−7
28	Pompano					1.5E−2	7.0E−3		
29	Wild gilthead seabream					7.8E−8	1.1E−7		
30	Gastropods					5.0E−3	9.5E−4	1.1E−4	1.1E−7
31	Bivalves		3.5E−6			2.0E−3	9.2E−4	1.7E−4	9.7E−6
32	Reared gilthead seabream								
33	Reared meagre								
34	Reared european seabass								
35	Mullets					1.4E−2	7.0E−3		
36	Round sardinella			6.0E−3		8.0E−8	1.0E−7		
37	Planktonic copepods				6.4E−2		1.2E−1	1.2E−1	4.9E−2
38	Phytoplankton						3.3E−1	1.2E−1	
39	Algae							6.2E−1	
40	Artificial food pellets	3.8E−1	3.9E−1	5.4E−1	1.6E−1	4.4E−1	1.9E−1	3.4E−2	4.4E−1
41	Detritus						2.1E−1	5.7E−2	4.5E−1

	Prey	Predator 25	26	27	28	29	30	31	32
1	Red scorpionfish								
2	Striped barracuda								
3	Great amberjack								
4	Bluefish								
5	Cephalopods								
6	Grey triggerfish								
7	Buccichi's goby								
8	Juveniles gilthead seabream								
9	Common eagleray								
10	Juv. pelagic plank. fishes								
11	Juveniles sparids								
12	Juveniles. pompano								

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Table 3 (*Continued*)

	Prey	Predator							
		25	26	27	28	29	30	31	32
13	Juveniles bogue								
14	Juveniles mullets								
15	Juv. med. horse mackerel								
16	Sparids								
17	Striped red mullet								
18	Medit. horse mackerel								
19	Comber								
20	Pelagic planktivorous fishes								
21	Crabs			9.5E−8		2.0E−3			
22	Shrimps			9.5E−8		6.7E−4			
23	Echinoderms					8.0E−3			
24	Mysids			2.1E−2	4.0E−3	6.0E−3			
25	Anphipods	8.5E−2	7.6E−2	1.9E−2	4.5E−2	8.0E−3			
26	Bogue								
27	Polychaetes	1.0E−3		2.1E−2		8.0E−3	1.0E−5		
28	Pompano								
29	Wild gilthead seabream								
30	Gastropods			4.9E−5		1.0E−3			
31	Bivalves			4.9E−5		6.7E−4			
32	Reared gilthead seabream								
33	Reared meagre								
34	Reared european seabass								
35	Mullets								
36	Round sardinella								
37	Planktonic copepods	2.8E−2	7.9E−4						
38	Phytoplankton	2.0E−1						9.1E−1	
39	Algae						8.8E−1		
40	Artificial food pellets	2.3E−1	6.5E−1		7.2E−1	6.2E−1	1.1E−2		1.0E+0
41	Detritus	4.5E−1		9.4E−1			1.1E−1	8.9E−2	

	Prey	Predator				
		33	34	35	36	37
1	Red scorpionfish					
2	Striped barracuda					
3	Great amberjack					
4	Bluefish					
5	Cephalopods					
6	Grey triggerfish					
7	Bucchichi's goby					
8	Juveniles gilthead seabream					
9	Common eagleray					
10	Juv. pelagic plank. fishes					
11	Juveniles sparids					
12	Juveniles. pompano					
13	Juveniles bogue					
14	Juveniles mullets					
15	Juv. med. horse mackerel					
16	Sparids					
17	Striped red mullet					
18	Medit. horse mackerel					
19	Comber					
20	Pelagic planktivorous fishes					
21	Crabs					
22	Shrimps					
23	Echinoderms					
24	Mysids					
25	Anphipods					
26	Bogue					
27	Polychaetes					
28	Pompano					
29	Wild gilthead seabream					
30	Gastropods					
31	Bivalves					
32	Reared gilthead seabream					
33	Reared meagre					
34	Reared european seabass					
35	Mullets					
36	Round sardinella					
37	Planktonic copepods					
38	Phytoplankton					6.3E−1
39	Algae					
40	Artificial food pellets	1.0E+0	1.0E+0	1.0E+0	1.0E+0	3.8E−2
41	Detritus					3.3E−1

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Table 4
Ecosystem properties for the fish farm model as computed by Ecopath.

Parameter	Value	Units
Sum of all consumption	31,059.83	tonnes/km^2/year
Sum of all exports	23,933.35	tonnes/km^2/year
Sum of all respiratory flows	13,812.25	tonnes/km^2/year
Sum of all flows into detritus	50,795.5	tonnes/km^2/year
Total system throughput	119,601	tonnes/km^2/year
Sum of all production	12,640	tonnes/km^2/year
Gross efficiency (catch/net p.p.)	3.449	
Calculated total net primary production	1604.958	tonnes/km^2/year
Total primary production/total respiration	0.116	
Net system production	−12,207.29	tonnes/km^2/year
Total primary production/total biomass	0.204	
Total biomass/total throughput	0.066	
Total biomass (excluding detritus)	7864.549	tonnes/km^2
Total catches	5535.782	tonnes/km^2/year
Mean trophic level of the catch	2	
Connectance index	0.191	
System omnivory index	0.129	

comparable to an immature ecosystem. The system omnivory index was in accordance with the latter result. However, the parameters derived from the information theory showed greater values for the fish farm, reflecting the greater power to maintain the system and face up future unexpected perturbations.

4. Discussion

The pelagic compartment was strongly affected by the large flux of organic matter. Artificial food pellets act as the main factor favouring the aggregation of wild fishes (Tuya et al., 2006), providing resources enough to determine the functioning of the system, i.e., most of the key species (e.g., mullets, round sardinella) fed on artificial food pellets (Fernández-Jover et al., 2008), which resulted in a low connectance and omnivory index in the whole system. Consequently, TLs of aggregated fish species were lower than the previous results for the Mediterranean (Stergiou and Karpouzi, 2002) and those reported in FishBase (Froese and Pauly, 2003), since the diet included an important proportion of food pellets, which TL is 1 by definition.

Opportunistic feeding around cages of piscivorous species contributed to the existence of some indirect effects among functional groups and/or human activities. Bluefish predates on the cultured and the aggregated fish assemblages, impacting negatively on the wild aggregated fishes and the three human activities considered in this study. Additionally, the lack of relevant positive effect of aggregated wild fish on both trammel net and recreational fisheries in our model exhibits the low interaction among these and fish farming.

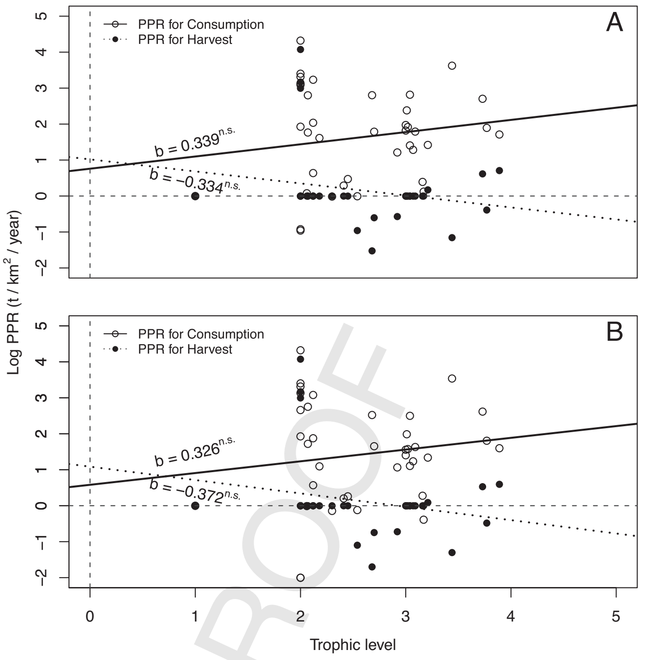

Fig. 5.

The high input and dependency on artificial food pellets to support food web, promotes great values of mutual information shared in the system and a considerable system's 'strength in reserve' from which, theoretically, it can draw to meet unexpected perturbations (Ulanowicz, 1986). It is both not due to the existence of a well structured and mature community, as predicted by the ecological theory Q6

Table 5
Comparison of several ecosystem statistics.

Index	Ecosystems					
	Fish farm	Sardinia Island, 1994[a]	Sardinia Island, 2006[a]	Cantabrian Sea[b]	South Catalan Sea[c]	Etang de Thau[d]
SC/TST	0.260	0.531	0.522	0.242	0.514	0.427
SR/TST	0.115	0.170	0.185	0.098	0.197	0.141
SFD/TST	0.425	0.235	0.221	0.355	0.252	0.360
SAP/TST	0.106	0.377	0.336	0.574	0.397	0.342
TPP/TR	0.116	1.370	1.090	4.897	1.180	1.511
TPP/TB	0.204	7.790	4.610	27.749	6.550	5.078
TB/TST	0.066	0.030	0.040	0.017	0.040	0.042
Connectance index	0.191	–	–	0.318	0.200	0.54
System omnivory index	0.129	0.190	0.160	0.268	0.190	0.354
Mean trophic level of the catch	2.000	–	2.000	3.660	3.120	2.19
Ascendancy	73,606.2	1790.600	4483.800	14,996.000	1815.422	38,348.400
Overhead	125,785	4970.300	11,371.400	24,884.800	5303.879	105,936.600
Capacity	199,391.2	6760.900	15,855.200	39,880.700	7119.300	144,285.000
Overhead/ascendency	1.709	2.776	2.536	1.659	2.922	2.762
Ecopath pedigree index	0.646	0.332	0.428	0.669	0.670	–

SC: sum of all consumptions; TST: total system throughput; SR: sum of respiration; SFD: sum of flows to detritus; SAP: sum of production; TR: total respiration; TPP: total primary production; TB: total biomass.

[a] Díaz-López et al. (2008).
[b] Sánchez and Olaso (2004).
[c] Coll et al. (2006).
[d] Palomares et al. (1993).

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(Christensen, 1995), but to high amount of resources available in the system in the form of artificial food pellets.

Compared with the other selected natural systems, the fish farm resulted in a heavily forced ecosystem sustained by the high loading of artificial food pellets, with a great total biomass dominated by both the reared and the pelagic wild fish assemblage, with a minimum dependence on the primary production of the system. These are features that usually characterise upwelling ecosystems (Coll et al., 2006). The inflow of matter and energy causes an increase of information in the system (Patten, 1959), which is not effectively integrated towards higher trophic levels (i.e., most of the biomass, the reared species, are not available for predators). However, the assessment of the developmental ecological stage of the fish farm *sensu* Odum's theory (Odum, 1971) resulted contradictory due to the minimum dependence on the primary production and the high amount of accumulated, both reared and wild, biomass. Habitat alteration through a build up of nutrients and over-sedimentation of food pellets cannot occur given that most of the biomass flows through the wild aggregated fish assemblage. As a final result, this study confirms that keeping wild fish around the cages reduces the environmental impact of fish farming.

5. Conclusions

We considered that the obtained model described what was happening in the fish farm ecosystem, given the current state showed by the study site. The model summarised most of the information existing about this system. It can be a valuable tool for understanding the effects of fish farming and predict changes on biodiversity, commercial fisheries or socioeconomic activities. It will allow the design of reliable short-term sustainable aquaculture policies at the system scale, such as the increase of the reared biomass or the exploitation of the aggregated wild fish assemblage, including the design of adaptive management experiments by means of manipulating some functional groups (e.g., implementing multi-trophic integrated aquaculture). This modelling approach evidenced the ecological role of the artificial food pellets related with the other components of the system, describing quite well the modifications induced on the system. In this framework, fish farm managers and governmental officers should be aware of the very important role that the aggregated fish assemblage could have in the system dynamics and structure.

Q7 Uncited references

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2012.08.028.

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