Food-web structure of and fishing impacts on the Gulf of Cadiz ecosystem (South-western Spain)

María Ángeles Torres [a,*], Marta Coll [b,c], Johanna Jacomina Heymans [d], Villy Christensen [c,e], Ignacio Sobrino [a]

[a] *Instituto Español de Oceanografía (IEO), Centro Oceanográfico de Cádiz, Puerto Pesquero, Muelle de Levante, s/n, PO Box 2609, E-11006 Cádiz, Spain*
[b] *Institut de Ciències del Mar (ICM-CSIC), Passeig Maritim de la Barceloneta, no 37-49, 08003 Barcelona, Spain*
[c] *Ecopath International Initiative Research Association, Barcelona, Spain*
[d] *Scottish Association for Marine Science (SAMS), Scottish Marine Institute, Dunbeg, Oban PA 37 1QA, Scotland*
[e] *Fisheries Centre, University of British Columbia, 2202 Main Mall, Vancouver, BC, V6T 1Z4 Canada*

ABSTRACT

The Gulf of Cadiz (North-eastern Atlantic, Spain) is an exploited ecosystem characterized by high marine biodiversity and productivity. Over the last decade, the landings of fish stocks such as anchovy (*Engraulis encrasicolus*), sardine (*Sardina pilchardus*) and hake (*Merluccius merluccius*) have been declining and currently remain low. A food-web model of the Gulf of Cadiz has been developed by means of a mass balance approach using the software EwE 6 to provide a snapshot of the ecosystem in 2009. The goals of this study were to: (1) characterize the food-web structure and functioning, (2) identify the main keystone groups of the ecosystem, (3) assess the impact of fishing to the Gulf of Cadiz compared to that in other essential marine ecosystems in the coastal area of Spain: Cantabrian Sea (North-eastern Atlantic) and Southern Catalan Sea (Mediterranean Sea), and (4) examine the limitations and weaknesses of the Gulf of Cadiz model for improvements and future research directions. The model consists of 43 functional groups, including the main trophic components of the system with emphasis target and non-target fish species. The main trophic flows are determined by the interaction between detritus, phytoplankton and micro- and mesozooplankton. Rose shrimp (*Parapenaeus longirostris*), cephalopods and dolphins present important overall effects as keystone species on the rest of the groups. The exploitation of fisheries composed mainly of trawlers, purse seiners and artisanal boats is intensive in the Gulf of Cadiz with all fleets exerting high impacts on most living groups of the ecosystem. The findings highlighted that the Gulf of Cadiz is a notably stressed ecosystem, displaying characteristics of a heavily exploited area. The comparative approach highlights that the three ecosystems display similarities with regard to structure and functioning such as the dominance of the pelagic fraction, a strong benthic-pelagic coupling, the important role of detritus, and the high impact of fishery exploitation.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

During the last decades, inefficient fisheries management together with illegal, unreported and unregulated (IUU) fishing practices in many marine ecosystems have caused the decline of fish stocks and therefore, major threats to marine biodiversity (e.g. Jackson et al., 2001; Agnew et al., 2009; Samhouri et al., 2009; Holt et al., 2011; Christensen and Walters, 2011). Consequently, fishing activities may alter the structure and functioning of marine food webs (Pauly et al., 1998a, 2002). This shows that fishery management based on single species is not sufficient and ongoing

efforts to develop an ecosystem-based approach to fisheries (EAF) are urgently needed for integrating sustainable exploitation and marine ecosystems conservation (Garcia et al., 2003; Garcia and Cochrane, 2005; FAO, 2008). For the EAF, new methodological tools have been developed, such as ecological models (e.g. Christensen and Walters, 2004; Plagányi, 2007) and ecosystem indicators (e.g. Cury and Christensen, 2005; Shin and Shannon, 2010). These tools provide a framework for assessing the impacts of interactions between species and fisheries and their implications for marine fisheries management (Coll and Libralato, 2012).

The Ecopath with Ecosim (EwE) approach is currently one of the most used ecosystem modeling tools for building ecological models within the context of ecosystem-based approaches to marine resources management (Polovina, 1984; Christensen and Pauly, 1992; Pauly et al., 2000; Christensen and Walters, 2004, 2011). This ecological modeling tool contributes to the science of an

* Corresponding author. Tel.: +34 956 29 42 09.
E-mail addresses: torresleal.ma@gmail.com, marian.torres@cd.ieo.es (M.A. Torres).

ecosystem-based approach by integrating human activities within an ecosystem context and evaluating their impacts on marine food webs, including environmental factors (Coll and Libralato, 2012). Results of this type of modeling can provide important insights into ecosystem structure and functioning, adding to our understanding the control of energy flows transferred through the food web while informing the practitioner as to the most appropriate management policies. In addition, these studies have also gathered a significant amount of information at an ecosystem level based on network analysis and information theory (Ulanowicz, 1986; Christensen and Pauly, 1993; Heymans and Baird, 2000; Heymans et al., 2007, 2012).

The Gulf of Cadiz marine ecosystem (ICES IXa South) connects the Atlantic Ocean with the westernmost part of the Mediterranean Sea (Fig. 1). This area is an important fishing ground with a high diversity and high productivity of exploited species (Sobrino et al., 1994). The abundance of marine resources is related to the bathymetric characteristics of its continental shelf and slope, the existence of a warm-temperate climate, the presence of oceanographic processes, and the enrichment produced by the outflows of important rivers such as Guadalquivir and Guadiana (Vila et al., 2004; Ramos et al., 2012). In addition, the Gulf of Cadiz is considered a highly suitable habitat for the reproduction of some commercial species due to the combination of warm and nutrient-rich waters and wind regimes (Jiménez et al., 1998; Millán, 1999). Several authors have shown the importance of the Guadalquivir River estuary, or related areas, in attracting spawning or juvenile development of commercial species such as anchovy and sardine (e.g. Baldó and Drake, 2002; Sobrino et al., 2005; García-Isarch et al., 2006).

The commercial fisheries of the Gulf of Cadiz use mainly mixed-species low selectivity trawlers, purse seiners, and artisanal boats (Millán, 1992; Sobrino et al., 1994; Silva et al., 2002; Jiménez et al., 2004). In 2009, the highest landings were provided by purse seiners, accounting for 54% of the total landings, and followed by trawlers (33%) and artisanal boats (13%) (Instituto Español de Oceanografía (IEO) Fishery Database). The main commercial species caught by the trawl fleet were rose shrimp (*Parapenaeus longirostris*), hake (*Merluccius merluccius*), common octopus (*Octopus vulgaris*), cuttlefish (*Sepia officinalis*), and horse mackerel (*Trachurus* spp.). For purse seiners, the main catches were sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*). Both pelagic resources accounted for almost 80% of the total reported purse seine landings, though mackerel (*Scomber* spp.) landings were also important in this fleet. Artisanal boats targeted cephalopods, sparids and flatfishes (Silva et al., 2002).

The Gulf of Cadiz marine ecosystem has a great socio-economic importance. In 2012, fishing activities generated landed value of approximately €100 millions. Additionally, these activities are a source of employment in the area, reaching 5000 and indirectly 30,000. Most jobs opportunities are associated to coastal towns, such as Isla Cristina, Punta Umbría, Sanlúcar, Chipiona, Conil, Barbate and Tarifa (JA, 2013).

On a spatial scale, the diverse nature of the substrata over the Gulf of Cadiz shelf leads to the coexistence of different fisheries. Consequently, the rocky bottoms in the eastern area (Cadiz coast) favor the artisanal fisheries targeting sea breams (mainly *Pagrus* spp., *Dentex* spp. and *Pagellus* spp.). Sand, mud and gravel bottoms in the western area (Huelva coast) are exploited mainly by trawl and gillnet fisheries which capture hake (*Merluccius merluccius*), wedge sole (*Dicologlossa cuneata*), crustaceans and cephalopods, among others (Ramos et al., 1996). Seasonal abundance of several commercial species determines the sequential development of different demersal and pelagic fisheries (Jiménez, 2002; Silva et al., 2002). Species catches vary largely in space and time in association with the highly diverse environmental traits encountered in the shelf as well as the species life cycles (Sobrino et al., 1994; Ramos et al.,

1996). In addition, anchovy and sardine biomass undergo large inter-annual fluctuations due to environmental changes (Sobrino et al., 2002).

In the Gulf of Cadiz, numerous studies have been undertaken mainly focusing on different fishing, biological, and ecological aspects (e.g. Jiménez et al., 2004; Torres et al., 2007; Gil et al., 2008; Vila et al., 2010; Silva et al., 2011). However, none have integrated all the available information to quantify fishing impacts in an ecosystem-based perspective despite the decline of the main stocks in the area (IEO Fishery Database). In addition, a recent study describing different features of the Gulf of Cadiz ecosystem required for the Marine Strategy Framework Directive has revealed that there are no studies about the food-web structure and trophic relationships of this marine exploited area (Ramos et al., 2012). Therefore, ecosystem modeling could be appropriate to fill this research gap, integrating all the available information on the Gulf of Cadiz marine ecosystem.

Hence, taking advantage of previous modeling work in surrounding areas, this study presents the development of the first food-web model of the Gulf of Cadiz (ICES IXa South) with the goals to: (1) characterize the food-web structure and functioning, (2) identify the main keystone groups of the ecosystem, (3) assess the impact of fishing to the Gulf of Cadiz compared to that in other essential marine ecosystems in the coastal area of Spain: Cantabrian Sea (North-eastern Atlantic) and Southern Catalan Sea (Mediterranean Sea), and (4) examine the limitations and weaknesses of the Gulf of Cadiz model for improvements and future research directions.

2. Material and methods

2.1. Area description and study period

The Gulf of Cadiz is located at the Southwestern end of the Iberian Peninsula and covers a large marine area of Spain, Portugal and Morocco. The Spanish area from the mouth of the Guadiana River, which borders Portugal in Ayamonte (Huelva), to the Cape of Tarifa (Cadiz) spans 303 km of coast (Sobrino et al., 1994). The modeled area is encompassed in ICES Subdivision IXa (South) and it covers 7224 km² with depths from 15 to 800 m (Fig. 1). The coastal area was excluded from the analyses because legal trawling fishing areas are only deeper than 15 m and since there is a lack of information necessary to parameterize the model. The food-web model developed in this study represents an annual average situation of the Gulf of Cadiz ecosystem in 2009 because this is the year when the best data were available, and most of the diet composition data for predators representing the marine food web were collected during this year (Torres, 2013).

2.2. The food-web model

The food-web model of the Gulf of Cadiz was constructed using the Ecopath with Ecosim (EwE) software version 6 (Christensen et al., 2008). In particular, we used the static Ecopath model that allows getting a snapshot representation of the resources in the ecosystem and their interactions in a specific period, namely the year 2009. The resources are represented by trophically linked biomass 'pools' in the form of functional groups (i). They consist of a single species or species groups representing ecological guilds (Christensen et al., 2008).

The model is parameterized based on two master equations. The first one describes how the production term for each functional group (i) of the model can be split into the following components: catches + predation mortality + net migration + biomass
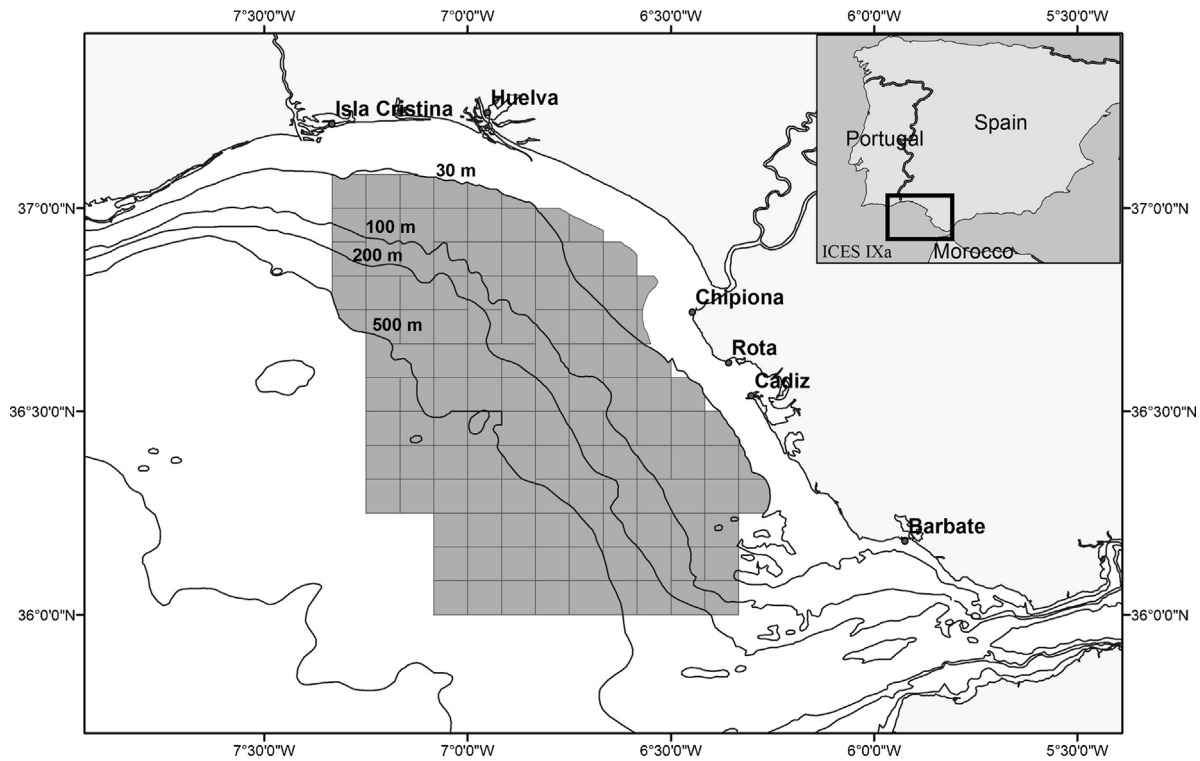
Fig. 1. The Gulf of Cadiz in the Atlantic waters of the South of Spain (ICES IXa South). The modeled area comprised the gray grids.

accumulation + other mortality:

$$\left(\frac{P}{B}\right)_i \cdot B_i = Y_i + \sum_{j=1}^n B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ji} + E_i + BA_i + \left(\frac{P}{B}\right)_i \cdot B_i (1 - EE_i)$$

(1)

where P_i is the total production rate of the functional group (i), B_i the biomass of the group (i), Y_i is the total fishery catch rate of (i), Q_i is the total consumption rate of (i), DC_{ji} is the contribution of the group (i) in the diet of predator (j), E_i the net migration rate of (i) (emigration–immigration), BA_i is the biomass accumulation rate of (i), while EE_i is the ecotrophic efficiency defined as the fraction of the production that is used in the system, i.e. either passed up the food web, used for biomass accumulation, migration or export (Christensen et al., 2008).

The second equation describes the energy balance of each group and it splits into:

Consumption (Q) = production (P) + respiration (R)

+ unassimilated food (U)   (2)

The model is parameterized through a system of linear equations for all the functional groups (Christensen and Walters, 2004), where for each equation at least three of the four basic parameters: B_i, $(P/B)_i$, $(Q/B)_i$ and EE_i have to be known for each group i. Usually EE is left unknown because it is difficult to estimate. Diet composition (DC) and catch (Y) are also needed for each functional group i. Further details, algorithms and equations are well described in Christensen and Walters (2004) and Christensen et al. (2008).

2.3. Input data and sources

The type of currency used in this study was wet weight biomass in t km^{-2} and wet weight production, consumption and catch in t km^{-2} year^{-1} for all functional groups. Where equations required dry weight, this value was properly changed into wet weight by using conversion factors. The detailed description of the functional groups, available datasets, equations and references used to build the Ecopath model of the Gulf of Cadiz is presented in Table A1, which provides all the species or taxa belonging to each functional group.

2.3.1. Functional groups classification

The ecological groupings used to build the food-web model were based mainly on species that had similar trophic roles in the ecosystem based on diet composition data (Torres, 2013), although other biological and ecological features (e.g. size, type of habitat, consumption, production and mortalities rates) were considered. The main species targeted by the fishery were modeled separately since better information about the different parameters was available for these groups (e.g. anglerfishes, mackerels, horse mackerels, common octopus, mullets, blue whiting, anchovy, sardine, rose shrimp, Norway lobster and mantis shrimp (Table A1)). European hake (*Merluccius merluccius*) was split into two multi-stanza groups (large hake, i.e. ≥20 cm of total length and small hake, i.e. <20 cm, with an age at transition of 12 months according to Piñeiro and Saínza (2003)) representing different life history stages or stanzas and ontogenetic changes in the diet (Torres and Sobrino, 2012). In addition, 20 cm is the recruitment size for the southern stock of hake including the Gulf of Cadiz (ICES, 2010a). This multi-stanza group was also similarly created in the other compared models in this study (Sánchez and Olaso, 2004; Coll et al., 2006, 2008). For this multi-stanza representation, the von Bertalanffy growth parameter $K = 0.165$ year^{-1} (Piñeiro, 2011) and the parameters obtained from its length-weight relationship in the study area ($W_{maturity}/W_{inf} = 0.0142$, Torres et al., 2012) were used.

Trawlers, purse seiners and artisanal boats were incorporated in the model as three separate fleets. Due to the lack of data and despite its great importance within the marine food web, the microbial loop was only indirectly modeled since it was parameterized as part of the detritus group, following previous ecosystem models in

the Atlantic Ocean and the Mediterranean Sea (Sánchez and Olaso, 2004; Coll et al., 2006, 2008; Tsagarakis et al., 2010).

2.3.2. Biomass estimates

Biomass estimates were generally taken from standard assessment methods performed in the study area.

In the case of demersal, benthopelagic, and benthic species, biomasses were estimated by using stratified and swept-area methods from two bottom-trawl surveys (ARSA: "Arrastre Región Sur-Atlántica") conducted seasonally (autumn and spring) in 2009 in the Gulf of Cadiz (Sobrino and Burgos, 2009; Vila et al., 2009). Biomass estimates for both surveys were averaged and used as representative for each functional group.

For pelagic fish, biomass estimates were taken from an acoustic survey (ECOCÁDIZ: "ECOsistema pelágico del Golfo de CÁDIZ") conducted in July 2009 (ICES, 2009; Iglesias et al., 2009). Pelagic hauls used for the acoustic energy allocation by species, although opportunistic, were carried out in such number and locations to ensure a relatively good sampling coverage (both geographically and in the depth range) of the neritic ichthyofauna of the Gulf of Cadiz ecosystem. The acoustic assessment was extended to all the schooling pelagic fish species (i.e. small and mid-sized species) occurring in the sampled area. Further details of this survey are well described in ICES (2009) and Iglesias et al. (2009).

Several studies of abundance of vulnerable groups such as seabirds, turtles, and marine mammals were considered to estimate their biomass (see details in Table A1).

Quantitative estimates of phytoplankton, by means of chlorophyll-a values obtained from sampling procedures and satellite images were used to calculate the biomass (Table A1). These data were assumed as reliable and suitable according to the modeled area and the study period. Additionally, as part of the analysis, the results obtained were supported by those presented in Ramos et al. (2012). Finally, previous studies undertaken in the Gulf of Cadiz were consulted but not used to calculate the phytoplankton biomass because they comprise an extended study area and a different study period (Reul et al., 2006; Navarro and Ruiz, 2006; Prieto et al., 2009).

Biomass of micro- and mesozooplankton was determined from samples collected during several ichthyoplankton surveys named "GOLFO" in 2006 (Jiménez et al., 2005). Detritus biomass was calculated empirically following the equation of Pauly et al. (1993):

$$\log D = -2.41 + 0.954 \cdot \log PP + 0.863 \log E \tag{3}$$

This equation links the production of detritus (D) with the average annual primary production (PP) (Navarro et al., 2006) and the average depth of the euphotic zone (E) (Ramos et al., 2012). Finally, a high value of EE (0.95) was entered (Table 1) to let EwE estimate the biomass for those groups with no biomass values provided in the area (i.e. commercial sparids (2), suprabenthos and macrozooplankton) following other models (Guénette et al., 2001; Neira and Arancibia, 2004; Okey et al., 2004). Under mass-balance conditions, biomass accumulation and other export terms were assumed equal to zero.

2.3.3. Production

According to Allen (1971), the production per unit of biomass (P/B) was assumed as the total mortality (Z), which is the sum of fishing mortality (F) and natural mortality (M). Fishing mortality (F) is the ratio between catches (Y) and biomass (B). In absence of catch-at-age data from unexploited populations, natural mortality for finfish species was estimated from the empirical equation proposed by Pauly (1980):

$$\log M = -0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634 \log T \tag{4}$$

linking natural mortality (M), the curvature parameter of the von Bertalanffy growth function (K), the asymptotic length (L_∞) calculated from Pauly (1984) where $L_\infty \approx L_{max}/0.95$ and the mean water temperature (T in °C). For finfish, maximum length values (L_{max}) were obtained from the bottom-trawl and acoustic surveys conducted in the area. Growth parameters were taken from studies performed in the area (e.g. Jiménez et al., 2001; Velasco et al., 2011a,b) or from literature. The mean water temperature in the Gulf of Cadiz in 2009 was 14.5 °C (Sobrino and Burgos, 2009; Vila et al., 2009).

For most invertebrate species (i.e. cephalopods, crustaceans, benthic invertebrates, bivalves, polychaetes), secondary production ratios were calculated following Brey's (2001) model or based on assumptions from other models (see Table A1). Due to the commercial importance and available information of rose shrimp in the area, natural mortality (M) was calculated from the empirical equation of Arce (2006) proposed for exploited marine invertebrates and taking into account information about its growth parameter (K) published in the area (Sobrino, 1998):

$$M = 1.325 \cdot K^{0.758} \tag{5}$$

Finally, for apex predators such as seabirds and dolphins, a P/Q value of 0.05 was assumed (Table 1) to let EwE estimate a P/B value for both groups (Christensen et al., 2008).

2.3.4. Consumption

Consumption per unit of biomass (Q/B) for finfish species was calculated following the empirical equation of Pauly et al. (1990):

$$\log\left(\frac{Q}{B}\right) = 6.37 - 1.5045\,T' - 0.168 \log W_\infty + 0.1399\,\mathrm{Pf}$$
$$+ 0.2765\,\mathrm{Hd} \tag{6}$$

where W_∞ is the asymptotic body weight (g), T' is an expression for the mean water temperature expressed using $T' = 1000/\mathrm{Kelvin}$ (Kelvin = °C + 273.15), and two variables expressing food type: Pf (1 for predators and zooplankton feeders and 0 for all others) and Hd (1 for herbivores and 0 for carnivores). For finfish species, W_∞ was estimated by using length-weight relationships published in the study area (Torres et al., 2012). Information related to the type of food was mostly taken from empirical data (Torres, 2013) or in absence of data from Fishbase (Froese and Pauly, 2012).

For seabirds, consumption was estimated by using the empirical equation proposed by Nilsson and Nilsson (1976):

$$\log(\mathrm{DR}) = -0.293 + 0.85 \cdot \log(W) \tag{7}$$

where DR is the daily ration (g) and W is the mean body weight (g) for each species. DR was converted to Q/B considering the biomass of each species and the time spent in the area.

In the case of marine mammals, consumption was calculated from the empirical equation of Innes et al. (1987):

$$R = 0.1 \cdot W^{0.8} \tag{8}$$

where R is the daily ration (kg) and W is mean body weight (kg) for each species. R was converted to Q/B considering the biomass of each species (see Table A1).

Due to the limited information available for crabs, benthic invertebrates carnivores and polychaetes, consumption was calculated as a function of body size following the equation of Cammen (1980):

$$\log(Q) = -0.420 + 0.742 \cdot \log(B) \tag{9}$$

where B is the average dry mass of each species within the groups. Mass/energy conversion factors were taken from Brey (2001). Consumption rates for all cephalopods, Norway lobster (Nephrops norvegicus) and mantis shrimp (Squilla mantis) were taken from

Table 1
Input parameters used for the Gulf of Cadiz food web model.

	Functional groups	B	P/B	Q/B	EE	P/Q	U/Q	T Y	PS Y	A Y	D
1	Seabirds	7E−05	3.03	60.53		0.05	0.2				1E−05
2	Killer whales	0.004	0.24	8.33			0.2				
3	Dolphins	0.031	0.69	13.72		0.05	0.2				6E−04
4	Loggerhead turtles	1E−04	0.15	2.54			0.2				2E−06
5	Sharks	0.140	0.85	5.46			0.2	0.012	3E−06	1E−03	0.069
6	Demersal piscivores	0.056	0.80	4.50			0.2	0.010	7E−06	2E−06	0.019
7	Anglerfishes	0.018	1.09	4.04			0.2	0.016	1E−05	1E−04	
8	Skates	0.061	1.05	3.67			0.2	0.028	5E−05	0.010	0.011
9	Large hake	0.246	0.88	4.62			0.2	0.142		0.007	0.006
10	Small hake	0.020	4.60	22.16			0.2	0.012			0.012
11	Mackerels	1.379	1.14	6.28			0.2	0.002	0.290	2E−04	0.550
12	Horse mackerels	0.559	0.64	6.47			0.2	0.065	0.041	0.001	0.030
13	Benthic cephalopods	1.060	1.91	6.45			0.2	0.135	2E−05		0.017
14	Common octopus	0.125	0.91	4.49			0.2	0.077		0.010	0.019
15	Benthopelagic cephalopods	0.995	1.24	6.90			0.2	0.030	5E−05	5E−04	0.003
16	Deep-sea fishes	0.283	0.31	3.36			0.2	0.005		5E−04	0.006
17	Large benthopelagic fishes	0.239	1.08	4.51			0.2	3E−06	3E−05	1E−06	0.026
18	Small benthopelagic fishes	2.958	0.96	9.02			0.2	0.009			0.022
19	Flatfishes	0.139	1.63	8.74			0.2	0.076	9E−06	1E−04	0.030
20	Demersal fishes	0.332	0.82	6.80			0.2	0.011	1E−06	5E−04	0.054
21	Mullets	0.034	1.61	5.51			0.2	0.041	3E−05	0.002	9E−06
22	Commercial sparids (1)	0.227	0.74	6.50			0.2	0.035	0.001		0.048
23	Commercial sparids (2)	0.337	0.82	7.03	0.95		0.2	0.019	0.004	0.043	0.005
24	Blue whiting	0.113	1.06	6.52			0.2	0.011	2E−06	1E−06	0.063
25	Small demersal fishes	1.961	1.84	11.65			0.2				0.004
26	Anchovy	2.817	1.65	9.16			0.2		0.405	1E−06	0.020
27	Sardine	4.350	1.04	8.37			0.2	0.000	0.930	5E−05	0.030
28	Rose shrimp	0.949	1.72	10.53			0.2	0.880			0.004
29	Norway lobster	0.037	0.93	4.05			0.2	0.018			0.000
30	Mantis shrimp	0.054	0.92	3.80			0.2	0.024			0.008
31	Crabs	1.730	2.11	9.84			0.2	6E−04		5E−04	0.029
32	Shrimps	6.445	1.70	11.74			0.2	0.014	2E−06		0.023
33	Gelatinous zooplankton	0.029	13.87	50.48			0.2				
34	Benthic invertebrates (C)	1.007	3.11	12.43			0.2				0.002
35	Polychaetes	4.888	2.53	18.42			0.4				
36	Suprabenthos	2.564	15.62	52.12	0.95		0.4				
37	Benthic invertebrates (F/D/S)	3.795	2.50	6.50			0.4				0.002
38	Bivalves	3.563	4.43	15.00			0.4	3E−05			0.022
39	Macrozooplankton	2.479	20.41	50.94	0.95		0.4				
40	Meso and microzooplankton	13.826	25.00	90.40			0.2				
41	Phytoplankton	20.170	158.04								
42	Detritus	70.946									
43	Discard	1.131									

Biomass (B: t km^{-2}); production/biomass ratio (P/B: year^{-1}); consumption/biomass ratio (Q/B: year^{-1}); ecotrophic efficiency (EE); production/consumption ratio or gross food conversion efficiency (P/Q); unassimilated consumption (U/Q); total trawl landings (T Y: year^{-1}); total purse seine landings (PS Y: year^{-1}); total artisanal landings (A Y: year^{-1}); total discards (D: year^{-1}).

daily feeding rate studies (see Table A1). Finally, for those groups with no information provided in the area, the values were assumed from other models involving similar species (Table A1).

2.3.5. Diet composition information

The diet composition matrix used in the parameterization of the model was constructed using local stomach-contents studies performed for the majority of the fish groups (Torres, 2013) and the European squid *Loligo vulgaris* (Vila et al., 2010) (Table 2). A detailed list of all species with diet composition information studied for this work is provided in Table A1. Diet composition data for those groups with no trophic information in the study area were taken from the literature (Table A1). Migratory species of seabirds and marine turtles were taken into account by modeling a proportion of their diet compositions as imports to the ecosystem following Coll et al. (2006).

2.3.6. Fisheries removals

The official landings data by species and by fleet with reference to 2009 were provided by the IEO Fishery Database. However, in order to give more reliable estimates, these data were corrected by considering: (1) discard information based on the results of the AMDES project conducted by the IEO in IXa ICES Division (Gulf of

Cadiz), (2) by-catch of vulnerable species from literature (Table A1), and (3) new estimates of illegal, unregulated or unreported (IUU) landings in the study area (Coll et al., 2013a; Torres, 2013). In order to quantify the IUU landings of the Gulf of Cadiz, landing declarations were compared with sale notes to cross-check and quantify the proportion of landed catch that was not declared in the sales notes in 2009 and therefore was not included in the official landing statistics (Torres, 2013).

2.4. Model balancing

Balancing of the Gulf of Cadiz model was undertaken manually following a top-down strategy. First, net food conversion efficiencies (P/Q [0.05–0.3]), respiration/assimilation (R/A [<1]) and production/respiration (P/R [<1]) ratios were checked to be within expected limits (Christensen et al., 2008). The pedigree data were used (see Section 2.5.1) to justify which parameters to change with the purpose of achieving the lowest possible level of uncertainty.

Initial results showed EE > 1 for most demersal, benthic, and benthopelagic groups. In the Gulf of Cadiz model, DC, P/B and Q/B for most fish groups were assumed to represent the most reliable data and the main errors were associated with biomass, in particular for benthopelagic, demersal, and benthic groups. Biomass values

Table 2

Diet composition matrix adjusted for the Gulf of Cadiz food web model.

	Prey/Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	Seabirds	0.00002																		
2	Killer whales																			
3	Dolphins																			
4	Loggerhead turtles																			
5	Sharks					0.002	0.005									0.0003				
6	Demersal piscivores					0.009	0.003		0.005	0.006										
7	Anglerfishes																			
8	Skates																			
9	Adult hake		0.184	0.030				0.429		0.009										
10	Juvenile hake					0.003	0.051	0.233		0.024	0.008			0.0001		0.0002				0.000001
11	Mackerels	0.051	0.121	0.065		0.203	0.220			0.064										
12	Horse mackerels	0.001		0.066		0.007	0.233			0.022						0.003				0.00001
13	Benthic cephalopods	0.002		0.012	0.100	0.013	0.011	0.088	0.006	0.018	0.028	0.070		0.011	0.140	0.024	0.0004	0.001	0.001	0.005
14	Common octopus			0.001		0.006														
15	Benthopelagic cephalopods		0.389	0.048		0.078	0.013		0.010	0.006	0.007			0.128		0.007				
16	Deep-sea fishes			0.020		0.010	0.028	0.026		0.002						0.003				
17	Large benthopelagic fishes					0.087	0.002			0.018	0.003					0.020				
18	Small benthopelagic fishes			0.011		0.045	0.070			0.024	0.020			0.012		0.033	0.0002	0.363	0.001	0.018
19	Flatfishes			0.009		0.018	0.022	0.089	0.025	0.038	0.011					0.00003				0.004
20	Demersal fishes					0.005	0.026	0.102	0.058	0.007						0.022				0.0002
21	Mullets																			
22	Commercial sparids (1)			0.003						0.008						0.000				
23	Commercial sparids (2)			0.412												0.002				
24	Blue whiting			0.026		0.010	0.030			0.015	0.001									
25	Small demersal fishes			0.003		0.000	0.046	0.018	0.010	0.071	0.117	0.075	0.086	0.038		0.037	0.004	0.001		0.189
26	Anchovy	0.089	0.026	0.076		0.047	0.066			0.298	0.193	0.078		0.059	0.185	0.300				
27	Sardine	0.171	0.010	0.176		0.053	0.029			0.191				0.264	0.204	0.160				0.00003
28	Rose shrimp			0.017		0.010	0.012	0.009	0.003	0.019	0.005			0.060	0.109		0.025			
29	Norway lobster																			
30	Mantis shrimp			0.003		0.00001														0.000005
31	Crabs				0.082	0.071	0.057		0.237	0.065	0.034		0.001	0.023	0.089	0.039	0.263	0.002		0.267
32	Shrimps		0.270	0.022		0.110	0.046	0.007	0.322	0.075	0.191	0.238	0.009	0.174	0.002	0.039	0.166	0.136	0.030	0.065
33	Gelatinous zooplankton				0.020		0.000					0.008								
34	Benthic invertebrates (C)				0.100	0.0001								0.011	0.105		0.007			0.003
35	Polychaetes					0.024	0.002		0.005		0.003			0.013	0.0001	0.052	0.018			0.109
36	Suprabenthos					0.079	0.002	0.084	0.015	0.207	0.003		0.057	0.013	0.0001	0.052	0.444	0.040	0.095	0.247
37	Benthic invertebrates (F/D/S)					0.002	0.005			0.011			0.021	0.0001			0.0003			0.014
38	Bivalves					0.000			0.215					0.031	0.166		0.00003			0.018
39	Macrozooplankton	0.002				0.103	0.0003		0.010	0.007	0.175	0.505	0.848	0.170		0.259	0.072	0.458	0.360	0.062
40	Meso and microzooplankton													0.004					0.513	0.000002
41	Phytoplankton																			
42	Detritus																			
43	Discard	0.281			0.250	0.004														
44	Import	0.404			0.448															
	SUM	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 2 (*continued*)

	Prey/Predator	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1	Seabirds																					
2	Killer whales																					
3	Dolphins																					
4	Loggerhead turtles																					
5	Sharks																					
6	Demersal piscivores																					
7	Anglerfishes																					
8	Skates																					
9	Adult hake																					
10	Juvenile hake																					
11	Mackerels				0.074																	
12	Horse mackerels	0.0004			0.006																	
13	Benthic cephalopods	0.009		0.023	0.071	0.014				0.011	0.006		0.001	0.005								
14	Common octopus	0.001	0.002																			
15	Benthopelagic cephalopods	0.013	0.001	0.015		0.006																
16	Deep-sea fishes	0.005																				
17	Large benthopelagic fishes																					
18	Small benthopelagic fishes	0.003				0.038				0.068	0.184		0.021	0.010								
19	Flatfishes			0.002																		
20	Demersal fishes											0.050										
21	Mullets				0.001																	
22	Commercial sparids (1)				0.029																	
23	Commercial sparids (2)																					
24	Blue whiting																					
25	Small demersal fishes	0.031	0.002	0.076	0.277	0.094	0.005							0.034								
26	Anchovy	0.010		0.007	0.066																	
27	Sardine																					
28	Rose shrimp	0.007	0.009																			
29	Norway lobster	0.005																				
30	Mantis shrimp				0.007																	
31	Crabs	0.174	0.243	0.047	0.028	0.003	0.054			0.021	0.130	0.140	0.005									
32	Shrimps	0.171	0.136	0.039	0.030	0.176	0.078			0.180	0.161	0.090	0.018	0.010								
33	Gelatinous zooplankton	0.007		0.001	0.002							0.096			0.050							
34	Benthic invertebrates (C)	0.025	0.014	0.053	0.101		0.025			0.005	0.048	0.200	0.050			0.050						
35	Polychaetes	0.013	0.185	0.196	0.111		0.136			0.180	0.048	0.070	0.140		0.024	0.050						
36	Suprabenthos	0.230	0.350	0.061	0.021	0.398	0.158			0.157		0.090	0.179	0.326								
37	Benthic invertebrates (F/D/S)	0.264	0.003	0.372	0.017		0.001			0.110	0.076	0.200	0.085	0.002		0.312						
38	Bivalves	0.0004	0.053	0.024	0.113		0.033			0.069	0.037		0.234	0.084		0.052						
39	Macrozooplankton	0.029	0.002	0.002	0.046	0.271	0.011			0.043	0.099		0.009	0.344								
40	Meso and microzooplankton	0.002	0.001	0.059			0.499	1	0.946	0.031	0.003		0.005		0.800	0.174		0.100			0.100	
41	Phytoplankton			0.023					0.054					0.004	0.050	0.082	0.100	0.050		0.500	0.100	1
42	Detritus									0.125	0.111	0.160	0.218	0.190		0.280	0.900	0.850	1	0.500	0.800	
43	Discard														0.100							
44	Import																					
	SUM	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

taken from trawl surveys appeared to be insufficient in relation to the requirements of the model itself. Therefore, these values were readjusted to achieve mass balance for those groups mentioned previously. This assumption was supported by previous studies which suggest that these groups are usually underestimated in trawl surveys, and the error introduced by the use of trawls can be up to 50% of the real value (Badaracco and Molinet, 1991; King, 1995; Wolff et al., 1998; Sánchez and Olaso, 2004). In fact, catchability in a trawl gear is affected by many factors such as species, population density, season, diurnal or lunar cycles, light intensity and body size, which all interact with the fishing gear (Trenkel and Skaug, 2005; Jennings and Dulvy, 2005; Fraser et al., 2007). Since no studies of catchability estimates by species and/or gear exist in the area and to achieve more reliable estimates of biomass, the catchability coefficients were adjusted and the original value ($q=1$) was corrected for those invertebrates groups and some benthic and demersal fishes, following the same strategy applied in other ecosystems (Alias, 2003; Mackinson and Daskalov, 2008; Tsagarakis et al., 2010). For pelagic fish species the biomass values were sufficient for mass balance (Table 1).

On the other hand, the unused consumption (U/Q) for those invertebrate groups composed of filters, detritivores, and suspensivores feeders (i.e. polychaetes, suprabenthos, benthic invertebrates, bivalves and macrozooplankton) was assumed to be 0.40 (Christensen et al., 2008) (see Table 1).

Finally, cannibalism within a group can cause problems with fitting a model and therefore it had to be decreased for small hake, cephalopods, small fishes and crustaceans groups. Because the diet composition was uncertain for the majority of invertebrates groups, the model was mostly balanced by gradually and slightly adjusting the diets of these groups (Table 2). Outputs estimated by the model are presented in Table 3.

2.5. Model analysis and ecosystem indicators

2.5.1. Pedigree index and quality of the model

The pedigree routine was used to quantify the uncertainty associated to the input values in the model (Christensen et al., 2008). This index varies from 0 (low-quality models, i.e. input data estimated or taken from other models) to 1 (high-quality models, i.e. well-sampled and high-precision local input data). The pedigree index is averaged over all parameters and groups in the model to provide an index of the quality of the input data of the model. In general, biomass, diet and catch data were mostly taken locally. However, P/B and Q/B for finfish and diet compositions for most invertebrates groups were scarce and hence they were calculated empirically or adopted from similar ecosystems.

2.5.2. Ecosystem properties and trophic flows

The general ecosystem status and its stage of development and maturity *sensu* Odum (1971) and Christensen (1995) were assessed by using ecological indicators. The total system throughput (TST), calculated as the sum of the all the flows of consumption, exports, respiration, import and flows to detritus, gives a representation of the overall ecosystem size in terms of flows (Ulanowicz, 1986; Christensen and Pauly, 1993). In addition, the following indicators describing the system maturity were obtained: total primary production/total system respiration (TPP/TR), total primary production/total biomass (TPP/TB), and total biomass/total system throughputs (TB/TST) ratios. The transfer efficiency is defined as the fraction of the total flows at each trophic level that is either exported or transferred to other TLs through consumption. The mean TE is calculated as a geometric mean from the TE in trophic levels (TL) II–IV (Christensen et al., 2005).

Finn's Cycling Index (FCI) (Finn, 1976) representing the percentage of flows recycled in the food web was also estimated. The

percentage of recycling after the removal of detritus is called Predatory Cycling Index (PCI) (Christensen et al., 2008). Finn's Mean Path Length (MPL), representing the mean number of nodes that energy inflow into the ecosystem passes through before exiting the network, was also included. Finally, network analysis indices based on the theoretical and computational methodology suggested by Ulanowicz (1986) were calculated. Ascendancy (A) is a measure of the average mutual information in a system, scaled by system throughput and provide information of the degree of development and maturity of an ecosystem (Ulanowicz, 1986). The upper limit for A is the 'development capacity' (C) and the difference between C and A is 'system overhead' (O). The overhead provide limits on how much the ascendancy can increase and reflect the system's 'strength in reserve' from which it can draw to meet unexpected perturbations (Ulanowicz, 1986). The ecological meaning of these indices is linked to the stability, resilience and maturity of the ecosystem (Odum, 1969; Ulanowicz and Norden, 1990; Heymans et al., 2007).

In addition, the system omnivory index (SOI) and the connectance index (CI) correlated with ecosystem maturity and complexity of the food web (Christensen, 1995) were calculated. SOI is based on the average omnivory index (OI) which is calculated as the variance of the TL of a consumer's prey groups indicating predatory specialization (Pauly et al., 1993). The connectance index (CI) is the ratio of the number of existing trophic links with respect to the number of possible links (Christensen et al., 2008).

The trophic structure was aggregated into a Lindeman spine, an analysis of discrete trophic levels (TL) *sensu* Lindeman (1942) and proposed by Ulanowicz (1995). In this routine, the system was aggregated into a linear food chain where import (on TL I only), consumption by predators, export, flow to the detritus, respiration, and throughput were calculated for each TL. The detritus box was separated from primary producers to show the amount of energy that is flowing through it. These flows were also represented by means of a flow diagram showing the trophic interactions between all groups within the ecosystem.

2.5.3. Mixed Trophic Impact and Keystoneness index

The Mixed Trophic Impact (MTI) analysis uses the Leontief (1951) matrix routine developed by Ulanowicz and Puccia (1990). This routine allows the quantification of all direct and indirect trophic impacts of all groups in the system. The MTI analysis estimates the relative impact that a hypothetical increase in the biomass of a group would produce on the other groups within the ecosystem, including fishing activities (Ulanowicz and Puccia, 1990). A positive or negative impact would mean an increase or decrease in the quantity of the impacted group. Further details or equations are well described in Christensen et al. (2008).

The keystoneness index (KS) was applied to evaluate the potential roles of each functional group as keystones in the system. This index is a function of a group's trophic impact on other groups in the ecosystem and its biomass. The methods proposed by Power et al. (1996) and Librarato et al. (2006) were compared. Both methods use the relative overall effect calculated from the MTI against the keystoneness (KS) and the contribution of each functional group to the total biomass of the food web.

2.5.4. Exploitation status of the fishery

The fisheries impacts were assessed by analyzing the mean trophic level of the catch (TLc), the exploitation rates (F/Z), the relative consumption of total production representing the proportion of total production that is consumed within the system by all the functional groups, fishing mortalities (F), the gross efficiency of the fishery (GE, catch/net primary production), and the percentage of primary production required (PPR) to evaluate the sustainability of fisheries (Pauly and Christensen, 1995; Tudela et al., 2005). In

Table 3
Outputs obtained from the Gulf of Cadiz food web model.

	Functional groups	TL	EE	P/Q	F	M2	M0	F/Z	OI	FD	R/A
1	Seabirds	3.09	0.05		0.147	0.001	2.878	0.049	1.08	0.00	0.94
2	Killer whales	4.55	0.00	0.03			0.235		0.20	0.01	0.96
3	Dolphins	4.49	0.03		0.018		0.668	0.027	0.15	0.11	0.94
4	Loggerhead turtles	3.18	0.09	0.06	0.013		0.137	0.088	1.25	0.00	0.93
5	Sharks	4.07	0.73	0.16	0.585	0.035	0.231	0.687	0.37	0.19	0.81
6	Demersal piscivores	4.29	0.98	0.18	0.515	0.271	0.016	0.642	0.09	0.05	0.78
7	Anglerfishes	4.84	0.82	0.27	0.890		0.201	0.816	0.08	0.02	0.66
8	Skates	3.70	0.76	0.29	0.802		0.252	0.761	0.26	0.06	0.64
9	Large hake	4.11	0.99	0.19	0.630	0.245	0.007	0.714	0.10	0.23	0.76
10	Small hake	3.70	0.96	0.21	1.192	3.247	0.161	0.259	0.26	0.09	0.68
11	Mackerels	3.57	0.85	0.18	0.611	0.356	0.170	0.538	0.31	1.97	0.77
12	Horse mackerels	3.20	0.80	0.10	0.246	0.269	0.128	0.383	0.09	0.79	0.88
13	Benthic cephalopods	3.89	0.93	0.30	0.143	1.638	0.129	0.075	0.26	1.50	0.63
14	Common octopus	3.92	1.00	0.20	0.847	0.062	0.003	0.928	0.29	0.11	0.75
15	Benthopelagic cephalopods	3.77	0.91	0.18	0.034	1.096	0.107	0.027	0.24	1.48	0.78
16	Deep-sea fishes	3.48	0.80	0.09	0.041	0.207	0.061	0.134	0.17	0.21	0.89
17	Large benthopelagic fishes	3.57	0.97	0.24	0.108	0.939	0.028	0.100	0.22	0.22	0.70
18	Small benthopelagic fishes	3.08	0.97	0.11	0.010	0.915	0.031	0.011	0.03	5.43	0.87
19	Flatfishes	3.59	0.86	0.19	0.760	0.648	0.227	0.465	0.24	0.28	0.77
20	Demersal fishes	3.48	0.97	0.12	0.197	0.593	0.028	0.241	0.24	0.46	0.85
21	Mullets	3.41	0.85	0.29	1.264	0.103	0.243	0.785	0.18	0.05	0.63
22	Commercial sparids (1)	3.27	0.97	0.11	0.373	0.350	0.021	0.501	0.29	0.30	0.86
23	Commercial sparids (2)	3.82		0.12	0.211	0.570	0.041	0.256	0.36	0.49	0.85
24	Blue whiting	3.41	0.99	0.16	0.652	0.392	0.012	0.617	0.22	0.15	0.80
25	Small demersal fishes	3.16	0.96	0.16	0.002	1.766	0.073	0.001	0.10	4.71	0.80
26	Anchovy	3.00	0.94	0.18	0.151	1.397	0.101	0.091	0.00	5.45	0.77
27	Sardine	2.95	0.95	0.12	0.221	0.772	0.052	0.211	0.05	7.51	0.84
28	Rose shrimp	3.17	0.88	0.16	0.932	0.587	0.200	0.542	0.38	2.19	0.80
29	Norway lobster	3.49	0.99	0.23	0.505	0.417	0.008	0.543	0.44	0.03	0.71
30	Mantis shrimp	3.27	0.98	0.24	0.590	0.312	0.016	0.643	0.48	0.04	0.70
31	Crabs	2.92	0.95	0.21	0.017	1.981	0.112	0.008	0.33	3.60	0.73
32	Shrimps	2.90	0.96	0.14	0.006	1.622	0.073	0.003	0.23	15.60	0.82
33	Gelatinous zooplankton	2.89	0.44	0.27		6.095	7.775		0.18	0.52	0.66
34	Benthic invertebrates (C)	2.67	0.86	0.25	0.002	2.657	0.450	0.000	0.28	2.96	0.69
35	Polychaetes	2.00	0.86	0.14		2.165	0.365		0.00	37.79	0.77
36	Suprabenthos	2.10		0.30		14.843	0.781		0.09	55.46	0.50
37	Benthic invertebrates (F/D/S)	2.00	0.85	0.38	4E−04	2.132	0.367	0.000	0.00	11.26	0.36
38	Bivalves	2.00	0.83	0.30	0.006	3.691	0.733	0.001	0.10	23.99	0.51
39	Macrozooplankton	2.10		0.40		19.390	1.021		0.09	53.05	0.33
40	Meso and microzooplankton	2.00	0.33	0.28		8.332	16.668		0.00	480.42	0.65
41	Phytoplankton	1.00	0.41			64.866	93.174			1879.33	
42	Detritus	1.00									
43	Discard	1.00	6E−05						0.27		

Trophic level (TL); ecotrophic efficiency (EE); production/consumption ratio or gross food conversion efficiency (P/Q); fishing mortality (F: year^{-1}); predation mortality (M2: year^{-1}); other natural mortality (M0: year^{-1}); exploitation rate (F/Z); omnivory index (OI); flow to detritus (FD: t km^{-2} year^{-1}) and respiration/assimilation ratio (R/A).

addition, available data enabled us to calculate the variations in the mean trophic level of the catch of the fishery from 1993 to 2009. These dataset were compared with modeling results and were used to set the modeling results in a temporal context.

2.5.5. Comparison of results with other ecosystems

The ecosystem properties and indicators obtained from the Gulf of Cadiz model were discussed and compared with results from available modeling exercises representing Spanish exploited marine ecosystems: the Cantabrian Sea (Sánchez and Olaso, 2004), on the Atlantic side, and the Southern Catalan Sea (Coll et al., 2006, 2008), in the Mediterranean Sea. This comparative analysis allowed a search for similarities and differences between these three exploited ecosystems and helped to provide a better understanding of the overall dynamic and structure of Spanish marine food webs. This comparison was possible because the three models followed similar criteria to estimate the input parameters and define the ecological grouping. Furthermore, the fishing gears and techniques used in the three ecosystems are similar and the major commercially exploited stocks are both pelagic and demersal fish, crustaceans and cephalopods. However, the analysis presented some limitations in the structure of each model due to the different

number of functional groups and fleets, the study period, and the depth ranges analyzed (Table 4).

3. Results and discussion

The pedigree index obtained in the Gulf of Cadiz model was 0.633, and ranked in the upper part of the range (0.164–0.676) of the 150 Ecopath models assessed worldwide by Morissette (2007). This value implies a reasonable quality of data and also is similar to the values obtained for the other ecosystem compared models here (Table 4).

3.1. Analysis at the functional group level

A total of 43 functional groups represented the Gulf of Cadiz ecosystem in 2009 including the main components of the food web. All groups were integrated into four TLs. In the Gulf of Cadiz, the TLs ranged from 1.0 for primary producers to 4.84 for anglerfishes (Table 3). In general, TLs for most groups were similar to those previously reported in other temperate ecosystems (Pauly et al., 1998b; Cortés, 1999; Stergiou and Karpouzi, 2002; Sánchez and Olaso, 2004; Coll et al., 2006; Ebert and Bizzarro, 2007; Lassalle et al., 2011). Anglerfishes were also found as top predators in the

Table 4

Summary statistics for the Gulf of Cadiz food web model, and comparison with the Spanish ecosystems of the Cantabrian Sea (Sánchez and Olaso, 2004) and the Southern Catalan Sea (Coll et al., 2006, 2008).

Statistics and indicators	Gulf of Cadiz	Cantabrian	Catalan	Units
Characteristics of the ecosystems				
Surface	7224	16000	4500	km^2
Study period	2009	1994	1994	Year
Number of functional groups	43	28	40	
Number of fleets	3	4	4	
Depth range	15–800	70–500	50–400	M
Ecosystem Theory Indices				
Total system throughput (TST)	7734.9	10143	4038.01	t km^{-2} year^{-1}
Sum of all consumption (TQ)	1946.9	2458.08	851.73	t km^{-2} year^{-1}
Sum of all exports (TE)	2233.7	3097.13	1251.89	t km^{-2} year^{-1}
Sum of all respiratory flows (TR)	955.1	990.82	326.86	t km^{-2} year^{-1}
Sum of all flows into detritus (TFD)	2599.2	3597.35	1607.52	t km^{-2} year^{-1}
Sum of all production (TP)	3704.4	5825	1851.31	t km^{-2} year^{-1}
Calculated total net primary production (NPP)	3187.7	4852.21	1577	t km^{-2} year^{-1}
Total primary production/total respiration (TPP/TR)	3.3	4.90	4.82	
Net system production (PP-TR)	2232.6	3861.399	1250.14	t km^{-2} year^{-1}
Total primary production/total biomass (TPP/TB)	39.8	27.749	26.74	
Total biomass/total throughput (TB/TST)	0.01	0.017	0.01	
Total biomass (excluding detritus) (TB)	80.02	174.86	58.97	t·km^{-2}·year^{-1}
Mean transfer efficiency (TTE)	14.9	33.3	12.2	%
Connectance Index (CI)	0.25	0.32	0.20	
System Omnivory Index (OI)	0.18	0.27	0.22	
Ecopath pedigree index	0.63	0.67	0.67	
Fishery Status Indices				
Total catches	4.55	11.63	5.36	t km^{-2} year^{-1}
Mean trophic level of the catch (TLc)	3.32	3.66	3.12	
Gross efficiency of the fishery (GE, catch/net PP)	0.0014	0.002	0.003	
Primary production required to sustain the fishery (PPR, considering PP)	12.97	30.53	9.54	%
Primary production required to sustain the fishery (PPR, considering PP+detritus)	16.45	40.7	10.6	%
Cycling Indices				
Predatory cycling index (PCI, of throughput without detritus)	8	3.55	3.33	%
Throughput cycled (excluding detritus)	2.14	107.91	27.39	t km^{-2} year^{-1}
Finn's cycling index (FCI, of total throughput)	3	4.89	6.77	%
Finn's mean path length (MPL)	2.43	2.99	2.56	
Information Indices				
Ascendency (A)	41.1	25.9	35.8	%
Overhead (O)	49.2	73	64.2	%
Capacity (C)	25810	29577.2	7119.3	Flowbits

Cantabrian Sea model (Sánchez and Olaso, 2004) and in the Southern Catalan Sea model (Coll et al., 2006, 2008), suggesting that these species have similar trophic roles in all ecosystems compared. In addition, marine mammals presented TL > 4 in the Gulf of Cadiz (Table 3). Regarding the fish community, anchovy (TL = 3.00) and sardine (TL = 2.95) showed the lowest TLs due to the importance of zooplankton and phytoplankton in their diet. Seabirds had a relatively low TL (Table 3) because of the presence of small-pelagic fishes in their diet and also because they feed on discard which is parameterized in the model as a detritus group (with TL of 1). The remaining fish groups, loggerhead turtles, cephalopods, and crustaceans (except crabs and shrimps) had TLs > 3.0 (Table 3). The second TL comprised mainly benthic invertebrates due to their detritus-based diet.

It is noteworthy that most groups showed high *EE* values (*EE* > 0.95), which indicated that the production of each group was extensively used in terms of predation or exploitation by fisheries within the ecosystem. In addition, these high *EE* values for some functional groups could be induced partly by the adjustment of their catchability coefficients. For fish, the *EE* indicated that 73–99% of the production was used within the system (Table 3). Most benthic invertebrates groups similarly had remarkably high *EE* values. This result appeared to be appropriate as they are highly consumed in the ecosystem (Table 2) accordingly to local diet composition studies (Torres, 2013). Conversely, lower values of *EE* were presented for apex predators such as seabirds, marine mammals and turtles (Table 3) indicating that they are scarcely preyed upon or

non-exploited by the fishery. In addition, low *EE* for phytoplankton and micro- and mesozooplankton indicated that a large percentage of these groups could go to detritus, corroborating previous studies (Huertas et al., 2006) which suggests that a high percentage of primary production is exported to the bottom as particulate organic matter where a large proportion is recycled, in particular in the shallowest waters. This feature of the primary producers was also demonstrated in the Cantabrian Sea model (Sánchez and Olaso, 2004), but not in the Southern Catalan Sea model (Coll et al., 2006, 2008) where these groups are highly consumed. These differences are mainly due to the lower productivity of the Mediterranean Sea in comparison with Atlantic ecosystems (Bosc et al., 2004).

The total biomass supported by the ecosystem (excluding detritus and discard) was 80 t km^{-2} in 2009, represented mainly by phytoplankton (25.2%), zooplankton groups (20.4%), benthic invertebrates (16.6%), crustaceans groups (14.7%), pelagic fishes (11.4%), demersal fishes (9%) and cephalopods (2.7%) (Table 1). These results highlight the great importance of the planktonic compartments, in addition to bottom communities and benthic producers in the area. Concerning pelagic fishes, anchovy, and sardine had the highest biomass values. This feature is common in upwelling and related ecosystems (Jarre-Teichmann, 1998; Guénette et al., 2001; Shannon et al., 2003; Neira and Arancibia, 2004; Heymans et al., 2004; Moloney et al., 2005) and it is also characteristic of the other two Spanish ecosystems (Sánchez and Olaso, 2004; Coll et al., 2006, 2008).

In fact, the highest flows to detritus (FD) were provided by sardine and anchovy in addition to the benthic groups (Table 3). Respiration to assimilation ratio (R/A) ranged from 0.332 to 0.965 t km^{-2} year^{-1}, with the highest values corresponding to top predators. Omnivory index (OI) of each group reached the lowest values in the demersal domain for demersal piscivores fishes and anglerfishes mainly due to their ichthyophagous behavior (Torres, 2013). Moreover, those consumers preying on planktonic groups (horse mackerel, small benthopelagic fishes, anchovy and sardine) and detritus (suprabenthos, polychaetes and macrozooplankton) presented low OI values (Table 3) and hence they were the most specialized consumers. By contrast, the most omnivorous fish group was the shark group (0.372) with a large number of prey items in its diet (Torres, 2013). This group was followed by crustaceans, suggesting more complexity in this part of the food web. Furthermore, these groups present a relatively wide trophic spectrum compared with detritus-based diet at lower level groups. In general, OI results were similar to those obtained for the Southern Catalan Sea model (Coll et al., 2006), indicating that most groups prey on similar TL resources in both ecosystems.

Mortality rates obtained for the model were split into predation mortality (M2), other natural mortality (M0), and fishing mortality (F). In the model, natural mortality (M) is the sum of predation mortality (M2) and other natural mortality (M0). When comparing natural mortality (M) from the model to M values from stock assessments, some differences were detected. Notably, for large hake (ICES, 2010a) and sardine (ICES, 2010b), the M values from stock assessments were considerably lower than M values from estimated by the Ecopath model. These differences were also identified in the Cantabrian Sea model (Sánchez and Olaso, 2004). Concerning predation mortality (M2), the highest values were for small hake, benthic invertebrates, crabs, small demersal fishes, benthic cephalopods, shrimps, and anchovy (Table 3). All of these groups comprise important sources of food for numerous predators in the Gulf of Cadiz ecosystem (Table 2). Other mortality (M0) estimated by the model presented the highest values for phytoplankton, micro- and mesozooplankton, gelatinous zooplankton, seabirds, macrozooplankton and suprabenthos. A high value of M0 implies a low representation of the species dynamic by the model and it is frequently associated to species that spend part of their time outside the studied area (such as seabirds) or are highly abundant (such as planktonic organisms) (Christensen et al., 2008). Regarding the fish groups, higher values of M0 were obtained for skates, mullets, sharks, flatfishes, and anglerfishes. Dolphins also presented a high value of M0 in addition to non-commercial benthic invertebrates.

Most of the biomass and production in the benthic and demersal domains were associated with detritus. Furthermore, detritus was an important compartment in terms of consumption (Table 2), constituting one of the main energy flow inputs similar to other Atlantic ecosystems such as the Cantabrian Sea and the Bay of Biscay (Sánchez and Olaso, 2004; Lassalle et al., 2011). This feature may be associated with the inputs of continental nutrients mainly from the Guadiana and Guadalquivir rivers, which increase the flow of the phytoplankton production to detritus and the biomass of many detritivores groups. Several studies of the spatial and temporal distribution of phytoplankton in the Gulf of Cadiz have highlighted the relevant role of this compartment within the food web. In fact, this group increases the exploitable biomass in the area (Reul et al., 2006; Navarro and Ruiz, 2006; Prieto et al., 2009).

The analysis of the consumption of production of the system, by excluding planktonic groups, suprabenthos, and detritus groups, emphasized the importance of crustaceans, sardine, and anchovy within the system as it was shown in other Mediterranean ecosystems (Coll et al., 2006, 2007; Piroddi et al., 2010).

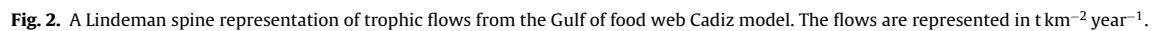### 3.2. Ecosystem properties and trophic flows

The summary statistics and indicators obtained from the Gulf of Cadiz model are presented in Table 4, and compared with the Cantabrian Sea and the Southern Catalan Sea ecosystems previously modeled. For the Gulf of Cadiz, TST was 7735 t km^{-2}, indicating that the sum of all flows in the ecosystem was larger in this area than in the Southern Catalan Sea (Coll et al., 2006, 2008), but lower than in the Cantabrian Sea (Sánchez and Olaso, 2004) according to the productivity regimes (Sherman and Hempel, 2009) of the three ecosystems and the overall surface modeled (Table 4). TST in the Gulf of Cadiz was mainly represented by flows to detritus (33.6%), followed by the flows of exports out of the system in terms of catches (28.9%), consumption (25.1%) and respiration (12.4%). Similar results were obtained in the other ecosystems compared (Table 4), highlighting that a significant amount of living biomass ends up as detritus.

TPP/TR ratio in the Gulf of Cadiz showed that the energy produced is approximately three times higher than balanced by the cost of maintenance (Table 4). According to Odum's (1969) maturity attributes, this value could indicate an undeveloped stage of the Gulf of Cadiz ecosystem. However, Christensen and Pauly (1993) found that most Ecopath models overestimate this value when decomposer organisms, like bacteria and fungi, are omitted in the model. TPP/TB ratio of the Gulf of Cadiz presented the highest value of the three compared models, reflecting a low level of biomass accumulation within the system compared with productivity. This feature may possibly be influenced by the Guadiana and Guadalquivir Rivers nutrients. The net system production results also pointed out an under development stage of the Gulf of Cadiz ecosystem (Christensen, 1995).

Concerning the indices related to the food-web complexity, the relatively low omnivory index of the system (SOI) suggested that the Gulf of Cadiz network is rather linear. This value indicated that in general consumers feed on a single trophic level which is in line with the diet composition studies in the area (Torres, 2013). In addition, SOI was similar to those obtained for temperate and upwelling ecosystems (Heymans et al., 2004; Coll et al., 2006, 2007, 2008; Barausse et al., 2009; Piroddi et al., 2010; Angelini and Vaz-Velho, 2011; Lassalle et al., 2011). Furthermore, the connectance index (CI) was similar to that obtained for the Southern Catalan Sea model (Coll et al., 2006, 2008), showing moderate-low inner linkages within the food web. However, the CI value obtained for the Cantabrian Sea model was higher (Sánchez and Olaso, 2004), suggesting more complexity and number of links in that food web.

Predatory Cycling Index (PCI), or recycling after cycles to detritus are removed, of the Gulf of Cadiz is higher than those of the other systems (Table 4), indicating that more energy is recycled when detritus is removed and suggesting that all net primary production is not directly used and entered in the food web through heterotrophic benthic organisms. PCI presented the highest value for the three ecosystems compared. This value implies a high level of community stress (Christensen, 1995) *sensu* Odum, possibly due to the high levels of fishing practices in the area. Mean Path Length (MPL) was similar to those values obtained for the Cantabrian Sea and the Southern Catalan Sea (Table 4), suggesting that a flow passes through a similar number of groups. This feature is also characteristic of upwelling ecosystems (Jarre-Teichmann and Christensen, 1998; Neira and Arancibia, 2004).

Ascendancy (%A) was higher in the Gulf of Cadiz than that obtained for Coll et al. (2006, 2008) in the Southern Catalan Sea and for Sánchez and Olaso (2004) in the Cantabrian Sea, showing less complexity and large flows through a few channels. This difference could be related to the different characteristics of the modeled areas, in particular to the different number of functional groups and the study periods (Table 4) (Sánchez and Olaso, 2004; Coll et al.,

Fig. 2. A Lindeman spine representation of trophic flows from the Gulf of food web Cadiz model. The flows are represented in t km^{-2} year^{-1}.

2006, 2008). During the late 2000s the Gulf of Cadiz was more affected by human disturbance, impacting the ecosystem structure and function. The system overhead (O%) of the Gulf of Cadiz was the lowest between the three ecosystems compared, indicating that the Gulf of Cadiz has the least redundancy for potential use against disturbances (Ulanowicz, 1986).

In general, the global indicators described above suggest that the Gulf of Cadiz is a relatively immature and stressed ecosystem (Odum, 1969; Finn, 1976; Ulanowicz, 1986, 1995; Christensen, 1995) and this characteristic may be partly explained by the intensive human exploitation since ancient times (Sobrino et al., 1994). This is in line with results observed from the other two modeled areas of the Iberian Peninsula (Table 4) highlighting the high impact that Spanish fisheries pose in marine food webs of the Spanish Economic Exclusive Zone (EEZ).

Concerning the analysis of biomass and trophic flows, the highest biomass values in the Gulf of Cadiz were concentrated at TLs II and III excluding primary producers (Fig. 2). These values corresponded mainly to benthic and planktonic compartments. The results of the *Lindeman spine* representation (Fig. 2) revealed the importance of TLs II and III in the Gulf of Cadiz ecosystem in terms of biomass, catch, and exportation. Indeed, 68.6% of total system biomass (excluding detritus) is within TLs II and III. About 22% of TST flows are from TL II. The importance of TLs II and III was also found in the Cantabrian Sea (Sánchez and Olaso, 2004) and in the Southern Catalan Sea (Coll et al., 2006, 2008). Flows to detritus mainly originated from TL II, similar to the Mediterranean ecosystem compared in this study.

The most efficient trophic transfer (TE) occurred from TL III to TL IV. TL I (primary production and detritus) generated over 75% of the TST of the entire system (Fig. 2), underlying once again the importance of these groups at the base of the food web within the ecosystem. The mean transfer efficiency (TE) for the whole system was similar to the value obtained for the Southern Catalan Sea model (Coll et al., 2006, 2008), but was lower than for the Cantabrian Sea (Sánchez and Olaso, 2004) (Table 4). This could be due to differences in productivity dynamics of the three areas, but also to different ways of calculating the phytoplankton biomass and production to parameterize the model, in line with the differences observed for the primary production required to sustain the catch (PPR). The TE in the Gulf of Cadiz was mainly derived from detritus and was higher than the general value of 10% estimated by Pauly and Christensen (1995). This percentage was lower than the average for detritus (17.8%) but slightly higher than for primary

producers (13.9%). Finally, the exports (i.e. catches) are mainly concentrated in TL III followed by TL IV and the high transfer efficiency from TL III underlines the strong exploitation by the fisheries on this TL.

The trophic flows representing the major trophic interactions by main functional group within the Gulf of Cadiz ecosystem are shown in Fig. 3. The main flows originated from the groups at the base of the food web (i.e. detritus, phytoplankton, and zooplankton), moving the energy to the upper TL groups. Among fish groups, small-pelagic fishes (i.e. sardine and anchovy) are the main components in terms of biomass, underlining the important role of these species within the system. These groups were also important components in the other two ecosystems compared (Sánchez and Olaso, 2004; Coll et al., 2006, 2008).

3.3. Mixed trophic impact analysis and Keystone index

In general, most groups had a negative impact on themselves, interpreted as reflecting increased within-group competition for resources (Fig. 4). In the Gulf of Cadiz model, large hake exerted a positive effect on small hake because this species cannibalizes itself, though the cannibalism represents less than 3% of the diet (Torres and Sobrino, 2012). This trophic behavior was not as significant as in the other ecosystems of the Iberian Peninsula compared (Sánchez and Olaso, 2004; Coll et al., 2006).

Most groups had a direct impact on their main prey through predation (Fig. 4). Otherwise, prey had positive impacts on their predators, e.g. phytoplankton had a strong positive impact on zooplankton, sardine, and anchovy. However, seabirds, killer whales, loggerhead turtles, sharks, deep-sea fishes, large benthopelagic fishes, blue whiting, Norway lobster, and mantis shrimp had a slight or no impact on other groups in the ecosystem likely because these groups exhibit low biomass levels and in some cases their prey are considered mostly imported. Therefore, these groups were not represented in Fig. 4. The MTI analysis underlined the fact that dolphins had a negative effect on its preferred prey group: commercial sparids (2).

Results also revealed that the main groups influencing the Gulf of Cadiz food web were at the base of the food web (detritus, phytoplankton, and zooplankton), having direct impacts on fish and invertebrates groups (Fig. 4). This fact highlights again the importance of these groups in the ecosystem and suggests possible bottom-up effects within the ecosystem. The important role of detritus in the area as a source of food and as a structuring
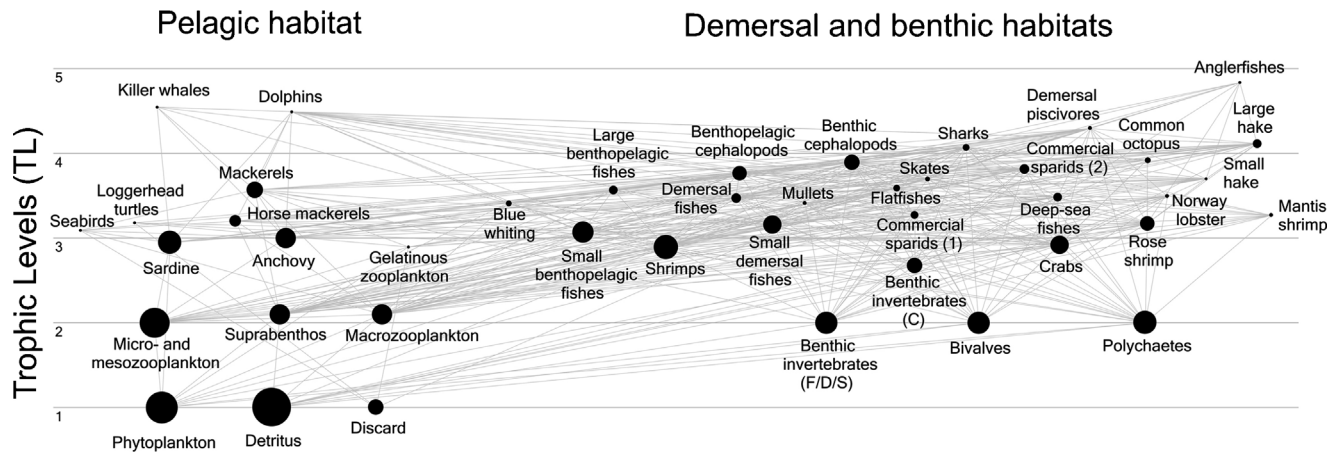
Fig. 3. Flow diagram of the Gulf of Cadiz food web. The size of each circle is proportional to the biomass of the functional group. All the functional groups are represented according to their trophic levels on the *y*-axis (TL) and connected to each other through light gray lines that represent prey–predator relationships. Groups are organized considering their pelagic, demersal and benthic habitats.

group (i.e. with a large biomass) in the Gulf of Cadiz food web was also highlighted by its positive effect on most groups including fisheries.

Some coupled pelagic-demersal relationships between cephalopods and small pelagic fishes or between medium-sized pelagic fishes (mackerel and horse mackerel) and demersal fish groups were identified (Fig. 4). This coupling is characteristic of upwelling and heavily exploited ecosystems (Sánchez and Olaso, 2004; Moloney et al., 2005; Coll et al., 2006).

When comparing the two indices of keystoneness (KS) proposed by Librarato et al. (2006) (Fig. 5a) and modified from Power et al. (1996) (Fig. 5b), the same keystone groups were identified: benthic cephalopods, commercial sparids (2), rose shrimp, and dolphins, suggesting that these groups had low biomass and high overall impact. However, some differences were observed between the two keystoneness methods as they weight differently the biomass proportion of the species within the ecosystem as previously highlighted (Coll et al., 2013b). Thus, the method proposed by Power
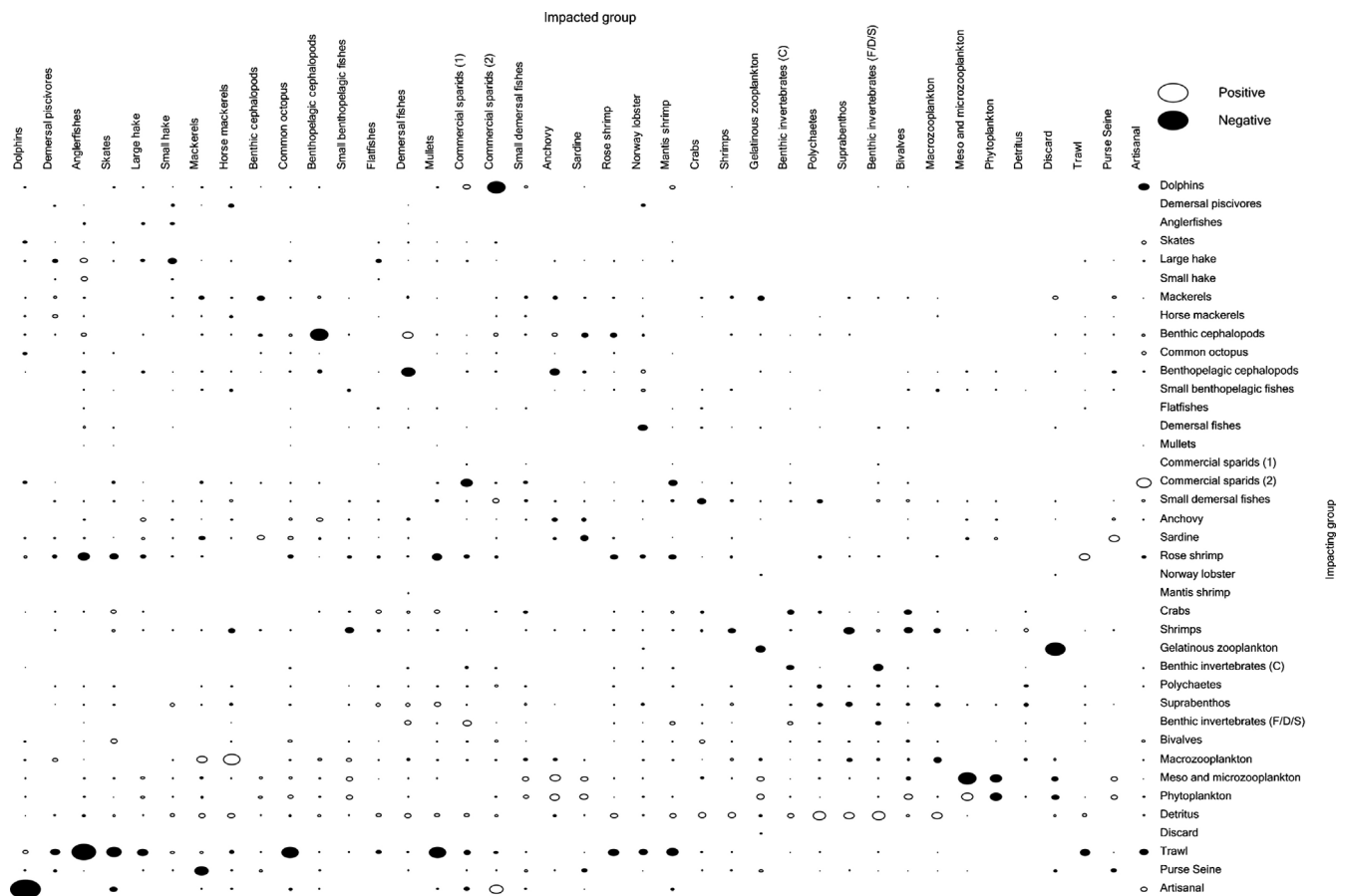
Fig. 4. Mixed Trophic Impact (MTI) analysis of the Gulf of Cadiz food web. The size of an ellipse represents the size of the trophic impact of the functional groups (white ellipses indicate positive impact, while black ellipses show negative impact). The three fishing fleets included in the model are represented at the bottom.

a

b

1 Seabirds	12 Horse mackerels	23 Commercial sparids (2)	34 Benthic invertebrates (C)
2 Killer whales	13 Benthic cephalopods	24 Blue whiting	35 Polychaetes
3 Dolphins	14 Common octopus	25 Small demersal fishes	36 Suprabenthos
4 Loggerhead turtles	15 Benthopelagic cephalopods	26 Anchovy	37 Benthic invertebrates (F/D/S)
5 Sharks	16 Deep-sea fishes	27 Sardine	38 Bivalves
6 Demersal piscivores	17 Large benthopelagic fishes	28 Rose shrimp	39 Macrozooplankton
7 Anglerfishes	18 Small benthopelagic fishes	29 Norway lobster	40 Micro- and mesozooplankton
8 Skates	19 Flatfishes	30 Mantis shrimp	41 Phytoplankton
9 Large hake	20 Demersal fishes	31 Crabs	42 Detritus
10 Small hake	21 Mullets	32 Shrimps	43 Discard
11 Mackerels	22 Commercial sparids (1)	33 Gelatinous zooplankton	

Fig. 5. Keystone Index (KI) analysis of the Gulf of Cadiz food web. The size of the circles are proportional to the biomass of each functional group (a) indicator *sensu* Librarato et al. (2006), and (b) indicator modified from Power et al. (1996).

et al. (1996) tends to overestimate the ecological importance of groups with low biomass and low impact (such as dolphins and commercial sparids (2)) in the study area.

Cephalopods had an important role in the Gulf of Cadiz as has been suggested by previous studies (Silva et al., 1998, 2011; Vila et al., 2010). These species hold an important trophic position as top-down structuring groups in the marine food web (Vila et al., 2010; Torres, 2013), and may be influenced by environmental factors and fishery exploitation (Sobrino et al., 2002). Cephalopods are, in fact, important groups in marine ecosystems and can proliferate in highly exploited areas (Piatkowski et al., 2001; Boyle and Rodhouse, 2005; Coll et al., 2013c).

Most of groups had a relatively high fishing and predation mortality. However, this was not the case for macrozooplankton and dolphins. Dolphins were also keystone groups in other temperate

and upwelling ecosystems (Ainsworth et al., 2002; Bundy, 2001; Coll et al., 2007; Barausse et al., 2009; Tsagarakis et al., 2010) due to the high feeding impact of the group relative to its biomass (excluding by-catch). Since this vulnerable group has been declining in most ecosystems it could be used as an ecological indicator to monitor fishing impact (Librarato et al., 2006). Dolphins were also identified as keystone species in other similar Mediterranean ecosystems such as the Northeastern Ionian Sea and the Southern Catalan Sea (Piroddi et al., 2010; Coll et al., 2006). Macrozooplankton is mainly composed of euphausiids and plays an important trophic role in the Gulf of Cadiz food web (Torres, 2013). As it is shown in Table 2, this group comprises an important source of food for most groups.

The method proposed by Librarato et al. (2006) identifies some keystone groups with high biomass and high trophic impact. In the
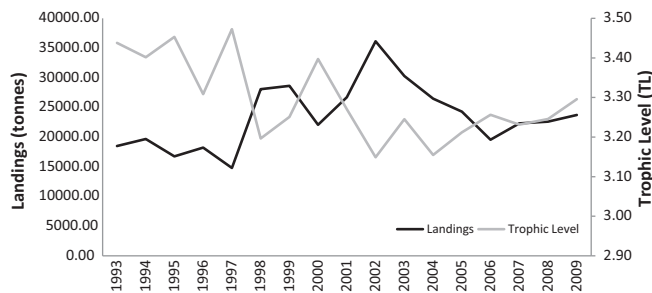
Fig. 6. Mean trophic level of total landings from the Gulf of Cadiz (1993–2009).

Gulf of Cadiz model, the groups in the lower part of the trophic web, such as phytoplankton and micro- and mesozooplankton were identified as keystone groups. These groups have a dominant role due to their abundance and therefore may also be defined as structuring groups (i.e. groups that have an important role in the ecosystem because have a large biomass) within the ecosystem (Heymans et al., 2012). It is also interesting that these groups were presented askeystone groups in other temperate ecosystems (Sánchez and Olaso, 2004; Coll et al., 2006; Lassalle et al., 2011), indicating possible bottom-up effects.

3.4. Fisheries impacts on the ecosystem

In general, the results of the Ecopath model of the Gulf of Cadiz revealed that the three ecosystems compared here presented similar levels of fishing impacts. In the Gulf of Cadiz, landings were dominated by species belonging to TL III.

Overall, the mean trophic level of the catches (TLc) in 2009 was 3.32 (Table 4) due to the dominance in the total catches of sardine, rose shrimp, anchovy, mackerels, large hake, benthic cephalopods, and horse mackerels with TLs between 2.95 and 4.11 (Table 3). Pauly et al. (1998a) suggested that the mean trophic level of the catch (TLc) can decline in an exploited ecosystem as a consequence of overexploitation of the highest trophic levels corresponding to large and slow growing long-lived predators. This phenomenon is known as 'Fishing Down Marine Food Web' (Christensen, 1996). With the aim of analyzing the status of exploitation of the Gulf of Cadiz ecosystem, estimates of the annual mean trophic level of the total catch (TLc) were calculated by combining the TLs obtained from the model (Table 3) and landings of the fishery operating in the Gulf of Cadiz since 1993–2009. In general, the analysis showed variations in the TLc with a declining trend from 1993 (TL = 3.44) until 2004 (TL = 3.15) with a rate of 0.19 per decade, two times higher than the global value (0.1) obtained by Pauly et al. (1998a). This suggests a heavy exploitation of the resources in the area from the beginning of the time series to 2004. However, from 2005 the TLc have shown an upward trend (Fig. 6). This trend is in line with the results obtained for Baeta et al. (2009) in nearby Portugal and may reflect a collapse of small-pelagic fish stocks rather than a recovery of higher trophic level species. The reason for the highest landing in 2002 may be related to the high landings for short-lived species such as anchovy (Engraulis encrasicolus) and rose shrimp (Parapenaeus longirostris) compiled in the IEO, Fishery Database. Both resources are of great economic importance in the area (JA, 2013). It should be noted that this high landing value in 2002 could also be related to certain oceanographic features that favored these species, similar to what it was suggested for other species in the area (Sobrino et al., 2002).

Regarding trawl fishery, the highest landings were accounted mainly for rose shrimp, large hake and benthic cephalopods (Table 1). However, the pelagic resources such as sardine, anchovy and mackerels were basically caught by the purse seine fishery. The

artisanal fleet targeted mainly commercial sparids (2) and common octopus. Octopus vulgaris is caught in the study area by the artisanal gear known as alcatruz (octopus pot) (Sobrino et al., 2011).

The most discarded group was mackerel (Table 1), mainly due to the presence of non-commercial size specimens of Scomber colias. The ratio landing/discard was 3.02 on average. In addition, high discard rates were also reached mainly for demersal fishes, such as sharks, blue whiting, commercial sparids, and flatfishes according to previous studies in the area (Pérez et al., 2005). Finally, the highest discard rates were achieved for other medium-sized pelagic fishes, in particular chub mackerel (Scomber solias), small demersal fishes, and also anchovy (ICES, 2010b).

Exploitation rates (F/Z) showed high values ranging from 0.714 to 0.928 for target demersal species such as common octopus, anglerfishes, mullets, skates, hake, sharks, and mantis shrimp in the area (Table 3). In the particular cases of common octopus and anglerfishes, the exploitation rates may be unsustainable because they are higher than the 0.8 suggested for demersal stocks (Mertz and Myers, 1998; Rochet and Trenkel, 2003). Nevertheless, anchovy and sardine presented low values of F/Z and none of them exceeded the recommended rate of 0.50 considered as overexploited stocks (Patterson, 1992; Mertz and Myers, 1998; Rochet and Trenkel, 2003).

The exploitation by fisheries was intensive in the Gulf of Cadiz, catching a total of 4.55 t km^{-2} in 2009 (Table 4), though not as high as in the Cantabrian Sea (Sánchez and Olaso, 2004) and in the Southern Catalan Sea (Coll et al., 2006). Mullets, small hake, rose shrimp, anglerfishes, and common octopus presented the highest levels of fishing mortality by trawling fleet, whereas F values were not very high for some other pelagic and invertebrates target species such as anchovy, sardine, the remaining cephalopods groups (Table 3). Concerning fishing mortalities (F), the general results obtained from the model are in line with the values obtained from southern hake, sardine, and blue whiting stock assessments in the Gulf of Cadiz in 2009 (ICES, 2010a,b,c). In the modeled area, the group most heavily impacted by fishing and predation was small hake. The same result was found in the Southern Catalan Sea (Coll et al., 2006).

Regarding the impact of the fishery on the ecosystem, the trawl fleet presented negative impacts on several groups, higher and much stronger than for the other gears considered in the model (Fig. 4). However, these fishing impacts are largely underestimated by the model because habitat destruction, modifications of the physical properties of seafloor sediments, water-sediment chemical exchanges, and sediment fluxes by trawling (Turner et al., 1999; Pauly, 2010; Puig et al., 2012) are not taken into consideration. The largest negative impacts were on its main target species, in particular sharks, anglerfishes, skates, common octopus, mullets, rose shrimp, and mantis shrimp, underlining the role of humans as predators in the ecosystem. Moreover, trawling had a negative impact on the artisanal fleet, which could be explained by the spatial competition in the different fisheries on the shelf of the Gulf of Cadiz (Vila et al., 2004).

The purse seine fleet had a negative effect on its target groups such as horse mackerels and blue whiting (Fig. 4). In contrast, this fleet had a positive impact on seabirds, benthic cephalopods, small demersal fishes, gelatinous zooplankton and sardine, by increasing or decreasing discard availability and through direct mortality. Finally, the artisanal fleet had an indirect positive impact on its main target group (commercial sparids (2)) possibly due to the decrease of its main predator (dolphins). This fleet had a very strong negative impact on this vulnerable group likely because it competes negatively with this group for prey. This gear seems to be the most selective, presenting the lower impacts in general on all groups. This result was also found in the other ecosystems compared (Sánchez and Olaso, 2004; Coll et al., 2006).

The primary production required to sustain the landings, PPR (%), was estimated at 751 t km^{-2} year^{-1} or 16.4% in the Gulf of Cadiz during 2009. This value was obtained taking into account the primary producers together with detritus and showed a low value compared to similar temperate ecosystems with PPR values ranging from 24.2% for tropical to 35.3% for non-tropical shelves reported by Pauly and Christensen (1995). When taking into account only the primary producers the value was 13%, suggesting the great importance of detritivorous organisms within the catch, e.g. rose shrimp. The major PPR fractions in the Gulf of Cadiz were to sustain mainly the catches of mackerel, rose shrimp and sardine. The PPR results reached lower values than those obtained for the Cantabrian Sea (Sánchez and Olaso, 2004), but slightly higher than for the Southern Catalan Sea (Coll et al., 2006). The gross efficiency of the fishery (GE = catch/net primary productivity) (Table 4) was higher that the mean global value (0.0002) calculated for a wide range of marine ecosystems (Christensen et al., 2005).

Finally, results indicating how much of the exploitable biomass is "consumed" by fisheries in relation to the other groups, highlight that the fishery consumed 5% of fished groups. Furthermore, the fishery had a strong impact (>50%) on demersal resources (e.g. mullets, anglerfishes, common octopus, large hake, Norway lobster, and mantis shrimp), indicating that the fishery was an important component of the Gulf of Cadiz food web in 2009.

4. Conclusions

The ecological model presented in this study is the first attempt to characterize the food-web structure and quantify the effects of fishery on the ecosystem of the Gulf of Cadiz (ICES IXa South) considering the main trophic components. This application enabled us to integrate previous studies and also identify important gaps in our present knowledge of this ecosystem for further research. In particular, information on the invertebrates and vulnerable groups is less abundant than that concerning other groups in the ecosystem. The major sources of uncertainty were associated with the biomass estimations for most groups. Additionally, better estimations of discards and IUUs regarding all fleets may be needed in the future. Synthetic indicators highlight that the Gulf of Cadiz is a relatively immature and notably stressed ecosystem, characteristics of heavily exploited areas. The model highlighted that the ecosystem is dominated by the lower trophic levels, which dominate most of the flows. In addition, a large percentage of primary production flows to detritus. Consequently, benthic invertebrates are important components within the ecosystem. In addition, strong relationships between the pelagic, demersal and benthic domains were identified due to key groups such as benthic cephalopods, commercial sparids (2), macrozooplankton, rose shrimp, benthopelagic cephalopods and dolphins. Small and medium-sized pelagic fishes presented high biomasses and catches, and played an important role in the ecosystem. Fisheries, in particular the bottom trawling feet, exerted large impacts on their main target species of the food web. The Gulf of Cadiz ecosystem displays similarities in terms of its structure and functioning with other ecosystems of the Iberian Peninsula such as the dominance of the pelagic fraction, strong benthic-pelagic couplings, the important role of detritus, and the high impact of fishery exploitation. These findings highlight that ecosystem-based management measures may be needed to reduce the impact of fishing and ensure the sustainability of marine resources of the Gulf of Cadiz in the future. Dynamics simulations using Ecosim and Ecospace would help clarify the exploitation status of the Gulf of Cadiz. The application of both modules would provide useful information to ensure the sustainability of the marine resources and to support comparative approaches.

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.2013.05.019.

References

Agnew, D., Pearce, J., Pramod, G., Peatman, T., Watson, R., Beddington, J.R., Pitcher, T.J., 2009. Estimating the worldwide extent of illegal fishing. PLos One 4 (1–8), e4570.

Ainsworth, C., Heymans, J.J., Pitcher, T., Vasconcellos, M., 2002. Ecosystem models of Northern British Columbia for the time periods 2000, 1950, 1990 and 1750. Fisheries Centre Research Reports 10 (4), 41.

Alias, M., 2003. Trophic model of the coastal fisheries ecosystem of the west coast of Peninsular Malaysia. In: Silvestre, G., Garces, I., Stobutzki, M., Ahmed, R.A., Valmonte-Santos, C., Luna, L., Lachica-Alio, P., Silvestre, L., Garces, I., Stobutzki, M., Ahmed, R.A., Valmonte-Santos, C., Luna, L., Lachica-Aliño, P., Munro, P., Christensen, V., Pauly, D. (Eds.), Assessment, Management and Future Directions for Coastal Fisheries in Asian Countries. World Fish Center Conference Proceedings, vol. 67. , pp. 313–332.

Allen, R.R., 1971. Relation between production and biomass. Journal of the Fisheries Research Board of Canada 28, 1573–1581.

Angelini, R., Vaz-Velho, F., 2011. Ecosystem structure and trophic analysis of Angolan fishery landings. Scientia Marina 75, 309–319.

Arce, C.A., 2006. Nuevos estimadores de Mortalidad Natural en Invertebrados marinos de áreas de surgencia. M.Sc. Thesis. Universidad de Concepción, Chile, pp. 35.

Badaracco, M.T., Molinet, R., M.Sc. Thesis 1991. Flujos de materia en el sistema demerso-pelágico de Golfo Triste, Edo Carabobo, Venezuela. Universidad Simón Bolivar, pp. 191.

Baeta, F., Costa, M.J., Cabral, H., 2009. Changes in the trophic level of Portuguese landings and fish market price variation in the last decades. Fisheries Research 97, 216–222.

Baldó, F., Drake, P., 2002. A multivariate approach to the feeding habits of small fishes in the Guadalquivir Estuary. Journal of Fish Biology 61, 21–32.

Barausse, A., Duci, A., Mazzoldi, C., Artioli, Y., Palmeri, L., 2009. Trophic network model of the Northern Adriatic Sea: analysis of an exploited and eutrophic ecosystem. Estuarine Coastal and Shelf Science 83, 577–590.

Bosc, E., Bricaud, A., Antoine, D., 2004. Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. Global Biogeochemical Cycles 18, http://dx.doi.org/10.1029/2003GB002034.

Boyle, P., Rodhouse, P., 2005. Cephalopods: Ecology and Fisheries. Blackwell Science Ltd., Oxford.

Brey, T., 2001. Population Dynamics in Benthic Invertebrates. A Virtual Handbook. http://thomas-brey.de/science/virtualhandbook

Bundy, A., 2001. Fishing on ecosystems: the interplay of fishing and predation in Newfoundland-Labrador. Canadian Journal of Fisheries and Aquatic Sciences 58, 1153–1167.

Cammen, L.M., 1980. Ingestion rate: an empirical model for aquatic deposit feeders and detritivores. Oecologia 44, 303–310.

Christensen, V., 1995. Ecosystem maturity—towards quantification. Ecological Modelling 77 (1), 3–32.

Christensen, V., 1996. Managing fisheries involving predator and prey species. Reviews in Fish Biology and Fisheries 6, 417–442.

Christensen, V., Pauly, D., 1992. ECOPATH II a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling 61, 169–185.

Christensen, V., Pauly, D., 1993. Trophic models of aquatic ecosystems. In: ICLARM Conf. Proc. vol. 26, p. 390.

Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling 172 (2-4), 109–139.

Christensen, V., Walters, C.J., 2011. Progress in the use of ecosystem models for fisheries management. In: Christensen, V., Maclean, J. (Eds.), Ecosystem Approaches to Fisheries: A Global Perspective. Cambridge University Press, Cambridge, pp. 189–205.

Christensen, V., Walters, C.J., Pauly, D., 154 pp 2005. Ecopath with Ecosim: a User's Guide, November 2005 edition. Fisheries Centre, University of British Columbia, Vancouver, Available online at www.ecopath.org

Christensen, V., Walters, C.J., Pauly, D., Forest, R., 2008. Ecopath with Ecosim 6 User Guide, November 2008 edition. Fisheries Centre, University of British Columbia, Vancouver, pp. 235.

Coll, M., Santojanni, A., Palomera, I., Tudela, S., Arneri, E., 2007. An ecological model of the Northern and Central Adriatic Sea: Analysis of ecosystem structure and fishing impacts. Journal of Marine Systems 67, 119–154.

Coll, M., Bahamon, N., Sarda, F., Palomera, I., Tudela, S., Suuronen, P., 2008. Ecosystem effects of improved trawl selectivity in the South Catalan Sea (NW Mediterranean). Marine Ecology Progress Series 355, 131–147.

Coll, M., Carreras, M., Cornax, M.J., Massutí, E., Morote, E., Pastor, X., Quetglas, T., Silva, L., Sobrino, I., Torres, M.A., Tudela, S., Harper, S., Zeller, D., Pauly, D., 2013a. Estimates of total fisheries removals from the Spanish Mediterranean Sea and Gulf of Cadiz (1950-2008). Fisheries Centre Research Report (in press).

Coll, M., Libralato, S., 2012. Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. Fish and Fisheries 13, 60–88.

Coll, M., Navarro, J., Olson, R., Christensen, V., 2013b. Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. Deep Sea Research II: Topical Studies in Oceanography, http://dx.doi.org/10.1016/j.dsr2.2013.08.020.

Coll, M., Navarro, J., Palomera, I., 2013c. Ecological role of the endemic Starry ray *Raja asterias* in the NW Mediterranean Sea and management options for its conservation. Biological Conservation 157, 108–120.

Coll, M., Palomera, I., Tudela, S., Sardà, F., 2006. Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. Journal of Marine Systems 59, 63–96.

Cortés, E., 1999. Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science 56, 707–717.

Cury, P.M., Christensen, V., 2005. Quantitative Ecosystem Indicators for Fisheries Management. ICES Journal of Marine Science 62, 307–310.

Ebert, D.A., Bizzarro, J.J., 2007. Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). Environmental Biology of Fishes 80, 221–237.

FAO, 2008. Fisheries Management. 2. The Ecosystem Approach to Fisheries. 2.1 Best Practices in Ecosystem Modelling for Informing an Ecosystem Approach to Fisheries. Suppl. 2, Add. 1. FAO, Rome, 78 pp.

Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. Journal of Theoretical Biology 56, 363–380.

Fraser, H.M., Greenstreet, S.P.R., Piet, G.J., 2007. Taking account of catchability in groundfish survey trawls: implications for estimating demersal fish biomass. ICES Journal of Marine Science 64, 1800–1819.

Froese, R., Pauly, D., 2012. FishBase. World Wide Web Electronic Publication. www.fishbase.org, version (08/2012).

Garcia, S.M., Cochrane, K.L., 2005. Ecosystem approach to fisheries: a review of implementation guidelines. ICES Journal of Marine Science 62 (3), 311–318.

Garcia, S.M., Zerbi, A., Aliaume, C., Do Chi, T., Lasserre, G., 2003. The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook. In: FAO Fisheries Technical Paper. No. 443. FAO, Rome, 71 pp.

García-Isarch, E., Juárez, A., Ruiz, J., Romero, Z., Jiménez, P., Baldó, F., 2006. Spawning and nursery habitat of the wedge sole *Dicologlossa cuneata* (Moreau, 1881) in the Gulf of Cadiz (SW Spain). Scientia Marina 70, 123–136.

Gil, J., Canoura, J., Vila, Y., Sobrino, I., 2008. Information about grenadiers from bottom trawl surveys in the Gulf of Cadiz. In: Orlov, A.M., Iwamoto, T. (Eds.), Grenadiers of the World Oceans: Biology, Stock Assessment, and Fisheries. Amer Fisheries Soc, Bethesda, pp. 49–63.

Guénette, S., Christensen, V., Pauly, D., 2001. Fisheries impacts on North Atlantic ecosystems: models and analyses. Fisheries Centre Research Reports 9 (4), 344.

Heymans, J.J., Baird, D., 2000. Network analysis of the northern Benguela ecosystem by means of NETWRK and ECOPATH. Ecological Modelling 131, 97–119.

Heymans, J.J., Coll, M., Libralato, S., Christensen, V., 2012. Ecopath theory, modelling and application to coastal ecosystems. In: Wolanski, E., McLusky, D.S. (Eds.), Treatise on Estuarine and Coastal Science. Elsevier, pp. 93–113.

Heymans, J.J., Guénette, S., Christensen, V., 2007. Evaluating network analysis indicators of ecosystem status in the Gulf of Alaska. Ecosystems 10, 488–502.

Heymans, J.J., Shannon, L.J., Jarre, A., 2004. Changes in the northern Benguela ecosystem over three decades: 1970, 1980 and 1990. Ecological Modelling 172, 175–195.

Holt, A.R., Godbold, J.A., White, P.C.L., Slater, A.M., Pereira, E.G., Solan, M., 2011. Mismatches between legislative frameworks and benefits restrict the implementation of the Ecosystem Approach in coastal environments. Marine Ecology Progress Series 434, 213–228.

Huertas, I.E., Navarro, G., Rodríguez-Gálvez, S., Lubián, L.M., 2006. Temporal patterns of carbon dioxide in relation to hydrological conditions and primary production in the northeastern shelf of the Gulf of Cadiz (SW Spain). Deep-Sea Research II 53, 1344–1362.

ICES, 2009. Report of the Working Group on Acoustic and Egg Surveys for Sardine and Anchovy in ICES Areas VIII and IX (WGACEGG) , 16–20 November 2009. Lisbon, Portugal. ICES CM 2009/LRC:20, 181 pp.

ICES, 2010a. Report of the Working Group on the Assessment of Southern Shelf Stocks of Hake, Monk and Megrim (WGHMM), 5–11 May 2010 , Bilbao, Spain. ICES CM 2010/ACOM:11, 599 pp.

ICES, 2010b. Report of the Working Group on Anchovy and Sardine (WGANSA) , 24–28 June 2010. Vigo, Spain. ICES CM 2010/ACOM:16, 290 pp.

ICES, 2010c. Report of the Working Group on Widely Distributed Stocks (WGWIDE) , 28 August–3 September 2010. Vigo, Spain. ICES CM 2010/ACOM:15, 612 pp.

Iglesias, M., Miquel, J., Oñate, D., Díaz, N., Tugores, P., Ramos, F., Millán, M., 2009. Acoustic assessment and distribution of the main pelagic fish species in the ICES Subdivision IXa South during the ECOCÁDIZ 0609 Spanish survey (June-July 2009). In: WD to the ICES Working Group on Acoustic and Egg Surveys for Sardine and Anchovy in ICES Areas VIII and IX (WGACEGG), p. 42 pp.

Innes, S., Lavigne, D.M., Earle, W.M., Kovacs, K.M., 1987. Feeding Rates of Seals and Whales. Journal of Animal Ecology 56 (1), 115–130.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–637.

Jarre-Teichmann, A., 1998. The potential role of mass balance models for the management of upwelling ecosystems. Ecological Applications 8 (1), 93–103.

Jarre-Teichmann, A., Christensen, V., 1998. Comparative analyses of trophic flows in upwelling systems: global vs. local changes. In: Durand, M.H., Cury, P., Medelssohn, R., Roy, C., Bakun, A., Pauly, D. (Eds.), Local vs. Global Changes in Upwelling Ecosystems. ORSTOM, Paris, pp. 423–443.

JA, 2013. Junta de Andalucía Consejería de Agricultura y Pesca. http://www.juntadeandalucia.es/agriculturaypesca/portal/ (access April 2013).

Jennings, S., Dulvy, N.K., 2005. Reference points and reference directions for size-based indicators of community structure. ICES Journal of Marine Science 62, 397–404.

Jiménez, M.P., 2002. Aplicación de análisis multivariantes para la obtención y estandarización de esfuerzos pesqueros en pesquerías multiespecíficas. Las pesquerías demersales del Golfo de Cádiz. PhD Thesis. Universidad de Cádiz, 328 pp.

Jiménez, M.P., Piñeiro, C., Sobrino, I., Ramos, F., 2001. Studies on age determination and growth pattern of the wedge sole *Dicologlossa cuneata* (Moreau,1881) in the Spanish waters of the Gulf of Cadiz (southwest Iberian Peninsula). Boletín Instituto Español de Oceanografía 13 (3–4), 279–285.

Jiménez, M.P., Romero, Z., Sobrino, I., 2005. Los recursos pesqueros del Golfo de Cádiz. Sector Litoral de Huelva. Informe Interno del Instituto Español de Oceanografía, 120 pp.

Jiménez, M.P., Sobrino, I., Ramos, F., 1998. Distribution pattern, reproductive biology, and fishery of the wedge sole *Dicologlossa cuneata* in the Gulf of Cadiz, southwest Spain. Marine Biology 131, 173–187.

Jiménez, M.P., Sobrino, I., Ramos, F., 2004. Objective methods for defining mixed-species trawl fisheries in Spanish waters of the Gulf of Cadiz. Fisheries Research 67, 195–206.

King, M., 1995. Fisheries Biology, Assessment and Management. Fishing New Books. Blackwell Science, pp. 341.

Lassalle, G., Lobry, J., Le Loc'h, F., Bustamante, P., Certain, G., Delmas, D., Dupuy, C., Hily, C., Labry, C., Le Pape, O., Marquis, E., Petitgas, P., Pusineri, C., Ridoux, V., Spitz, J., Niquil, N., 2011. Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf food web: implications for ecosystem management. Progress in Oceanography 91, 561–575.

Leontief, W.W., 1951. The Structure of the U.S. Economy. Oxford University Press, New York.

Librarato, S., Christensen, V., Pauly, D., 2006. A method for identifying keystone species in food web models. Ecological Modelling 195 (3–4), 153–171.

Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. Ecology 23, 399–418.

Mackinson, S., Daskalov, G., 2008. An Ecosystem Model of the North Sea to Support an Ecosystem Approach to Fisheries Management: Description and Parameterisation, vol. 142. Sci. Ser. Tech Rep., Cefas Lowestoft, pp. 195 pp.

Mertz, G., Myers, R.A., 1998. A simplified formulation for fish production. Canadian Journal of Fisheries and Aquatic Sciences 55, 478–484.

Millán, M., 1992. Descripción de la pesquería de cerco en la Región Suratlántica Española y Atlántico-Norte Marroquí. Informes Técnicos, vol. 136. Instituto Español de Oceanografía, pp. 70.

Millán, M., 1999. Reproductive characteristics and condition status of anchovy Engraulis encrasicolus L. from the Bay of Cadiz (SW Spain). Fisheries Research 41, 73–86.

Moloney, C.L., Jarre, A., Arancibia, H., Bozec, Y.M., Neira, S., Roux, J.P., Shannon, L.J., 2005. Comparing the Benguela and Humboldt marine upwelling ecosystems with indicators derived from inter-calibrated models. ICES Journal of Marine Science 62, 493–502.

Morissette, L., 2007. Complexity, Cost and Quality of Ecosystem Models and their Impact on Resiliance: A Comparative Analysis, with Emphasis on Marine Mammals and the Gulf of St. Lawrence. PhD. Thesis. University of British Columbia, Vancouver, 260 pp.

Navarro, G., Ruiz, J., 2006. Spatial and temporal variability of phytoplankton in the Gulf of Cadiz through remote sensing images. Deep-Sea Research II 53, 1241–1260.

Navarro, G., Ruiz, J., Huertas, I.E., García, C.M., Criado-Aldeanueva, F., Echevarría, F., 2006. Basin-scale structures governing the position of the deep fluorescence maximum in the Gulf of Cádiz. Deep Sea Research Part II: Topical Studies in Oceanography 53, 1261–1281.

Neira, S., Arancibia, H., 2004. Trophic interactions and community structure in the upwelling system off Central Chile (33-39 degrees S). Journal of Experimental Marine Biology and Ecology 312, 349–366.

Nilsson, S.G., Nilsson, I.N., 1976. Numbers, food consumption, and fish predation by birds in Lake Möckeln, southern Sweden. Ornis Scandinavica 7, 61–70.

Odum, E.P., 1969. The strategy of ecosystem development. Science 104, 262–270.

Odum, E.P., 1971. Fundamentals of Ecology. W. B. Saunders Co., Philadelphia, pp. 574.

Okey, T.A., Banks, S., Born, A.R., Bustamante, R.H., Calvopina, M., Edgar, G.J., Espinoza, E., Farina, J.M., Garske, L.E., Reck, G.K., Salazar, S., Shepherd, S., Toral-Granda, V., Wallem, P., 2004. A trophic model of a Galapagos subtidal rocky reef for evaluating fisheries and conservation strategies. Ecological Modelling 172, 383–401.

Patterson, K., 1992. Fisheries for small pelagic species: an empirical approach to management targets. Reviews in Fish Biology and Fisheries 2, 321–338.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. Journal du Conseil international pour l'Exploration de la Mer 39, 175–192.

Pauly, D., 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM, Studies and Reviews 8, 325 pp.

Pauly, D., 2010. 5 Easy Pieces. The Impact of Fisheries on Marine Ecosystems. Island Press, Washington, USA, ISBN 9781597267199, pp. 193 pp.

Pauly, D., Christensen, V., 1995. Primary production required to sustain global fisheries. Nature 374, 255–257.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998a. Fishing down marine food webs. Science 279, 860–863.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. Nature 418, 689–695.

Pauly, D., Christensen, V., Sambilay, V., 1990. Some Features of Fish Food Consumption Estimates Used by Ecosystem Modelers. ICES CM 1990/G:17, Session O, 9 pp.

Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science 57 (3), 697–706.

Pauly, D., Soriano-Bartz, M., Palomares, M.L., 1993. Improved construction, parameterization and interpretation of steady-state ecosystem models. In: Christensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM Conference Proceedings No. 26. , pp. 1–13.

Pauly, D., Trites, A.W., Capuli, E., Christensen, V., 1998b. Diet composition and trophic levels of marine mammals. ICES Journal of Marine Science 55, 467–481.

Pèrez, N., Silva, L., Arujo, H., Aranda, G., 2005. Results on the Spanish Gulf of Cadiz Discard Pilot Survey (ICES Division IXa for 2005). Informe Interno del Instituto Español de Oceanografía., pp. 24 pp.

Piatkowski, U., Pierce, G.J., Da Cunha, M.M., 2001. Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. Fisheries Research 52, 5–10.

Piñeiro, C., 2011. Edad y crecimiento de la merluza europea Merluccius merluccius (Linnaeus, 1758) del Noroeste de la Península Ibérica: Evolución de un paradigma. PhD Thesis. Universidad de Vigo, 202 pp.

Piñeiro, C., Saínza, M., 2003. Age estimation, growth and maturity of the European hake (Merluccius merluccius (Linnaeus, 1758)) from Iberian Atlantic waters. ICES Journal of Marine Science 60, 1086–1102.

Piroddi, C., Bearzi, G., Christensen, V., 2010. Effects of local fisheries and ocean productivity on the northeastern Ionian Sea ecosystem. Ecological Modelling 221, 1526–1544.

Plagányi, E.E., 2007. Models for an Ecosystem Approach to Fisheries. FAO Fisheries Technical Paper No. 477. Report no 477. FAO, Rome, 108 pp.

Polovina, J.J., 1984. Model of a coral reef ecosystems I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs 3 (1), 1–11.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the Quest for Keystones. BioScience 46, 609–620.

Prieto, L., Navarro, G., Rodríguez-Gálvez, S., Huertas, I.E., Naranjo, J.M., Ruiz, J., 2009. Oceanographic and meteorological forcing of the pelagic ecosystem on the Gulf of Cadiz shelf (SW Iberian Peninsula). Continental Shelf Research 29, 2122–2137.

Puig, P., Canals, M., Company, J.B., Martín, J., Amblas, D., Lastras, G., Palanques, A., Calafat, A.M., 2012. Ploughing the deep sea floor. Nature 489, 286–289.

Ramos, F., Gil, J., Torres, M.A., Silva, L., Vila, Y., Sánchez, R., Jiménez, M.P., Baldó, F., Fernández-Salas, F., Rueda, L.M., Díaz del Rio, V., Vázquez, J.T., López-González, N., Lens, S., Bellas, J., Besada, V., Viñas, L., González-Quijano, A., Franco, A., Fumega, J., 2012. Estrategias Marinas. Demarcación Marina Sudatlántica.

Parte I. Marco General: Características de la demarcación marina. Ministerio de Agricultura, Alimentación y Medio Ambiente (MAGRAMA), Instituto Español de Oceanografía (IEO), Centro de Estudios de Puertos y Costas-Centro de Estudios y Experimentación de Obras Públicas (CEPYC-CEDEX), Madrid, pp. 127 pp.

Ramos, F., Sobrino, I., Jiménez, M.P., 2006. Cartografía temática de caladeros de la flota de arrastre en el Golfo de Cádiz. Inf. Tecn. 45/96. Consejería de Agricultura y Pesca. Junta de Andalucía, pp. 29 pp.

Reul, A., Muñoz, M., Criado-Aldeanueva, F., Rodríguez, V., 2006. Spatial distribution of phytoplankton 13 μm in the Gulf of Cadiz in relation to water masses and circulation pattern under westerly and easterly wind regimes. Deep-Sea Research II 53, 1294–1313.

Rochet, M.J., Trenkel, V.M., 2003. Which community indicators can measure the impact of fishing? A review and proposals. Canadian Journal of Fisheries and Aquatic Sciences 60, 86–99.

Samhouri, J., Levin, P., Harvey, C., 2009. Quantitative evaluation of marine ecosystem indicator performance using food web models. Ecosystems 12, 1283–1298.

Sánchez, F., Olaso, I., 2004. Effects of fisheries on the Cantabrian Sea shelf ecosystem. Ecological Modelling 172, 151–174.

Shannon, L.J., Moloney, C.L., Jarre, A., Field, J.G., 2003. Trophic flows in the southern Benguela during the 1980 and 1990. Journal of Marine Systems 39, 83–116.

Sherman, K., Hempel, G. (Eds.), 2009. The UNEP Large Marine Ecosystem Report: A Perspective on Changing Conditions in LMEs of the World's Regional Seas. UNEP Regional Seas Report and Studies No. 182. United Nations Environment Programme, Nairobi, Kenya.

Shin, Y.J., Shannon, L.J., 2010. Using indicators for evaluating, comparing and communicating the ecological status of exploited marine ecosystems. 1. The IndiSeas project. ICES Journal of Marine Science 67, 686–691.

Silva, L., Gil, J., Sobrino, I., 2002. Definition of fleet components in the Spanish artisanal fishery of the Gulf of Cadiz (SW Spain ICES division IXa). Fisheries Research 59, 117–128.

Silva, L., Vila, Y., Torres, M.A., Sobrino, I., Acosta, J.J., 2011. Cephalopod assemblages, abundance and species distribution in the Gulf of Cadiz (SW Spain). Aquatic Living Resources 24, 13–26.

Silva, L., Sobrino, I., Ramos, F., 1998. Fishing exploitation pattern of the common octopus, Octopus vulgaris Cuvier, 1797 in the Spanish waters of the Gulf of Cadiz. In: Report of the Working group on Cephalopod Fisheries and Life History. ICES CM 1998/G:7., pp. 39–45.

Sobrino, I., 1998. Biología y pesca de la gamba blanca (Parapenaeus longirostris, Lucas 1846) en el Atlántico Nororiental. PhD Thesis. Universidad de Sevilla, 218 pp.

Sobrino, I., Baldó, F., García-González, D., Cuesta, J.A., Silva-García, A., Fernández-Delgado, C., Arias, A.M., Rodríguez, A., Drake, P., 2005. The effect of estuarine fisheries on juvenile fish observed within the Guadalquivir Estuary (SW Spain). Fisheries Research 76, 229–242.

Sobrino, I., Burgos, C., 2009. Informe de la campaña ARSA 1109. MIEMO, Instituto Español de Oceanografía, 62 pp.

Sobrino, I., Jiménez, M.P., Ramos, F., Baro, J., 1994. Descripción de las pesquerías demersales de la Región Suratlántica Española, vol. 151. Boletín Instituto Español de Oceanografía, 76 pp.

Sobrino, I., Juarez, A., Rey, J., Romero, Z., Baro, J., 2011. Description of the clay pot fishery in the Gulf of Cadiz (SW Spain) for Octopus vulgaris: Selectivity and exploitation pattern. Fisheries Research 108, 283–290.

Sobrino, I., Silva, L., Bellido, J.M., Ramos, F., 2002. Rainfall, river discharges and sea temperature as factors affecting abundance of two coastal benthic cephalopod species in the Gulf of Cádiz (SW Spain). Bulletin of Marine Science 71, 851–865.

Stergiou, K.I., Karpouzi, V.S., 2002. Feeding habits and trophic levels of Mediterranean fish. Reviews in Fish Biology and Fisheries 11, 217–254.

Torres, M.A., Jiménez, M.P., Sobrino, I., Vila, Y., 2007. Deep fish communities of the Gulf of Cadiz (SW Spain). In: Buj, I., et al. (Eds.), Proc. XII European Congress of Ichthyology. Cavtat (Dubruvnic).

Torres, M.A., 2013. Modelización Ecológica del Golfo de Cádiz. Relaciones Tróficas, Estructura de la Comunidad e Impacto de la Pesca en el Ecosistema. University of Cadiz, in press.

Torres, M.A., Ramos, F., Sobrino, I., 2012. Length-weight relationships of 76 fish species from the Gulf of Cadiz (SW Spain). Fisheries Research 127–128, 171–175.

Torres, M.A., Sobrino, I., 2012. Feeding habits of European hake Merluccius merluccius (L. 1758) in the Gulf of Cadiz. In: Final Proceedings in International Symposium of the Marine Science (ISMS), Cádiz (Spain).

Trenkel, V.M., Skaug, H., 2005. Disentangling the effects of capture efficiency and population abundance on catch data using random effects models. ICES Journal of Marine Science 62, 1543–1555.

Tsagarakis, K., Coll, M., Giannoulaki, M., Papakonstantinou, C., Machias, A., 2010. Food-web traits of the North Aegean Sea continental shelf (Eastern Mediterranean, Greece) and comparison with other Mediterranean ecosystems. Estuarine Coastal and Shelf Science 88, 233–248.

Tudela, S., Coll, M., Palomera, I., 2005. Developing an operational reference framework for fisheries management on the basis of a two-dimensional index of ecosystem impact. ICES Journal of Marine Science 62, 585–591.

Turner, S.J., Thrush, S.F., Hewitt, J.E., Cummings, V.J., Funnell, G., 1999. Fishing impacts and the degradation or loss of habitat structure. Fisheries Management and Ecology 6, 401–420.

Ulanowicz, R.E., 1986. Growth and Development: Ecosystem Phenomenology. Springer Verlag (reprinted by iUniverse, 2000), New York, 203 pp.

Ulanowicz, R.E., 1995. Ecosystem trophic foundations: lindeman exonerata. Chapter 21 p. In: Patten, B.C., Jørgensen, S.E. (Eds.), Complex Ecology: The Part-Whole Relation in Ecosystems. Englewood Cliffs, Prentice Hall, pp. 549–560.

Ulanowicz, R.E., Norden, J.S., 1990. Symmetrical overhead in flow and networks. International Journal of Systems Science 21 (2), 429–437.

Ulanowicz, R.E., Puccia, C.J., 1990. Mixed trophic impacts in ecosystems. Coenoses 5, 7–16.

Velasco, E.M., Del Árbol, J., Baro, J., Sobrino, I., 2011a. Age and growth of the Spanish chub mackerel Scomber colias off southern Spain: a comparison between samples from the NE Atlantic and the SW Mediterranean. Revista de Biología Marina y Oceanografía 46, 27–34.

Velasco, E.M., Jiménez-Tenorio, N., Del Árbol, J., Bruzón, M.A., Baro, J., Sobrino, I., 2011b. Age, growth and reproduction of the axillary seabream,

Pagellus acarne, in the Atlantic and Mediterranean waters off southern Spain. Journal of the Marine Biological Association of the United Kingdom 91, 1243–1253.

Vila, Y., Burgos, C., Sánchez, R., 2009. Informe de la campaña ARSA 0309. MIEMO. Instituto Español de Oceanografía, pp. 89.

Vila, Y., Silva, L., Millán, M., Ramos, F., Gil, J., Jiménez, M.P., 2004. Los recursos pesqueros del Golfo de Cádiz: estado actual de explotación. Informes Técnicos. Instituto Español de Oceanografía, pp. 200 pp.

Vila, Y., Silva, L., Torres, M.A., Sobrino, I., 2010. Fishery, distribution pattern and biological aspects of the common European squid Loligo vulgaris in the Gulf of Cadiz. Fisheries Research 106, 222–228.

Wolff, M., Koch, V., Bautista, J., Vargas, J.A., 1998. A trophic flow model of the Golfo the Nicoya, Costa Rica. Revista de biologia tropical 46, 63–79.