Community Ecology 20(2): 161-171, 2019
1585-8553 © Akadémiai Kiadó, Budapest
DOI: 10.1556/168.2019.20.2.6

Trophic interactions in the coastal ecosystem of Morocco: An Ecopath approach

H. Essekhyr, K. Khalil, Z. Damsiri, G. Derhy and K. Elkalay[1]

Laboratory of Applied Sciences for the Environment and Sustainable Development, School of Technology, Cadi Ayyad University, Essaouira Al Jadida, Route d'Agadir, BP 383, Essaouira, Morocco
[1]Corresponding author. E-mail: k.elkalay@uca.ma Telephone: +(212) 524792776 / 524792064

Keywords: Ecopath model; Food chain; Moroccan Atlantic coast; Trophic flux.

Abstract: The Moroccan Atlantic coast is considered as one of the richest fishing areas in the world, having rich biodiversity, and supporting the fisheries sector. However, studies have shown that the ecosystem presently suffers from overexploitation of fishery resources and environmental degradation. To quantify these impacts, the characterization of the ecosystem is essential. In this work, an Ecopath model (EwE), which assumes steady-state and mass-balanced conditions for the Moroccan Atlantic coast ecosystem, was developed and balanced. Network analysis included in the Ecopath software package was used to estimate trophic interactions and the maturity of the ecosystem. The model consisted of 29 functional groups. The results showed a Total System Throughput (TST) which is comprised mainly of flows into detritus, followed by export, consumption, and respiration. Systemic indicators, suggest that the Moroccan Atlantic coast is an immature and developing ecosystem. Further observations on the functioning and dynamics of the ecosystem are discussed.

Nomenclature: Stanford and Guénette (2001).

Abbreviations: DRH–Département des Ressources Halieutiques; EBFM–Ecosystem-Based Fisheries Management; EwE–Ecopath with Ecosim; INRH–Fisheries Research Institute; MTI–Mixed Trophic Impacts;TST–Total System Throughput.

Introduction

Coastal areas have been described as complex ecosystems formed by interactions between natural and societal systems. They provide important services to society and contribute more than 60% of the total economic value of the biosphere (Martinez et al. 2007). They also play important ecological (Beck et al. 2001, Hughes et al. 2005) economic and social roles (Balmford et al. 2002).

The conservation and sustainable use of these resources can help to improve the Moroccan economy. The Moroccan maritime zone is about 66 000 km^2 and the exclusive economic zone is about 1 170 000 km^2 (Chafik 2014). The Canaries currents provide upwelling in the Moroccan Atlantic coast (Belvèze 1984). The seasonal upwelling of the northern zone (26 ° N and 33 ° N) and the permanent upwelling of the southern zone (21 ° N-26 ° N), provides the nutrients for the ecosystem and makes the Moroccan Atlantic coast one of the richest fishing areas in the world (INRH 2015).

This has given the fishing industry the privilege of being an important sector for the country's economy since the 1930s. In the 1980s, this industry expanded considerably with two distinct subsectors, including coastal fishing and high sea fishing. In recent decades, the fishery sector continues to grow. However, the sector suffers from many problems that need to be addressed to ensure sustainable use of resources and environmental management. Over this period, particularly from the 1980s, the concept of fishery management evolved from a single species management paradigm to a more comprehensive approach called ecosystem-based fisheries management (EBFM) (Christensen and Pauly 1993).

One of the most important tools used for EBFM is Ecopath (EwE), a tool we have employed to evaluate and assess the challenges of fisheries management on the Atlantic Coast of Morocco. The EWE software (www.ecopath.org) is widely used for ecosystems, fisheries and resources modeling in marine and aquatic ecosystems worldwide (Christensen and Walters 2011, Colleter et al. 2015). There are more than 400 ecosystem models already published, (Colleter et al. 2015) and more than 700 citations of these models per year (Coll et al. 2006).

EWE allows the description of food webs and their interactions, the simulation of overfishing scenarios (Wang et al. 2016), and description and analyses of the flow of food webs (Odum 1969, Coll et al. 2006). EwE also makes it possible to simulate the trophic dynamics of an ecosystem under different management strategies (Eddy et al. 2017, Kumar et al. 2016). Recently, EWE is being used to study the effects of ocean warming (Bentley et al. 2017, Serpetti et al. 2017), invasive species (Corrales et al. 2017), and pollutants (Tierney et al. 2018, Walters and Christensen 2018). Ecopath models have also been used in comparative ecosystem studies (Rodriguez-Zaragoza et al. 2016) by employing them for ecological network analysis (Christensen and Pauly 1992).

Only one ecosystem model using EWE was published for the Moroccan Atlantic coast (Stanford and Guénette

2001) and it mainly attempted to summarize data available for this ecosystem. In this study, we developed and describe an Ecopath model with 29 functional groups representing the main trophic components of the ecosystem along the Atlantic Coast of Morocco. In our model we describe ecological groups based on their trophic roles in the ecosystem, and also on the economic importance of these groups.

This study makes important contributions to ecosystem modeling of the Atlantic coasts and also contributes to increased understanding of the functioning and structure of the ecosystem. Moreover, we also aim in this study to describe the trophodynamic and thermodynamic links of the ecosystem of the Moroccan Atlantic coast, because understanding the dynamics of this ecosystem is fundamental for the sustainable management of marine resources and for future projections of the impact of fishing on the functioning of this ecosystem. We compare results of our model to models of the Gulf of Cadiz (Torres et al. 2013) and Gran Canaria (Couce-Montero et al. 2015), using the ecological indices of the models.

Materials and methods

Study area

The Atlantic coast of Morocco covers more than 3000 km, between latitudes 36 °N (Cape Spartel) and 21 °N (Cape Blanc), and has a north-south-west orientation. Following the historical development of the fishery (INRH/DRH 2015), three major fishing areas are identified: the northern area between Tanger and Safi, the center area between Safi and Cape Boujdour, and the southern area between Cape Boujdour and White Cape in Laguira (Fig. 1). Most of the fishery resources distributed over these three areas are concentrated in the central and southern Atlantic, with 80% of catches by volume represented by small pelagic fishes (INRH/DRH 2016).

The food-web model

The Moroccan Atlantic coast food web model was constructed using EWE software version 6.4.4, to quantify trophic interactions and energy flows among the compartments of the ecosystem. The parameterization of the model was based on satisfying two master equations with Equation 1 describing production, consumption and biomass terms for functional groups in the ecosystem:

$$(P/Bi).Bi = Yi + \\ + \Sigma_j Bj.(Q/Bi).DCij + Ei + BAi + (P/Bi).Bi(1-EEi), \quad (1)$$

where (P/Bi) is the production/biomass ratio of (i), Bi is the biomass of group (i); Yi is the total fishery catch rate of (i), Bj is the biomass of the predators (j), Q/Bi is the food consumption per unit biomass of the predators (j); $DCij$ is the fraction (%) of (i) in the diet of (j), Ei the net migration rate of (i) (emigration–immigration), BAi is the biomass accumulation rate of (i), EEi is the ecotrophic efficiency of (i), and j=1,...,n with n as the number of species.

The second equation describes the energy balance of each group:

$$Qi = Pi + Ri + Ui \;, \quad (2)$$

where Qi is the consumption of a prey (i) from the system; Pi is the production consumed by predators, or exported out of the system, or converted into detritus; Ri is the respiration of (i), and Ui is the non-assimilated food of (i).

Functional groups

The Moroccan Atlantic coast model includes 29 functional groups. Groupings were based on habitats, size, trophic roles of individual species in the ecosystem, data availability, and commercial importance. It is convenient to separate commercial fish groups by size to reduce cannibalism (Stanford et al. 2001). The 29 functional groups are commercial pe-

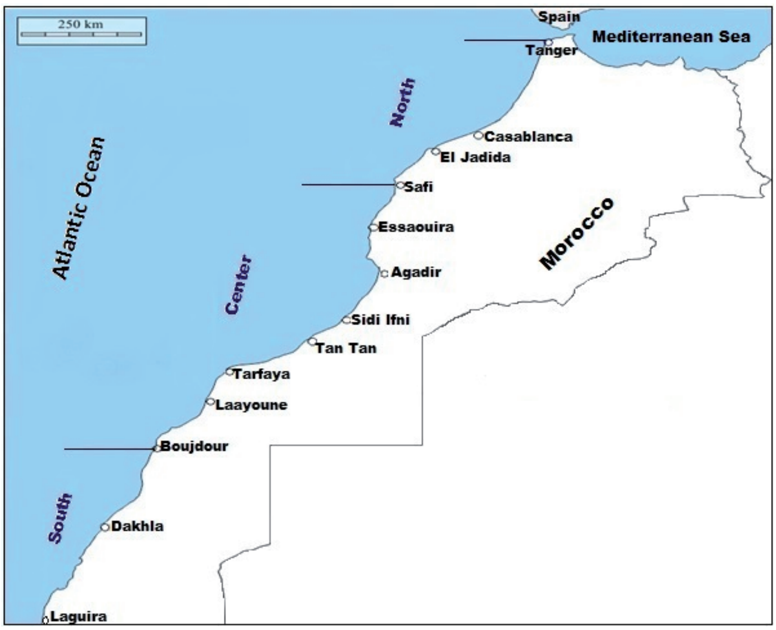

Figure 1. Map illustrating the Moroccan Atlantic coast with three fishing areas: Northern area (between Tanger and Safi), center area (between Safi and Boujdour) and southern area (between Boujdour and Laguira).

lagic sharks, small demersal sharks, commercial rays, large pelagic, commercial large demersal sharks and rays, small deep-water benthic, tunas, commercial very large demersal, large demersal, large bathypelagic, commercial large deep-water benthic, medium pelagic, commercial large demersal, commercial medium demersal, very large demersal, small bathypelagic, small demersal, large deep-water benthic, commercial medium demersal, medium pelagic, sardines, and mesopelagic prey species. Six groups of invertebrates were included, including lobsters, cephalopods, shrimp, detrital feeders and herbivores, small and large zooplankton. The other groups are primary producers and detritus.

Model parametrization

Input parameters. In the development of an EwE model, it is necessary to include at least three of the four main input parameters the ratio of production/biomass (*P/B*), the consumption/biomass ratio (*Q/B*), biomass (*B*) and the ecotrophic efficiency (*EE*) (Christensen and Pauly 1993, Christensen et al. 2005). *EE* which is the proportion of functional group that is, used in the system was generally the parameter that was estimated by *EwE*.

Biomass (B). The biomass was expressed in t km^{-2} of wet weight. The information on trophic groups was difficult to provide for the Moroccan Atlantic coast. Biomass estimates were left, for Ecopath to estimate, by assuming an ecotrophic efficiency of 0.95 based on Ricker (Ricker 1968) assumed for some groups as a qualified hypothesis, assuming natural mortality (M) to be low. This value was used in the Polovina model (Polovina 1984) and later models.

Production/biomass (P/B)

The Production/Biomass (P/B) ratio is expressed per year^{-1}. The P/B ratio is equivalent to total mortality (Z), otherwise expressed as sum of fishing mortality (F) and natural mortality (M). F was calculated as the ratio of catches and biomass ($F = Y/B$) mainly for commercial species. Natural mortalities for fish groups were calculated using Pauly's equation (1980):

$$\log(M) = -0.066 - 0.279*\log(L\infty) + 0.6543*\log(K) + 0.4634*\log(T)\ , \quad (3)$$

where $L\infty$ is the fish length (total length in cm), K is the Von Bertalanffy growth parameter (year^{-1}), and T (°C) is the mean annual water temperature in which the population is maintained.

Consumption rates (Q/B). This parameter (*Q/B*) expresses the number of times a given population consumes its own weight per year. This quantity was estimated for each consumer eco-group following the empirical relationship suggested by Palomeras and Pauly (1998):

$$Q/B = 10^{6.37} * 0.0313\ Tk * W_{inf} 0.168 * 1.38\ Pf * 1.89\ Hd, \quad (4)$$

where Tk = 1000*(Temperature in °C 273.1) –1, W_{inf} = asymptotic weight in g, Pf = 1 for predators and planktivores, zero for herbivores and detritivores, zero for omnivores; Hd = zero for carnivores and omnivores, 1 for detritivores and herbivores. *Winf = a Linfb* is taken from the location closest to Morocco in FishBase (Froese and Pauly 2000).

Diet composition

Dietary data for fish groups were determined from FishBase (www.fishbase.org) and the literature (Gibson and Ezzi 1987, MacPherson and Roel 1987, Bennett 1989, Sala and Ballesteros 1997, Carrasson and Matallanas 1998).

Model balancing

Following the best practices in Ecopath modeling (Heymans et al. 2016), balancing an Ecopath model requires adjusting the input parameters and diets of groups (Table 1) such that none of the EE values exceeds 1 (Table 2). Most *P/Q* ratios (gross efficiency, *GE*) calculated should be in the range between 0.1 and 0.3; respiration/assimilation rate values are < 1.0; respiration rate/biomass values range from 1 to 10 for fish compartments and 50 to 100 for groups with higher turnover rates (higher *P/B* and *Q/B* values). Once balanced, the model can be used, to study the feeding behavior and strategy for each compartment using the Omnivory Index (Christensen et al. 2008).

Results

We analyzed the food webs structure, measured and quantified the overall state of ecosystem development and trophic interactions (Ulanowicz 1980, Borrett et al. 2018), by using the Finn's Cycling Index, total Primary Production/total respiration (TPP/TR), total Primary Production/total biomass (TPP/TB), and Total biomass/total system throughput (TB/TST). We also quantified the direct and indirect trophic effects between network nodes using the Mixed trophic impact parameter (Ulanowicz and Puccia 1990). Furthermore, we used Libralato et al. (2006) and Valls et al. (2015) keystoneness index to identify species with the greatest influence in the food web in relation to their biomasses (Paine 1995).

Analysis of the functional groups and input parameters

Configuration of the Ecopath model was based on available ecological information and fishing data for Moroccan continental shelf fisheries. Input parameters and resulting output of the balanced model are shown in Table 2. A total of 29 functional groups represent the Moroccan Atlantic coast ecosystem, organized into four discrete trophic levels (TL) from 1 to 4. The highest TL are large bathypelagic, pelagic sharks, and tunas (Table 2). Trophic flows between the different functional groups of the ecosystem are presented in Figure 2. *EE* values are high for most fished groups except the top predators (large bathypelagic, pelagic sharks, tunas) whereas they are low for phytoplankton and detritus (Table 2).

Table 1. Diet composition matrix adjusted for the Moroccan Atlantic coast food web model.

	Prey \ predator	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**
1	Primary producers	1	0.58	0.32		0.5				0.088	0.21	0.25		0.14			0.035				0.04		0.1			0.006	0.005	
2	Sm. zooplankton		0.06	0.1						0.3	0.2		0.05	0.12			0.2		0.63	0.18	0.2	0.097	0.44	0.01			0.085	0.16
3	lg. zooplankton		0.1		0.47		0.079	0.016	0.001	0.18	0.26	0.25	0.09	0.15		0.03	0.25		0.38	0.59	0.18		0.38	0.043	0.16	0.003	0.0004	0.3
4	Shrimp			0.02			0.084	0.34	0.001	0.009	0.18	0.37	0.66	0.34		0.08	0.16			0.12	0.1		0.025	0.007	0.36	0.23		0.28
5	Lobsters						0.08				0.006	0.013																
6	Detrital feeders																										0.0002	0.007
7	Sm. deep-water benthic								0.05			0.006		0.005		0.001	0.01				0.007			0.034	0.001		0.08	
8	Lg. deep-water benthic																									0.001	0.032	
9	Comm Lg. deep-water benthic																											0.09
10	Sm. demersal				0.52		0.42		0.25	0.005	0.081	0.0002	0.05	0.088	0.27	0.067								0.02	0.027		0.004	0.027
11	Med. demersal						0.016		0.16			0.0002	0.022	0.004	0.27	0.19								0.047	0.018	0.037	0.07	
12	comm med. demersal						0.11	0.32	0.33			0.008	0.029	0.005	0.26	0.04								0.097	0.03	0.055	0.004	
13	Lg. demersal								0.09			0.001	0.031			0.13						0.057			0.004	0.038	0.006	
14	comm lg. demersal						0.01														0.05	0.024			0.026	0.053	0.0004	
15	V. lg. demersal																				0.007					0.029		
16	Comm v. lg. demersal								0.033				0.016			0.01								0.04	0.022	0.03	0.05	
17	Sm. bathypelagic											0.001	0.008				0.07	0.27						0.019	0.15	0.039		0.058
18	Lg. bathypelagic																	0.02						0.008	0.011			0.001
19	Mesopelagic prey								0.041		0.001	0.042					0.16			0.1	0.027			0.02	0.025			0.041
20	Med. pelagic								0.021							0.09	0.11					0.4		0.049		0.001		
21	comm med. pelagic															0.06		0.17				0.33		0.14		0.056	0.08	0.067
22	Lg. pelagic															0.075		0.17			0.028	0.04		0.048				
23	Sardines						0.2				0	0.038	0.031	0.082		0.12					0.28	0.05		0.21	0.023	0.044	0.17	0.02
24	Tunas																					0.0001		0.053	0.001	0.005	0.001	
25	Sm. demersal sharks rays													0.001		0.05										0.021	0.022	
26	Lg. demersal sharks rays																							0.003		0.004		
27	Pelagic sharks																									0.002		
28	Cephalopods			0	0.01			0.32	0.023		0.001	0.003	0.017	0.037	0.2	0.064		0.37			0.04			0.15	0.14	0.26	0.29	0.033
29	Detritus		0.26	0.56		0.37				0.26	0.028	0.021	0	0.006									0.05			0.091		
	Import					0.13				0.16	0.037	0	0	0.015							0.037					0.001		
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 2. The compartments and input parameters for the Moroccan Atlantic model. Parameter estimate by the model are in bold, including: trophic level (TL); biomass (B; t km^{-2}); production/biomass ratio (P/B; year^{-1}); consumption/biomass ratio (Q/B; year^{-1}); ecotrophic efficiency (EE); and P/Q is the production / consumption ratio (Lg=Large, Sm= Smal, V. Lg= very large).

Group name	Trophic level	B (t km^2)	P/B (year^{-1})	Q/B (year^{-1})	EE	P/Q	SOI
Lg. bathypelagic	4.59	0.24	0.44	4.34	**0.55**	**0.10**	0.01
Pelagic sharks	4.28	0.20	0.36	2.57	**0.02**	**0.14**	0.32
Tunas	4.27	0.06	0.64	3.77	**0.47**	**0.17**	0.29
Lg. Pelagic	4.18	**1.61**	0.78	3.21	0.95	**0.24**	0.24
Comm v. lg. demersa.	4.10	0.50	2.30	4.89	**0.29**	**0.47**	0.27
Comm lg. deep-water	3.98	**0.09**	0.53	4.47	0.95	**0.12**	0.12
V. lg. demersal	3.94	**0.12**	0.16	3.88	0.95	**0.04**	0.07
Lg. demersal sharks rays	3.85	0.20	0.32	3.20	**0.05**	**0.10**	0.70
Lg. deep-water benthic	3.80	**0.07**	0.27	2.98	0.95	**0.09**	0.28
Sm. deep-water benthic	3.72	**1.87**	0.35	2.17	**0.95**	**0.16**	0.11
Sm. demersal sharks rays	3.71	0.33	0.66	5.71	**0.74**	**0.12**	0.42
Comm med. pelagic	3.49	**3.45**	0.94	6.31	0.95	**0.15**	0.37
Sm. bathypelagic	3.46	**1.94**	1.77	12.65	0.95	**0.14**	0.37
Lobsters	3.42	**2.61**	0.28	5.85	**0.95**	**0.05**	0.06
Cephalopods	3.40	**1.22**	3.10	11.70	**0.95**	**0.26**	0.27
Lg. demersal	3.31	**1.68**	0.49	7.45	0.95	**0.07**	0.18
Med. pelagic	3.23	**4.66**	1.13	8.47	**0.95**	**0.13**	0.09
Comm lg. demersal	3.12	2.24	0.82	5.99	**0.07**	**0.14**	0.35
Mesopelagic prey	3.07	**4.42**	2.38	13.00	**0.95**	**0.18**	0.01
Comm med. demersal	2.94	1,86	1.26	7.92	**0.72**	**0.16**	0.42
Sardines	2.92	17.64	1.10	11.10	**0.52**	**0.10**	0.16
Med. demersal	2.89	3.61	0.69	8.56	0.95	**0.08**	0.28
Sm. demersal	2.62	**11.44**	1.45	10.96	**0.95**	**0.13**	0.29
Lg. zooplankton	2.18	**56.21**	6.00	25.00	0.95	**0.24**	0.17
Shrimp	2.12	**33.35**	1.70	11.33	**0.95**	**0.15**	0.11
Detrital feeders	2.00	**0.19**	0.55	2.16	**0.95**	**0.26**	0.01
Sm. zooplankton	2.00	**20.20**	25.00	90.4	**0.61**	**0.28**	
Primary producers	1.00	**102.50**	84.55		**0.32**		
Detritus	1.00	-			**0.10**		0.10

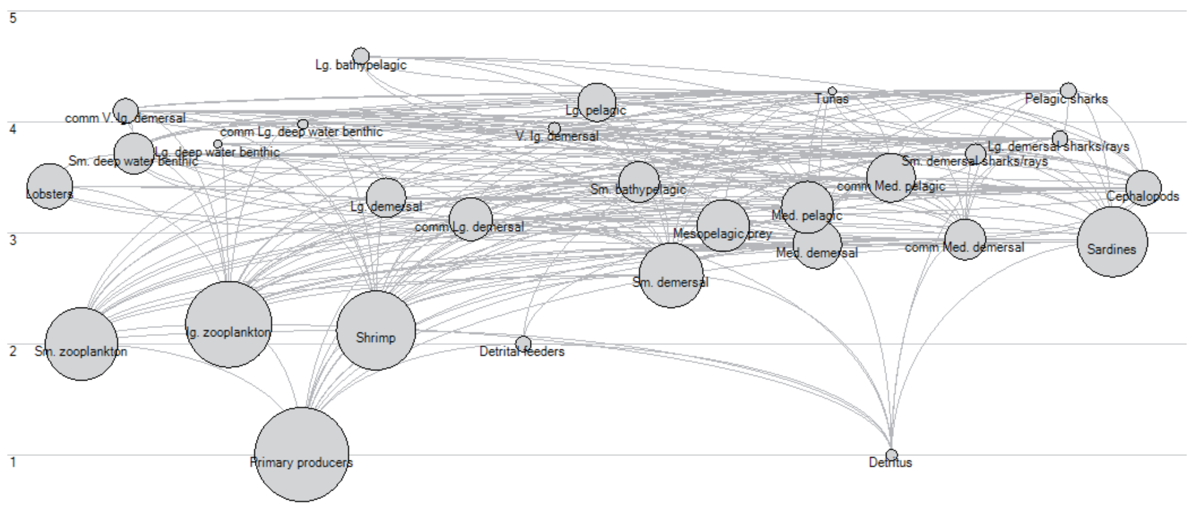

Figure 2. Flow diagram of the Moroccan Atlantic coast food web, representing the functional groups according to their trophic levels. The size of each circle is proportional to the biomass of each functional group. The lines represent the energy flow and the trophic level of the group denoted on the y-axis.

Analysis of trophic levels and representation of a Lindeman spine

A routine in Ecopath (Lindeman spine analysis) aggregates the entire system into discrete trophic levels (Christensenet al. 2005). Five discrete trophic levels were identified in this study with the Lindeman spine subroutine (Fig. 3). The Lindeman spine is a popular tool for analyzing flows between discrete trophic levels in the ecosystem (Christensen and Walters 2004, Christensenet al. 2005). The trophic flows (t km^{-2} yr^{-1}) in an ecosystem include consumption, production, respiration, exports, imports and flow to detritus. Analysis of our results shows that most groups of fish and invertebrates were at the TL II and III. The majority of flows within the ecosystem occur in the first two levels I and II, which together represent 63.44% of the total system throughput. TL I represents 45.42% of the total TST, while 18.02% is represented by TL II, which is mostly made up of small zooplankton (20.20 t km^{-2}), large zooplankton (56.21 t km^{-2}), and shrimp (33.35 t km^{-2}). These groups are very important in terms of biomass, comprising 40% of the total biomass excluding detritus.

Flows from primary producers and detritus were combined to evaluate trophic level transfer efficiency. The average transfer efficiency for the system is 11.7%. The highest transfer efficiency (TE) is for the TL II, and these decreases as the trophic levels increase (Fig. 3). Total biomass supported by the ecosystem excluding detritus was 274.47 t km^{-2} (Table 3).

Analysis of mixed trophic impacts and Keystone index

The analysis of mixed trophic impacts (Fig. 4) shows that some fish groups such as commercial large deep-water benthic, commercial large demersal, commercial very large demersal, and mesopelagic prey, have minimal or no impact on other groups due to their relatively low biomass or low Q/B ratios. On the other hand, among the fish groups, pelagic sharks, cephalopods, large demersal sharks rays and commercial very large demersal, all demonstrate impacts on a large number of groups in the system through predation or competition. Cephalopods have a negative impact on detrital feeder, commercial small bathypelagic, and medium pelagic.

Pelagic sharks have a significant negative impact on benthic fishes, notably on large deep-water benthic species. Commercial very large demersal have negative impacts on most of the other demersal groups, while large demersal sharks rays produce positive impacts on demersal fish, and negative impact on the deep-water benthic groups. Keystone indices results (Fig. 5) reveal that the group pelagic shark have the highest total impact and total MTI in this ecosystem, followed by the commercial very large demersal and large demersal shark rays.

Ecosystem indicators

The system summary statistics for the model are summarized in Table 3, and compared with similar Atlantic ecosystems–Gulf of Cadiz (Torres et al. 2013), and the Gran Canaria ecosystem (Couce-Montero et al. 2015). Total system throughput (TST), which is the sum of all flows in the model and an overall measure of the "ecological size" of the system was 19248.77 t km^{-2} $year^{-1}$ of which consumption accounted for 21.78%, export 29.86%, respiration 15.26% and flows into detritus 33.1%. The net system production is 5725.11 t km^{-2} $year^{-1}$. The value of TPP/TR ratio in this study is 2.95, while TPP/TB and B/TST ratios were 31.56 and 0.01 respectively (Table 3). Total biomass (excluding detritus) of the system is 274.46 t km^{-2}, connectance index (the ratio between the number of existing links between the groups and the number of theoretically possible connections), and the system omnivory index value for Moroccan Atlantic coast, were 0.30 and 0.20 respectively (Table 3).

The Finn's cycling index, FCI (Finn 1976), is the proportion of the total system throughput (TST) recycled in the system.

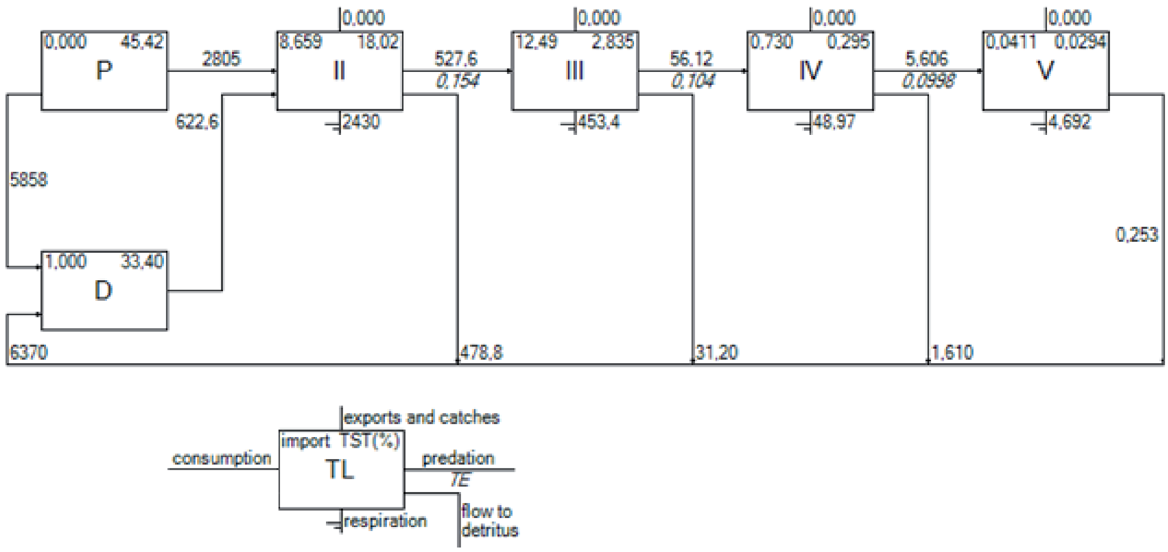

Figure 3. Lindeman spine representation of trophic flows of Moroccan Atlantic coast model. Primary producers (P) and detritus (D) are separated to clarify the representation. TST is the total system throughput.

Table 3. Summary statistics for the Moroccan Atlantic coast food web model, and comparison with the Spanish ecosystems of the Gulf of Cadiz (Torres et al. 2013) and the Gran Canaria ecosystem (Couce-Montero et al. 2015).

Parameters	Morocco	Cadiz	Gran Canaria	Units
Ecosystem properties				
Sum of all consumption (TC)	4192.04	1946.9	2684.883	t km^{-2}.y^{-1}
Sum of all exports (TE)	5748.10	2233.7	1189.410	t km^{-2}.y^{-1}
Sum of all respiratory flows (TR)	2937.90	955.1	1009.388	t km^{-2}.y^{-1}
Sum of all flows into detritus (TD)	6370.73	2599.2	2268.251	t km^{-2}.y^{-1}
Total system throughput (TST)	19248.77	7734.9	7151.932	t km^{-2}.y^{-1}
Sum of all production (TP)	9636.11	3704.4	3052.556	t km^{-2}.y^{-1}
Total net primary production (NPP)	8663.01	3187.7	2192.650	t km^{-2}.y^{-1}
Net system production (NSP)	5725.11	2232.6	1183.262	t km^{-2}.y^{-1}
Total biomass (excluding detritus) (TB	274.47	80.02	253.566	t km^{-2}
Ecosystem maturity				
Total primary production/total respiration (TPP/TR)	2.95	3.3	2.172	-
Total primary production/total biomass (TPP/TB)	31.56	39.8	8.647	-
Total biomass/total throughput (TB/TST)	0.01	0.01	0.035	y^{-1}
Food web structure				
Connectance Index (CI)	0.30	0.25	0.152	-
System Omnivory Index (SOI)	0.20	0.18	0.340	-
Finn'sCycling Index (FCI)	1.36	3	12.60	% TST
Finn's mean path length (FML)	2.22	2.43	3.253	-
Ascendancy (AS)	41.00	41.1	25.5	%
System Overhead (SO)	59.0	49.2	74.5	%
Model reability				
Transfer efficiency total	11.7	14.9	15.8	%

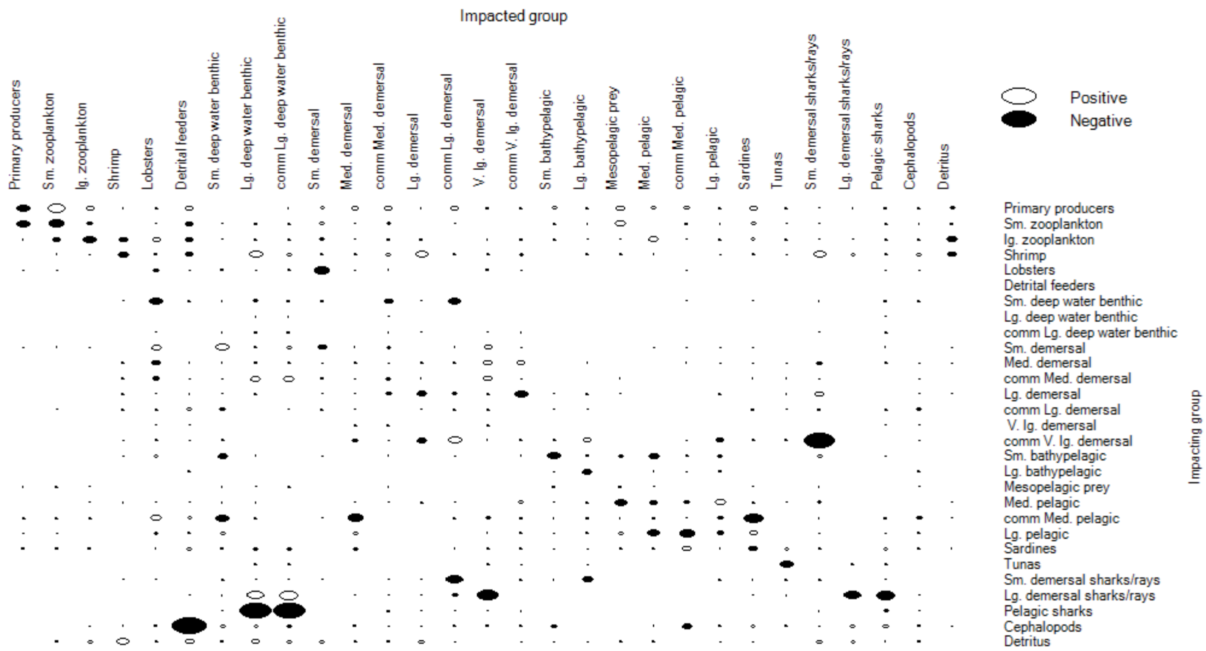

Figure 4. Mixed Trophic Impact (MTI) analysis of the Moroccan Atlantic coast food web. The size of an ellipse represents the size of the trophic impact of the functional groups (white ellipses indicate positive impact, while black ellipses show negative impact).

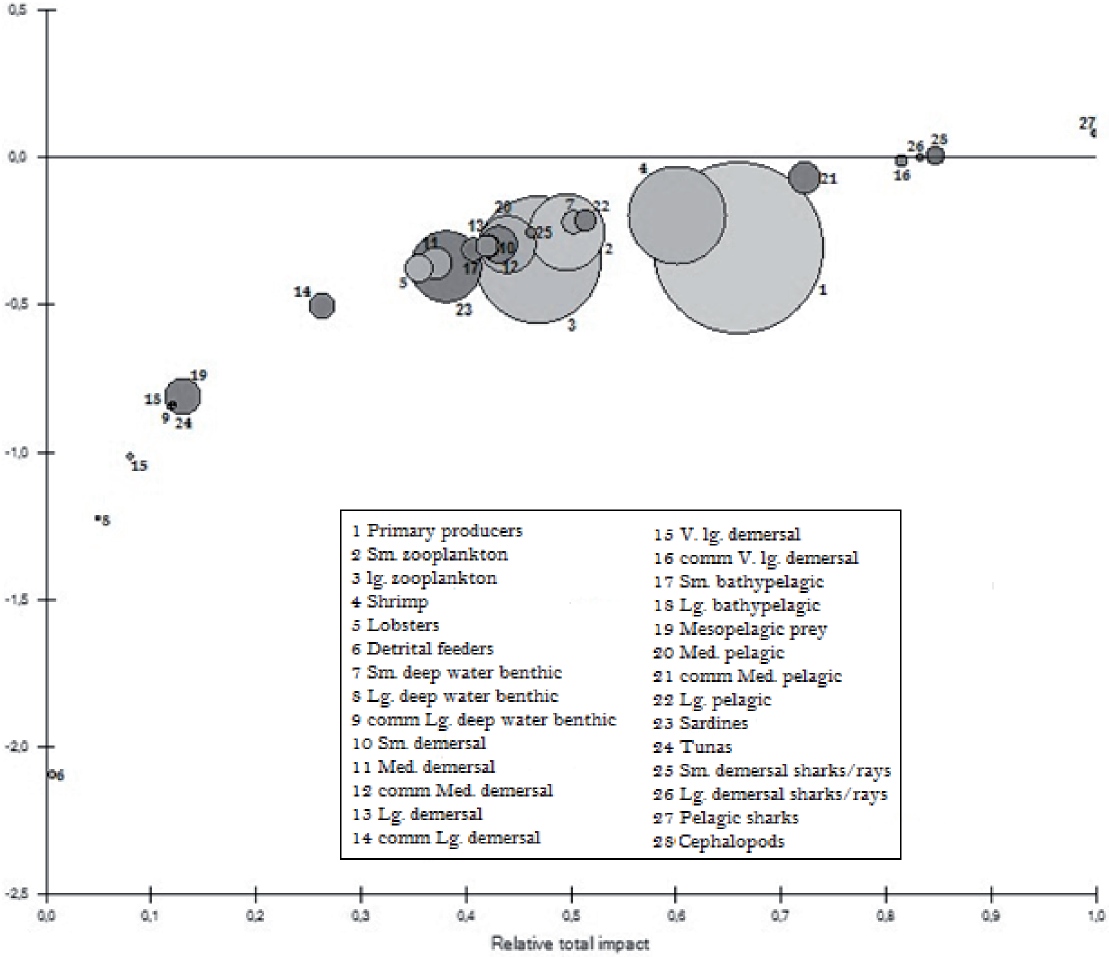

Figure 5. Keystone Index (KI) analysis of the Moroccan Atlantic coast web. The size of the circles is proportional to the biomass of each functional group indicator.

This index is related to ecosystem maturity (Christensen and Pauly 1993). Odum (1969) suggested that as systems mature, they become more dependent on detritivory than herbivory. The TPP/TR ratio is a functional index of the relative maturity of an ecosystem (Odum 1969). The ratio approaches 1 as a system matures, or in other words, energy fixed tends to be balanced by the energy cost of maintenance in the mature stages.

The FCI estimated for the system was 1.36% of the total system throughput, while the value of mean path length (the average number of groups that a flow passes through) (Finn, 1976), was 2.22% and the ascendancy, a measure of maturity that depicts the degree of development of an ecosystem was estimated to be 41.0%, while 59.0% was for the overhead, a measure that provides limits on how much the ascendency can increase and reflects how resilient an ecosystem is to unexpected perturbations (Ulanowicz 1986).

Discussion

Pedigree index

The data for this study were obtained from published literature and models that describe similar consumer organisms (Stanford et al. 2001). We used the pedigree index to quantify uncertainty associated with input values in the model (Christensen et al. 2008). The average value for this model was 0.13 on a scale of 0 to 1. This model will make an important contribution and fill gaps in our current knowledge about trophic interactions documented for the Moroccan Atlantic coast and the ecosystem functions therein that are currently poorly understood.

Structure and trophic levels flows

Four discrete trophic levels were identified in this study. The low EE for phytoplankton suggests that a large percentage of this group enter detritus. Ecotrophic efficiency (EE) values are high for most fish groups (EE > 0.95), except for the top predators (large bathypelagic, pelagic sharks, tunas), which indicates that production of each group was extensively used up by both predation and or exploitation by fisheries. The mean transfer efficiency (TTE) was 11.7% approaching the value of 10% estimated by Pauly and Christensen (1995). Primary producers and detritus, located at TL I, generated more than 23% of the TST, followed by TL II which was composed mainly of zooplankton (small and large) and shrimp, that contributed 15.4% of the TST. Also based on the high consumption values, our model shows the important link between TL II and detritus.

Ecological roles and trophic interactions

In general, most groups had negative within group impact reflecting increased competition for resources among conspecifics, looping effects, and perhaps cannibalism (Fig. 4). Most groups directly impact their main prey through predation, e.g., an increase in large zooplankton leads to a decrease in the biomass of the small zooplankton. The groups, pelagic sharks, cephalopods, large demersal sharks rays, and commercial very large demersal, demonstrated impacts on a largest number of groups in the system through predation or competition.

Biomass increase in pelagic sharks can have a negative impact on deep-water benthic groups, and deep-water benthic groups have a negative impact on some demersal groups, revealing the importance of coupled benthic–demersal and benthic–pelagic interactions. The MTI results also revealed that the main groups influencing the Moroccan Atlantic coast food web were at the top of the food web (pelagic shark, cephalopods, and large demersal sharks rays). These groups have direct impacts on the fish and invertebrate groups modeled in this study (Fig. 4), highlighting the importance of the groups in the ecosystem and suggesting possible top-down effects within the ecosystem. The MTI and keystone indices show the relevance of the pelagic sharks group on the functioning of the system of the Moroccan Atlantic coast model (Figs 4 and 5), Commercial very large demersal and large demersal sharks rays can also be considered keystone groups as these also show a relatively high total impact with a high total MTI (Fig. 5).

Ecosystem properties

We present a comparison between the model for Moroccan Atlantic coast and two adjacent ecosystems – the Gulf of Cadiz (Torres et al. 2013) and the ecosystem of Gran Canaria (Couce-Montero et al. 2015) (Table 3), using network analysis for each model. The similarities and differences observed between these three exploited ecosystems, may be explained by the nature and different number of functional groups included in each study, and the study period. The estimated value of TST for the Moroccan Atlantic coast was 19248,7 t km^{-2} y^{-1} (Compare to 7734.9 for the Gulf of Cadiz, and 7151.9 for Gran Canaria) indicating that the size in terms of total flows for this system is high compared to the two other ecosystems.

TST for the ecosystem we modeled mainly comprised 33.1%, flows to detritus, 29.86% exportation, 21.78% consumption and 15.26% respiration, and it was similar to the other ecosystems we compared to. The ratio of total net primary production to total respiration (TPP / TR) is an indicator of the state of maturity of the system (Odum 1971). Based on 41 Ecopath models analysis, the TPP/TR ratio ranges from 0.8 to 3.2 (Christensen and Pauly 1993). The value obtained for this model was 2.95 which indicates an underdeveloped stage for the Moroccan Atlantic coast, affirmed by the low value of *TB/TST* = 0.01 y^{-1}. The same results were obtained for the Gulf of Cadiz and the Gran Canaria ecosystem. On the other hand, the value of *TPP/TB* = 31.56 was slightly lower than those obtained in the Gulf of Cadiz (Torres et al. 2013) but higher than those obtained in the Gran Canaria ecosystem. These results show low levels of biomass accumulation within the Gulf of Cadiz and Moroccan Atlantic coast when compared to the Grand Canaria ecosystem.

The omnivorous index (OI) and the connectance index (CI) can also be used to assess the maturity of an ecosystem since the system at the stage of maturity can change from linear to web-like (Odum 1971). The system omnivory index (SOI) was highest for large demersal sharks rays followed by commercial medium demersal and small demersal sharks rays (*SOI* > 0.4), suggesting dietary flexibility. Mesopelagic prey, lobsters, very large demersal and medium pelagic functional groups showed the lowest value (*SOI* < 0.1) (Table 2). The SOI for the Moroccan Atlantic coast was 0.20; a value similar to those obtained for Gulf of Cadiz (Torres et al. 2013), suggesting that both systems are linear more than web-like networks. The connectance index (CI) of the Moroccan Atlantic coast showed the highest value of the three compared models, reflecting more complexity and linkages within the food web.

The average mean path length (MPL), of 2.22, was similar to those obtained for Gulf of Cadiz, 2.43, suggesting that the flow crosses a similar number of groups, but relatively lower than those for Gran Canaria 3.25. Ascendancy (% A) 41.0% for the Moroccan Atlantic coast, which is similar to the value obtained for Gulf of Cadiz, suggesting less complexity and large flows through a few channels. The Gran Canaria model (Couce-Montero et al. 2015), showed the highest value of overhead 74% compared to the Moroccan Atlantic 59%, and the Gulf of Cadiz 49.2% (Torres et al. 2013), suggesting that this system is more resilient to unexpected perturbations when compared to the other two ecosystems. The results obtained from the global indicators for the three ecosystems suggest that the ecosystem of Moroccan Atlantic coast as well as the Cadiz Gulf ecosystem show less advanced stages of development and maturation when compared to Gran Canaria, and are less complex and resistant to unexpected perturbations

Conclusions

This article presents an ecological model to characterize the ecosystem of the Moroccan Atlantic coast. In this model, we assumed equilibrium and mass balance conditions for the system during the year 2018. In this respect, we consider that a one-year period is an appropriate time scale, that is, it is short enough to avoid the impacts of environmental changes in the system. Biomass estimation for most groups is the main source of uncertainty for this model. New, up-to-date, data can be added to this model to improve the results. This study is an attempt to provide a summary of knowledge on biomass, consumption, production, food web and trophic structure. The model also provides a tool for quantitatively studying the trophic state of the ecosystem by describing how matter and energy propagate through the food web.

Parametrized results follow that most fish and invertebrate groups were at the second and third trophic levels, respectively. The ecosystem structure along five discrete TLs is dominated by lower trophic levels. The average transfer efficiency for this ecosystem is 11.7%. Ecological indicators related to the theory of ecosystem development indicate that the ecosystem is not yet a mature system and is resistant to perturbations. This characteristic can partly be explained by the energy transfer estimation through the food web that suggests about 20% of the energy produced by the primary producers in this area is needed to sustain the current fisheries (Kifani et al. 2008).

It is noteworthy that, out of the 11 exploited stocks that are included in fishing access agreements with the European Union (EU), 9 are overfished and 2 are unassessed. A recent study showed that ecosystems negatively affected by anthropogenic activities undergo changes in their networks and reduction in development, organization, and ecosystem health (Arias González et al. 2017). The results from the ecological indicators we obtained from the Moroccan Atlantic coastal ecosystem revealed a general methodological problem with EwE that cannot be solved; since we assume equilibrium for our modeled ecosystem for a period of 1 year while the system is obviously developing. It is therefore essential to specify the period over which the model should have predictive power. However, the choice of an appropriate time scale for models of upwelling systems such as the Moroccan Atlantic Coast seems debatable because of the fundamental role of variability in mediating spatial and temporal scales (Shannon and Jarre-Teichmann 1999). The model we present is a baseline representation to which new data can be added in the future to improve model results, and for continued dynamic simulation and exploration of fishery policies in Moroccan Atlantic Coastal fisheries.

Acknowledgements: This work was financially supported by the CNRST (project, PPR). The authors would like to acknowledge also K. Erzini, S. Libralato, S. Ray with his Phd student, E. Daili and T. Adebola for the improvement of the paper.

References

Arias-González, J.E., Fung, T., Seymour, R.M., Garza-Pérez, J.R., Acosta-González, G. Bozec, Y-M. and Johnson, C.R. 2017. A coral–algal phase shift in Mesoamerica not driven by changes in herbivorousfish abundance. *PLoS ONE* **??**

Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R.E., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J., Munro, K.,... Myers, N., Naeem, S., Paavola, J., Rayment, M., Rosendo, S., Roughgarden, J., Trumper, K. and Turner, R.K. 2002. Economic reasons for conserving wild nature. *Science* 297:950–953

Beck, Jr. M.W., Heck, K.L., Able, K. W., Childers, D., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G:, Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F. and Weinstein, M.P. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 8:633–641.

Belvèze, H. 1984. Biologie et dynamique de populations de sardine peuplant les cotes atlantique marocaines et propositions pour aménagement des pecheries. *Thèse de doctorat d'Etat*, Université de Bretagne Occidental.

Bennett, B.A. 1989. The diets of fish in three south-western Cape estuarine systems. *S. Afr. J. Zool.* 24(3):163–177.

Bentley, J.W., Serpetti, N. and Heymans, J.J. 2017. Investigating the potential impacts of ocean warming on the Norwegian and Barents Seas ecosystem using a time-dynamic food-web model. *Ecol. Model*. 360:94–107.

Borrett, S.R., Sheble, L., Moody, J. and Anway, E.C. 2018. Bibliometric review of ecological network analysis: 2010–2016. *Ecol. Model*. 382:63–82.

Carrasson, M. and Matallanas, J. 1998. Feeding habits of *Alepocephalus rostratus* (Pisces: Alepocephalidae) in the Western Mediterranean Sea. *J. Mar. Biol. Assoc. UK*. 78:1295–1306.

Chafik, A. 2014. Littoral, Activités humaines et stratégie de développement durable: Cas du Maroc. Rapport d'expertise élaboré pour le compte du Projet du Grand Ecosystème marin du Courant des Canaries (*CCLME*) mai 2014.

Christensen, V. and Pauly, D. 1993. Trophic models of aquatic ecosystems. In: *ICLARM Conf. Proc*., 26, 390 pp.

Christensen, V. and Walters, C.J. 2004. Ecopath with Ecosim: Methods, capabilities and limitations. *Ecol. Model*. 172:109–139.

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

Christensen, V., Walters, C.J. and Pauly, D. 2005. Ecopath with Ecosim: a user's guide. Fish Centre, Univ. British Columbia, Vancouver. November 2005 edition.

Christensen, V., Walters, C., Pauly, D. and Forrest, R. 2008. Ecopath with Ecosim version 6 User Guide. Fish. Centre, Univ. British Columbia, Vancouver. 281:1–235.

Coll, M., Shannon, L.J., Moloney, C.L., Palomera, I. and Tudela, S. 2006. Comparing trophic flows and fishing impacts of a NW Mediterranean ecosystem with coastal upwelling systems by means of standardized models and indicators. *Ecol. Model*. 198:53–70.

Colleter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D. and Christensen, V. 2015. Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecol. Model*. 302:42–53.

Corrales, X., Ofir, E., Coll, M., Goren, M., Edelist, D., Heymans, J.J. and Gal, G. 2017. Modeling the role and impact of alien species and fisheries on the Israeli marine continental shelf ecosystem. *J. Mar. Syst*. 170:88–102.

Couce-Montero, L., Christensen, V. and Castro, J.J. 2015. Effects of small-scale and recreational fisheries on the Gran Canaria ecosystem. *Ecol. Model*. 312:61–76.

Eddy, T.D., Lotze, H.K., Fulton, E.A., Coll, M., Ainsworth, C.H., de Araújo, J.N., Bulman, C.M., Bundy, A., Christensen, V., Field, J.C., Gribble, N.A., Hasan, M., Mackinson, S. and Townsend, H. 2017. Ecosystem effects of invertebrate fisheries. *Fish Fish*. 18:40–53.

Finn, J.T. 1976. Measures of ecosystem structure and function derived from analysis of flows. *J. Theor. Biol*. 56:363–380.

Froese, R. and D. Pauly (eds), 2000. *FishBase 2000.Concepts, Design and Data Sources.* ICLARM, Los Baños, Laguna, Philippines.

Gibson, R. N. and Ezzi, I. A. 1987. Feeding relationships of a demersal fish assemblage on the west coast of Scotland. *J. Fish Biol.* 31:55–69.

Heymans, J.J., Coll, M., Link, J.S., Mackinson, S., Steenbeek, J., Walters, C. and Christensen, V. 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecol. Model*. 331:173–184.

Hughes, T., Bellwood, D., Folke, C., Steneck, R. and Wilson, J. 2005. New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol Evol* , 20(7):380–386.

INRH/DRH. 2015. *Rapport annuel de l'etat des stocks et des pêcheries marocaines* 2015.

INRH/DRH. 2016. *Rapport annuel de l'etat des stocks et des pêcheries marocaines* 2016.

Kifani, S., Masski, H. and Faraj, A. 2008. The need of an ecosystem approach to fisheries: The Moroccan upwelling-related resources case. *Fish. Res*. 94:36–42.

Kumar, R., Varkey, D. and Pitcher, T. 2016. Simulation of zebra mussels (*Dreissena polymorpha*) invasion and evaluation of impacts on Mille Lacs Lake, Minnesota: An ecosystem model. *Ecol. Model.* 331:68–76.

Libralato, S., Christensen, V. and Pauly, D. 2006. A method for identifying keystone species in food web models. *Ecol. Model.* 195:153–171.

MacPherson, E. and Roel, B. A. 1987. Trophic relationships in the demersal fish community off Namibia. *S. Afr. J. Mar. Ssci.* 5:585–596.

Martínez, M.L., Intralawan, A., Vázquez, G., Pérez-Maqueo, O., Sutton, P. and Landgrave, R. 2007. The coasts of our world: Ecological, economic and social importance. *Ecol. Econ*. 63: 254–272.

Odum E.P. 1969. The strategy of ecosystem development. *Science*. 164(3877):262–270.

Odum E.P. 1971 . *Fundamentals of Ecology.* Saunders, Philadelphia.

Paine, R.T. 1995. A Conversation on refining the concept of keystone species. *Conserv. Biol*. 9:962–964.

Palomares, M.L.D. and Pauly, D. 1998. Predicting food consumption of fish populationsas functions of mortality, food type, morphometrics, temperature and salinity. *Mar. Freshwater Res*. 49:447–453.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *ICES J Mar Sci* 39(2):175–192.

Pauly, D. and Christensen, V. 1995. Primary production required to sustain global fisheries. *Nature* 376:279.

Polovina, J. J. 1984. Model of a coral reef ecosystem I. The Ecopath model and its application to French Frigate Shoals. *Coral Reefs*, 3:1–11.

Ricker, W. E. 1968. Food from the sea. In: *Resources and Man, a Study and Recommendation Report of the Committee on Resources and Man*. US National Academy of Sciences, W.H. Freeman, San Francisco. pp. 87–108.

Rodríguez-Zaragoza, L., Ortiz, M., Berrios, F., Campos, A., de Jesús-Navarrete, A., CastroPérez, J., Hernández-Flores, M., García-Rivas, M., Fonseca-Peralta, F. and Gallegos-Aguilar, E. 2016. Trophic models and short-term dynamic simulations for benthic-pelagic communities at Banco Chinchorro Biosphere Reserve (Mexican Caribbean): a conservation case. *Community Ecol.* 17:48–60

Sala, E. and Ballesteros, E. 1997. Partitioning of space and food resources by the fish genus *Diplodus* (Sparidae) in a Mediterranean rocky infralittoral ecosystem. *Mar. Ecol. Prog. Ser.* 152:273–283.

Serpetti, N., Baudron, A.R., Burrows, M.T., Payne, B.L., Helaouët, P., Fernandes, P.G. and Heymans, J.J. 2017. Impact of ocean warming on sustainable fisheries management informs the Ecosystem Approach to Fisheries. *Sci. Rep.* 7:1–15.

Shannon, L. J. and A. Jarre-Teichmann. 1999. A model of trophic flows in the northern Benguela upwelling system during the 1980s. *S. Afr. J. Mar. Sci.* 21: 349–366.

Stanford, R.J. and Guénette, S. 2001. A preliminary ecosystem model for the atlantic coast of Morocco in the mid-s1980s .In: Guénette, S., Christensen, V. and Pauly, D. (eds.), *Fisheries Impacts on North Atlantic Ecosystems: Models and Analyses. FCRR* 9(4), pp. 314–344.

Tierney, K.M., Heymans, J.J., Muir, G.K.P., Cook, G.T., Buszowski, J., Steenbeek, J., Walters, W.J., Christensen, V., MacKinnon, G., Howe, J.A. and Xu, S. 2018. Modelling marine trophic transfer of radiocarbon (14C) from a nuclear facility. *Environ. Model. Softw.* 102:138–154.

Torres, M.Á., Coll, M., Heymans, J.J., Christensen, V. and Sobrino, I. 2013. Food-web structure of and fishing impacts on the Gulf of Cadiz ecosystem (South-western Spain). *Ecol. Model*. 265:26–44.

Ulanowicz, R.E. 1980. An hypothesis on the development of natural communities. *J. Theor. Biol*. 85:223–245.

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

Valls, A., Coll, M., Christensen, V. and Ellison, A.M. 2015. Keystone species: Toward an operational concept for marine biodiversity conservation. *Ecol. Monogr*. 85:29–47.

Walters, W.J. and Christensen, V. 2018. Ecotracer: analyzing concentration of contaminants and radioisotopes in an aquatic spatial-dynamic food web model. *J. Environ. Radioactiv*. 181:118–127.

Wang, Y., Hu, J., Pan, H., Li, S. and Failler, P. 2016. An integrated model for marine fishery management in the Pearl River Estuary: Linking socio-economic systems and ecosystems. *Mar. Policy* 64:135–147.

Received March 9, 2019
Revised June 5, 2019
Accepted June 14, 2019