Community Ecology (2026) 27:57–75
https://doi.org/10.1007/s42974-026-00301-9

ORIGINAL ARTICLE

Structure and functioning of the Moroccan Mediterranean marine ecosystem: a trophic perspective

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Received: 1 June 2025 / Accepted: 5 January 2026 / Published online: 1 April 2026

Abstract

The Moroccan Mediterranean region has experienced significant development in various sectors, including tourism, fishing, industry, agriculture, and construction. However, the trophic functioning of its ecosystem and its vulnerability to these developments remain largely unexplored. To address this gap, an in-depth examination of the Moroccan Mediterranean Sea ecosystem was conducted using the Ecopath with Ecosim modelling approach from 2000 to 2003. This study aimed to describe the structure, functioning and state of the system. The model incorporated 40 functional groups, including 21 fish, 12 invertebrates, 2 primary producers, and 2 detritus groups, as well as individual groups for marine mammals, seabirds, and turtles. Analysis revealed that the functional groups were organized into five trophic levels, with swordfish and bluefin tuna occupying the highest level. Results also indicated that the ecosystem structure relies heavily on high flows into detritus and exports. Transfer efficiencies values are within the typical range for aquatic environments. The model's pedigree scored of 0.49 indicates that it was built from data of generally acceptable quality- a notable achievement given the limited availability of data for the Mediterranean Sea in Morocco. Across the entire study area, the total biomass of the modeled ecosystem (excluding detritus) was estimated at 93 $t \cdot km^{-2}$. Indicators of omnivory showed low values across most groups. Pelagic sharks, large pelagic fish, and hake were identified as ecologically important groups within the ecosystem.

Keywords Ecopath · Moroccan Mediterranean Sea · Food web · Trophic flow · Ecosystem dynamics · Ecosystem modelling · Ecosystem-based management (EBM)

Introduction

The Mediterranean Sea is the largest and deepest quasi-enclosed sea on Earth (Coll et al. 2010), bordered by southern Europe and Anatolia to the north, North Africa to the south, and the Levant to the east. Covering approximately 2,510,000 km^2 and stretching between latitudes 30° and 46° N (Zingone et al. 2021), it is connected to the Atlantic Ocean to the west via the narrow, 900-meter-deep Strait of Gibraltar. To the East, it connects to the Black Sea through the Dardanelles and the Bosphorus, while the Suez Canal, opened in 1869 and recently expanded, provides a link to the Red Sea in the southeast (Zingone et al. 2021). Although it represents just 0.32% of the ocean's total volume, the Mediterranean's geomorphological history supports high biodiversity, with 7–10% of all known marine species, a significant proportion of which are endemic (Garrabou et al. 2022).

Fisheries, valued at over 3 billion dollars, are a primary economic contributor to the Mediterranean region alongside tourism (Randone et al. 2017). However, Mediterranean fisheries have been significantly impacted by human activities for thousands of years (Lotze et al. 2010), including overfishing, coastal degradation, and pollution (Vilas et al.

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2020; Aboussalam et al. 2025). The consequences of these activities are evident: many commercial demersal species are heavily exploited or overfished, while non-commercial demersal species have experienced declines in abundance and biomass (Sardà et al. 1998; Colloca et al. 2013; Tsikliras et al. 2015; Vilas et al. 2020). Over 90% of assessed stocks are currently overexploited, contributing to a phenomenon known as "fishing down the food web" (Pauly et al. 1998; Petetta et al. 2021).

Located in northwest Africa and bordered by the North Atlantic and the Mediterranean Sea, Morocco has a substantial human population, many of whom rely on the Sea for their livelihood. With an extensive 3,500 km shoreline (Darasi and Aksissou 2019), Morocco boasts rich marine and terrestrial biodiversity, making it one of the most biodiverse nations in the Mediterranean Basin (Department of Environment, 2003Masski and De Stéphanis 2018; Mghili et al. 2022a, 2023). In recent decades, the Moroccan Mediterranean region has seen significant growth in tourism, construction, industry, agriculture, and fishing (Mghili et al. 2020). Despite its high coastal biodiversity and many endemic marine species (Department of Environment, 2003; Mghili et al. 2022a, 2022b), this region faces considerable challenges, mainly due to human activities, population growth, and economic development (Mghili et al. 2022b). These pressures have led to issues such as invasive species introductions, pollution, overexploitation of resources, and habitat destruction (Nachite et al. 2019; FAO, 2020; Mghili et al. 2020, 2022b; El Kabdani et al. 2025). The rising demands of tourism and global markets also increase the pressure on fishing communities to manage resources sustainably, with the risk of stock depletion due to overexploitation (Belhabib et al. 2013).

To better understand the functioning of this ecosystem, predict the effects of multiple drivers (e.g., overfishing, species invasions, pollution), and manage fisheries resources effectively, advancing towards system-level modelling is essential. In this context, the Ecopath with Ecosim (EwE) model, a software widely applied globally since the 1980 s, is instrumental in providing food web representation (Pauly et al. 2000; Christensen and Walters 2004). Numerous ecosystem modelling studies have focused on the Mediterranean Sea (Carrer and Opitz 1999; Pinnegar and Polunin 2004; Coll et al. 2008, 2013; Barausse et al. 2009; Libralato et al. 2010; Bănaru et al. 2013; Hattab et al. 2013; Michailidis et al. 2019; Corrales et al. 2020; García-Rodríguez et al. 2021; Keramidas et al. 2022; Sánchez-Zulueta et al. 2023). However, no Ecopath model has yet been applied specifically to the Moroccan Mediterranean Sea (MMS), while the Atlantic part of Morocco (Essekhyr et al., 2019; Damsiri et al., 2022) and nearby areas (Patrício and Marques 2006; Torres et al. 2013) have been modelled. To this end, this work aimed at developing the first food web reconstruction for the MMS. The food web is built using both a classical expert-based balancing approach in EwE and a novel approach based on Monte Carlo reconstruction of food webs. The aim of the work is to analyse the functioning and structure of the MMS, in terms of biomass and the entire food web, from primary producers to top predators.

Materials and methods

Study site

The Moroccan Mediterranean region lies between latitudes 35° and 36° north and longitudes 6° and 2° east (Srour et al. 2002) (Fig. 1). It is bounded by the Atlantic Ocean to the West, the North Western Mediterranean to the North and the South Western Mediterranean to the East. Its length is about 512 km, from Cape Spartel in the west to the Moroccan-Algerian border in the east. The region's 18,302 km^2 Exclusive Economic Zone (EEZ) includes the continental shelf (4933 km^2). 13 Marine Protected Areas span 222 km^2 (Marine Conservation Institute 2020), which is equivalent to 1% of Morocco's EEZ in the Mediterranean Sea (Belhabib et al. 2016). The sea depths are very irregular and the bottom relief is very uneven (Srour et al. 2002).

This region is not only a favored tourist destination but also supports a thriving fishing industry (Bouzekry et al. 2022). it harbors diverse fisheries resources (Zoubi 1999), and has seen significant changes in fishing practices since the 1980 s, resulting in an increase in the number of fishing units (Slimani and Hamdi 2004). In seven ports (M'diq, Jebha, Al Hoceima, Tangier, Nador, Ras Kebdana, Cala Iris), as well as in over ninety artisanal fishing grounds, fishing is the main commercial activity. In 2022, 40% of the Moroccan Mediterranean inshore fleet were made up of trawlers, 25% of longliners and 31% of seiners. The artisanal fleet numbers 2264 active units (El Arraf et al. 2024).

Modelling approach

The Ecopath with Ecosim (EwE) approach is widely used to model the aquatic ecosystems and to explore trophic organization (Polovina 1984; Pauly et al. 2000; Christensen and Walters 2004; Christensen et al. 2005). EwE software version 6.6.8 was applied to set up and represent the trophic mass-balanced model of the Moroccan Mediterranean Sea (MMS). In the EwE framework, the ecosystem's total biomass is distributed among different compartments. In this study, species with high economic and fisheries importance in Moroccan Mediterranean were represented as single-species functional groups to accurately capture their trophic

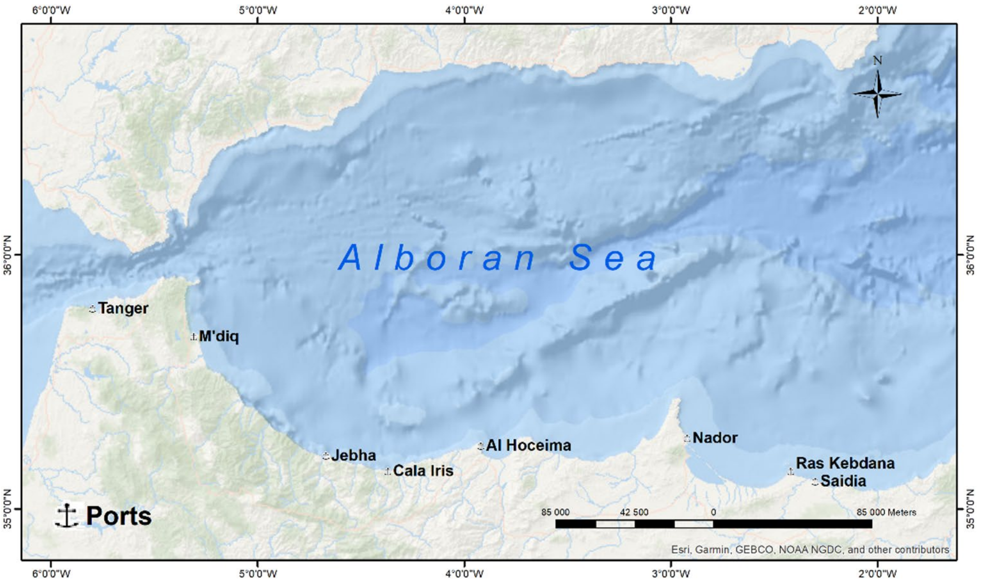


Fig. 1 Study area of the Moroccan Mediterranean Sea

roles, exploitation patterns, and contributions to the national economy. In contrast, species with similar ecological traits (e.g., diet composition, habitat, growth rate, trophic level) and limited available data were aggregated into multispecies functional groups, following standard Ecopath modeling practices (Christensen et al. 2008a, 2008b; Heymans et al. 2016).

For each functional group, Ecopath solves a set of linear equations based on two master equations to describe and parameterize trophic interactions and estimate unknown parameters. The first equation describes the total production for each functional group *i* and its components (Christensen and Walters 2004; Heymans et al. 2016):

$$\left(\frac{P}{Bi}\right).Bi = Yi + \sum jBj.\left(\frac{Q}{Bi}\right)j.DCij + Ei + BAi + \left(\frac{P}{Bi}\right).Bi(1 - EEi) \tag{1}$$

where P/B_i is the production/biomass ratio for a prey (*i*), B_i is the biomass of *i*, Y_i is the total fishery catch rate of (*i*;) B_j is the biomass of predator (*j*); $(Q/B)_j$ is the consumption/biomass ratio of *j*; DC_{ij} is the fraction of *i* in the diet of *j*; E_i is the net migration rate of *i*; BA_i for the biomass accumulation of *i*;and $(1-EE_i)$ represents mortality not due to predation or fishing, where EE_i is the proportion of the production that is used in the system (for predation or export).

The second equation ensures energy balance within each functional group:

$$Q_i = P_i + R_i + U_i \tag{2}$$

where Q_i is consumption, P_i is the production rate, R_i is respiration and U_i is the ratio of unassimilated food to consumption.

To run the Ecopath model, each functional group required data on biomass (t/km2), diet composition (DC prey proportion in the predator diet), catches (t/km2/y), unassimilated food, production/biomass ratio (P/B); total mortality (y-1); consumption/biomass ratio (Q/B; y-1) and ecotrophic efficiency (EE; proportion of the group's production used in the ecosystem through fishing, predation, or migration). This model provided one input parameter per functional group and per equation, either P/B, Q/B, B or EE (Christensen and Walters 2004; Christensen et al. 2008a, 2008b). The model's mass-balance was ensured using the thermodynamic and ecological principles (Christensen and Walters 2004; Heymans et al. 2016). The pedigree assigns scores ranging from 0 to 1, where values close to 1 indicate highly reliable and well-documented input data, and values close to 0 reflect greater uncertainty or lower data quality (Christensen and Walters 2004).

Moreover, an iterative approach for developing the food web model was employed (Loschi et al. 2023; Russo et al. 2025). This approach consists in a iterative random sampling of the set of parameters for building the food web within the input distribution ranges that were opportunely set on the basis of data uncertainty. At each iteration the set of randomly chosen parameters were used to develop the food web and a-posteriori check for ecological realism of the reconstructed food web was done using the same thermodynamic and ecological rules of Ecopath (Christensen and Walters 2004; Heymans et al. 2016). Uniform distribution were chosen for simplicity and ranges (10%, 20%, 30%, 50% and 80%) were set on the basis of uncertainty of data available (from local reliable information to general, model-based inputs). By randomly sampling the parameters develop several food webs that meet or do not meet the criteria for ecological realism: the unrealistic food webs discharged can be from thousands to millions depending on the consistency of dataset and range of parameters given. The iterative process, anyway, stops when at least 1000 reconstructed food webs meet the criteria for ecological realism. Although the approach is machine time consuming it has the characteristics of objectivity in balancing, has no assumptions on distribution of the inputs, can work with qualitative data and allows to embed all the uncertainty in the inputs (Loschi et al. 2023; Russo et al. 2025).

Input data

The Moroccan Mediterranean Sea's food web was defined and organized into 40 functional groups, ranging from primary producers to top predators, during the years 2000–2003 (see Online Resource). This includes 2 detritus groups, 2 primary producers, 12 invertebrates, 20 fishes, and separate groups for marine mammals, seabirds, and turtles. Groupings were based on size, habitat types and commercial significance in local fisheries. Additionally, some fish species were divided into functional categories specific to a single species due to their commercial value and/or to facilitate further specific management simulations. These species include blackspot seabream (*Pagellus bogaraveo*), hake (*Merluccius merluccius)*, bluefin tuna (*Thunnus thynnus)*, blue whiting (*Micromesistius poutassou)*, anchovy (*Engraulis encrasicolus)*, sardine (*Sardina pilchardus*), common octopus (*Octopus vulgaris)*, and deep-water rose shrimp (*Parapenaeus longirostris).*

A database of diet-related data was created, and the diet composition matrix (DCij) was assembled using available data from stomach content analyses conducted in the Mediterranean Sea (references are included in the Online Resource). The biomass of the two main producer groups, the detritus groups, and the three top predator groups was obtained from local studies (see Online Resource) and expressed in tonnes of wet weight per square kilometer of the species' habitat. This approach aimed to constrain the model and address the lack of direct assessments of biomass. The model estimated the biomass for the remaining groups, assigning distinct values of EE to each group. Diet compositions were adjusted to balance the model. The P/B ratio was determined as the total mortality (Z), expressed as the sum of fishing mortality ($F = Y/B$) and natural mortality (M) for finfish, following Pauly et al. (2000) (Eq. 1; see Online Resource). Parameters $L\infty$, K, and T were obtained from FishBase (Froese and Pauly 2000). Secondary production ratios for invertebrates were computed using Brey's (2001) model, while natural mortality (M) for deep-water rose shrimp was calculated with the empirical formula of Arce (2006), based on growth data from Froese and Pauly (2000) (Eq. 2; see Online Resource). A P/Q value of 0.05 was assumed for apex predators such as seabirds and marine mammals to allow EwE to estimate P/B values (Christensen et al. 2008a, 2008b).

The Q/B ratio for finfish was determined using the empirical relationship developed by Lourdes and Pauly (1998) (Eq. 3; see Online Resource). Consumption estimates for seabirds and marine mammals were calculated using the equations of Nilsson and Nilsson (1976) and Innes et al. (1987), respectively (Eqs. 4 and 5; see Online Resource), and those for invertebrates followed the body-size function of Cammen (1979) (Eq. 6; see Online Resource).

The target species, fishing methods, spatial distribution, and type of gear used were employed to categorize the fishing fleet. The Moroccan fleet was divided into artisanal, subsistence, and recreational sectors, while the industrial fleet was divided into purse seine and bottom trawl categories. The Spanish fleet was classified into purse seine, pots and traps, and longline, while the Portuguese fleet was divided into purse seine, longline, and pole and line.

Catch data (landings and discards) for the Moroccan fleet from 2000 to 2003 were sourced from local studies (Slimani and Hamdi 2004; Belhabib et al. 2013; Khalfallah et al. 2018; Ministère de l'agriculture, de la pêche maritime, du développement rural et des eaux et forêts, 2018, 2020, 2021, 2022; INRH 2020; Ayoubi et al. 2021; FAO, 2024a). The catch data for the Spanish and Portuguese fleets was taken from ICCAT (2006) and FAO (2024b).

When applying the iterative approach, the range of the input data was defined on general rules based on the perceived uncertainty of the input data and coherent with the settings used in the Ecopath pedigree (Heymans et al. 2016). Thus the ranges were considered as follows: 10% for the biomass of primary producers, seabirds and turtles for locally available data and 80% of uncertainty for the biomass of all other functional groups that were estimated only indirectly from the model; the uncertainty of the P/B and Q/B parameters was set at 50% for all groups because these parameters were derived from general empirical relationships; the uncertainty of the catch data was set as 30% of the values used in the reference model: this value reflects the fact that local values were used but little information on discards were available; 20% of uncertainty was used for the diet proportions of all groups because these inputs were taken from local studies (except for turtles, for which 80% was used). In order to make the results of the ecosystem indicators comparable between the MMS Ecopath model and the Monte Carlo approach, discards were used as imports for the respective functional groups. The iterative random approach with posterior identification of valid models (Loschi et al. 2023) implemented a search using uniform distributions within these ranges. The approach provides distributions and ranges for both valid inputs and outputs thus providing insights on the integrated model uncertainty.

Ecosystem indicators and model analysis

In Ecopath, the Lindeman spine represents the ecosystem as a series of discrete trophic levels (Lindeman 1942). Although each group is assigned a fractional trophic level based on the weighted average of its prey, the Lindeman spine allocates flows to integer trophic levels to depict the structure of the food chain. This framework enables the analysis of energy or biomass flows from primary producers and detritus through consumers, accounting for predation, export, respiration, and detritus production. It also allows the calculation of transfer efficiencies between levels, offering insights into energy transfer across the food web and facilitating the construction of a trophic pyramid that reflects the ecosystem's structure and functioning (Lalli and Parsons 1997; Pauly and Christensen 1995).

A set of indicators were estimated by EwE in order to measure the functioning, development, and the maturity of the ecosystem (Odum 1969; Christensen 1995). These indicators are the total system throughput (TST) which is the sum of all the flows (respiration, flows into detritus, export and consumption) and it is an indicator of the ecological size of the system (Ulanowicz 1986; Christensen and Pauly 1993; Heymans et al. 2014), total primary production to total respiration ratio (TPP/TR) is a maturity indicator of a system, that is closer to 1 for systems that are more mature (Odum 1969). Total primary production to total biomass ratio (TPP/TB) also refers to the system's maturity, as the biomass accumulates over time or as a system matures, the ratio reduces. Finn's cycling index (FCI) is the recycled proportion of the TST in an ecosystem (Finn 1976), while Finn's mean path length (FML) is the average of the number of groups a flow passes through or out of and expected to become higher with the maturation of the system (Christensen 1995). System Omnivory Index (SOI) is a measure of trophic interactions within the systems (Christensen et al. 2005). The Connectance Index (CI) is the number of both links, possible and actual in the food-web (GARDNER and ASHBY, 1970). Ascendency is a concept from information theory that represents the average mutual information in a system, normalized by system throughput. It was first described by (Ulanowicz and Norden, 1990). The system overhead (SO) is the difference between the capacity and the ascendency of an ecosystem. It represents the limits of increasing ascendency and reflects the "reserve force" that the system must draw upon to respond to disturbances or unexpected changes (Ulanowicz 1986). These ecosystem indicators were estimated for the reference MMS food web (expert based balancing) and for the 1000 food webs reconstructed using the iterative approach: this provides basis for identifying the consistency of indicators between the two approaches and their range of distribution useful for comparing with other systems.

To assess the impact of direct and indirect interactions in the food web, the Mixed Trophic Impact (MTI) routine was used (Ulanowicz and Puccia, 1990). It reveals what an increase of one functional group's biomass would have on the biomass of the other groups, including the fishing fleets that are treated as a functional groups (Christensen et al. 2008a, 2008b). Keystone species are identified by the index of keystoneness developed by (Valls et al. 2015). A keystone species is defined as one with important role in the ecosystem but having a low biomass (Power et al. 1996).

Results

Basic estimation

Input and output parameters of the MMS estimated by the software Ecopath are presented in Table 1. A dimensionless index of trophic level (TL) presented in the first column (Christensen et al. 2000). Five discrete trophic level were identified with the topmost functional groups, swordfish with TL of 4.85 and bluefin tuna with TL of 4.81. The ecotrophic efficiencies are high for most of the groups because they are preyed upon by many groups or are harvested by fisheries. However, groups with zero ecotrophic efficiency (sea turtles, seabirds, marine mammals) mean that they are not under predation pressure. The diet composition of the modeled functional groups is illustrated in Fig. 2, which shows the proportional distribution of prey items.

The flow diagram (Fig. 3) illustrates each functional group as a circle proportional to its biomass and reveals the interaction between these groups. The boxplot (Fig. 4) shows the estimated trophic levels of MMS functional groups, highlighting variability through Monte Carlo simulations. Most groups follow a clear trophic gradient, with low variability in lower levels (e.g., primary producers) and higher uncertainty in mid-to-top predators (e.g., groups 23 (Bluefin tuna), 25 (anglerfish), 28 (piscivores)).

Mixed trophic impact (MTI) and keystone index

The MTI analysis highlighted notable effects, both direct and indirect, from hypothetical changes in biomass of the functional groups (Fig. 5). An increase in piscivorous biomass could have positive effects (shown in the blue boxes) for medium-sized pelagic fish, sparids, sharks and demersal rays, sardines and Norway lobster, probably due to their predation on these species's predators. Conversely, such an increase in biomass may negatively impact (illustrated in the red boxes) anchovy, blue whiting, benthopelagic fish,

Table 1 Input and main output parameters for the MMS ecosystem model, with in brackets the median and interquartile range [median; IQR] for the 1000 models reconstructed with the iterative method. Bold numbers in the table correspond to values estimated by the model

	Group name	TL	Biomass (t/km^2)	*P*/B (/year)	Q/B (/year)	EE	*P*/Q (/year)	OI
1	Phytoplankton	1 [1;0]	4.28 [4.28;0.44]	114.6 [116.6;56.58]	- [0;0]	**0.45** [0.42;0.35]	– [0;0]	**0** [0;0]
2	Benthic macrophite	1 [1;0]	4.24 [4.25;0.41]	1.08 [1.1;0.52]	- [0;0]	**0.57** [0.37;0.33]	– [0;0]	**0** [0;0]
3	Gelatinous plankton	2.78 [2.77;0.05]	**0.01** [0.01;0.01]	13.57 [12.78;6.19]	49.38 [46.79;24.4]	0.94 [0.38;0.3]	**0.27** [0.29;0.15]	**0.26** [0.26;0.02]
4	Annelids	2.05 [2.04;0.01]	**27.69** [33.31;18.78]	2.71 [2.26;1.05]	5.91 [6.13;2.99]	0.94 [0.79;0.24]	**0.45** [0.41;0.11]	**0.05** [0.04;0.01]
5	Zooplankton	2.1 [2.09;0.02]	**0.94** [1.19;0.56]	41.7 [43.62;17.08]	120.82 [119.88;59.1]	0.95 [0.8;0.21]	**0.34** [0.37;0.12]	**0.1** [0.09;0.02]
6	Other benthic invertebrates	2.06 [2.05;0]	**18.37** [19.05;14.93]	0.71 [0.86;0.29]	5.62 [4.72;2.97]	0.95 [0.68;0.35]	**0.12** [0.16;0.1]	**0.06** [0.05;0]
7	Bivalves	2.11 [2.09;0.02]	**29.63** [30.1;22.56]	0.61 [0.78;0.19]	10.97 [9.91;5.34]	0.95 [0.5;0.33]	**0.05** [0.07;0.03]	**0.1** [0.09;0.02]
8	Norway lobster	2.64 [2.62;0.05]	**0.005** [0;0]	1.13 [1.25;0.53]	7.26 [6.12;3.69]	0.95 [0.49;0.31]	**0.15** [0.19;0.12]	**0.41** [0.39;0.01]
9	Lobsters and crabs	2.71 [2.71;0.04]	**2.84** [2.55;2.12]	1.93 [2.03;0.78]	7.07 [5.54;2.65]	0.95 [0.61;0.27]	**0.27** [0.37;0.16]	**0.35** [0.35;0.01]
10	Shripms	2.87 [2.8;0.14]	**3.45** [2.92;2.71]	1.17 [1.37;0.48]	15.43 [10.83;5.45]	0.95 [0.6;0.27]	**0.07** [0.11;0.06]	**0.32** [0.33;0.03]
11	Deep-water rose shrimp	3.05 [3.04;0.03]	**0.1** [0.11;0.08]	0.92 [0.84;0.41]	2.66 [2.38;1.19]	0.95 [0.53;0.33]	**0.34** [0.38;0.13]	**0.24** [0.23;0.03]
12	Common octopus	3.26 [3.24;0.06]	**0.15** [0.16;0.1]	0.91 [1.11;0.31]	4.49 [3.62;2.02]	0.95 [0.71;0.26]	**0.2** [0.29;0.16]	**0.37** [0.35;0.04]
13	Squids	3.2 [3.18;0.03]	**1.71** [2.03;1.16]	1.84 [1.6;0.72]	3.91 [3.71;1.63]	0.95 [0.7;0.28]	**0.47** [0.47;0.06]	**0.15** [0.12;0.03]
14	Cuttelfishs	3.41 [3.33;0.17]	**0.36** [0.39;0.26]	1.91 [2.08;0.79]	6.45 [5.37;2.17]	0.95 [0.7;0.27]	**0.29** [0.4;0.15]	**0.28** [0.3;0.11]
15	Sardine	2.98 [2.97;0.03]	**0.77** [0.9;0.47]	1.65 [2.03;0.6]	9.16 [8.56;4.37]	0.95 [0.64;0.31]	**0.18** [0.22;0.12]	**0.12** [0.11;0.02]
16	Anchovy	3.1 [3.09;0.02]	**0.43** [0.48;0.32]	1.65 [2;0.63]	9.16 [8.37;4.47]	0.95 [0.64;0.32]	**0.18** [0.22;0.12]	**0** [0;0]
17	Coastal fish	3.83 [3.72;0.14]	**0.03** [0.03;0.02]	0.44 [0.49;0.2]	1.56 [1.38;0.68]	0.95 [0.79;0.22]	**0.28** [0.36;0.16]	**0.2** [0.17;0.12]
18	Blue whiting	3.11 [3.1;0.01]	**1.23** [1.24;0.91]	1.06 [1.29;0.42]	6.52 [4.65;2.7]	0.95 [0.6;0.31]	**0.16** [0.25;0.16]	**0.02** [0.01;0]
19	Blackspot seabream	3.71 [3.6;0.23]	**0.01** [0.01;0]	1.04 [1.14;0.44]	2.72 [2.63;1.02]	0.95 [0.87;0.2]	**0.38** [0.46;0.08]	**0.59** [0.44;0.22]
20	Benthopelagic fish	4.31 [4.12;0.26]	**0.43** [0.43;0.31]	1.08 [1.24;0.41]	4.51 [3.17;1.23]	0.95 [0.65;0.31]	**0.23** [0.39;0.15]	**0.25** [0.22;0.09]
21	Pelagic sharks	4.72 [4.64;0.08]	**0.00000609** [0;0]	0.26 [0.36;0.07]	2.67 [1.77;0.87]	0.95 [0.84;0.23]	**0.1** [0.18;0.1]	**0.53** [0.47;0.08]
22	Demersal sharks and rays	4.49 [4.39;0.07]	**0.08** [0.07;0.06]	0.88 [0.87;0.43]	4.25 [2.68;1.05]	0.95 [0.18;0.14]	**0.2** [0.3;0.18]	**0.32** [0.26;0.12]
23	Bluefin tuna	4.82 [4.68;0.14]	**0.03** [0.04;0.02]	1 [1.03;0.42]	2.9 [2.48;1.04]	0.95 [0.77;0.26]	**0.34** [0.44;0.09]	**0.35** [0.28;0.1]
24	Other demersal fish	3.62 [3.3;0.99]	**0.49** [0.62;0.28]	3.67 [3.2;1.36]	7.71 [7.25;2.99]	0.95 [0.69;0.24]	**0.47** [0.47;0.05]	**0.21** [0.32;0.16]
25	Angler fish	4.21 [4.08;0.29]	**0.01** [0.01;0.01]	1.09 [1.04;0.51]	4.04 [2.9;1.22]	0.95 [0.3;0.3]	**0.26** [0.36;0.17]	**0.32** [0.27;0.03]
26	Red mullets	3.33 [3.3;0.04]	**0.04** [0.04;0.03]	2.35 [2.45;1.09]	7.14 [6.54;2.98]	0.95 [0.66;0.34]	**0.32** [0.39;0.13]	**0.13** [0.11;0.03]
27	Sparids	3.18 [3.08;0.16]	**1.07** [1;0.85]	0.31 [0.37;0.11]	4.73 [3.53;1.83]	0.95 [0.51;0.36]	**0.06** [0.09;0.05]	**0.39** [0.31;0.17]
28	Piscivores	4.35 [4.21;0.36]	**0.24** [0.2;0.18]	0.46 [0.53;0.21]	5.04 [3.23;1.56]	0.95 [0.55;0.33]	**0.09** [0.14;0.08]	**0.23** [0.2;0.05]
29	Groupers	4.11 [4.01;0.08]	**0.01** [0.01;0]	0.78 [0.97;0.28]	3.6 [3.13;1.67]	0.95 [0.82;0.27]	**0.21** [0.31;0.17]	**0.16** [0.15;0.03]
30	Swordfish	4.85 [4.68;0.23]	**0.01** [0.02;0.01]	1 [1.11;0.4]	3.34 [2.8;1.08]	0.95 [0.74;0.29]	**0.3** [0.42;0.12]	**0.39** [0.29;0.14]
31	Flatfishes	3.17 [3.15;0.02]	**0.02** [0.02;0.01]	1.86 [1.74;0.9]	5.86 [5.43;2.79]	0.95 [0.5;0.3]	**0.31** [0.35;0.16]	**0.04** [0.04;0]
32	Hake	4.28 [4.19;0.1]	**0.4** [0.31;0.29]	1.02 [1.1;0.48]	5.16 [3.17;1.09]	0.94 [0.53;0.32]	**0.19** [0.32;0.15]	**0.15** [0.13;0.03]
33	Small pelagic fish	3.01 [3;0.02]	**0.19** [0.21;0.14]	3.01 [2.55;1.24]	6.61 [6.61;3.11]	0.95 [0.66;0.32]	**0.45** [0.43;0.11]	**0.09** [0.09;0.01]
34	Medium pelagic fish	4.16 [4.03;0.17]	**0.3** [0.27;0.23]	1.99 [1.74;0.89]	5.09 [4.07;2.03]	0.95 [0.69;0.28]	**0.39** [0.47;0.07]	**0.4** [0.33;0.11]
35	Large pelagic fish	3.84 [3.81;0.07]	**0.18** [0.17;0.15]	0.72 [0.65;0.31]	2.49 [1.85;0.84]	0.95 [0.32;0.15]	**0.29** [0.36;0.16]	**0.73** [0.72;0.07]
36	Marine mammals	3.5 [3.48;0.09]	0.04 [0.04;0]	0.31 [0.41;0.1]	6.34 [3.95;1.71]	**0** [0;0]	0.05 [0.09;0.04]	**1** [0.95;0.1]
37	Seabirds	3.7 [3.64;0.14]	0.000000836 [0;0]	4.45 [5.89;1.39]	89 [59.99;31.37]	**0** [0;0]	**0.05** [0.08;0.04]	**1.29** [1.2;0.15]
38	Sea turtles	3.3 [3.29;0.15]	0.005 [0;0]	0.175 [0.22;0.05]	3.5 [3.06;1.82]	**0** [0;0]	0.05 [0.06;0.03]	**0.79** [0.04;0.03]

Table 1 (continued)

	Group name	TL	Biomass (t/km²)	*P*/B (/year)	Q/B (/year)	EE	*P*/Q (/year)	OI
39	Detritus	1 [1;0]	1 [1.03;0.76]	– [0;0]	– [0;0]	**0.99** [0.06;0.29]	– [0;0]	**0.41** [0;0]
40	Discards	1	0.25	–	–	–	–	**0**

The IQR represents the 25th–75th percentile interval of the Monte Carlo simulations. *TL* trophic level, *P/B* production/biomass, *Q/B* consumption/biomass, *EE* ecotrophic efficiency, *P/Q* production/consumption, *OI* omnivory index

bluefin tuna and other demersal fish, as they serve as sources of prey. In addition, the mixed trophic impact highlights the significant negative influence of fishing fleets on certain groups (e.g., benthopelagic fish), particularly from the Moroccan artisanal fleet. The results from the two keystoneness indexes (Fig. 6a) suggest that hake (f.g. 32), swordfish (f.g. 30), sparids (f.g. 27), pelagic sharks (f.g. 21), and flatfishes (f.g. 31) may be considered keystone species according to the criteria established by Libralato et al. (2006). Additionally, the index proposed by Power et al. (1996) (Fig. 6b) also identified Hake and Sparids as keystone species. Furthermore, several groups with low trophic levels, such as annelids (f.g. 4), bivalves (f.g. 7), and other benthic invertebrates (f.g. 6), were recognized as structuring species due to their significant biomass and high trophic impact.

Summary statistics and transfer efficiency

A comparison of summary statistics was performed for the two versions of the Moroccan Mediterranean Sea model: the expert-based balanced model (MMS) and the iterative random food-web developer version (MMS*). These were further compared with models from other regions, including the Gulf of Gabes (GG), the Southern Catalonia Sea (SCS), and the Adriatic Sea (AS) (Table 2).

The MMS showed a total discharge of 5430.65 t/km²/year, of which 43.35% was attributed to detritus flows, 36.01% to exports, 12.73% to consumption and 7.89% to total respiration. In the AS, detritus flows were also the highest (36.09%), but were followed by consumption (33.95%), exports (18.99%) and respiration (10.95%). Contrasting percentages were observed for the GG and the SCS. Consumption represented the highest percentage in both cases (36.92% and 51.42%, respectively), followed by detritus flux (29.92% and 25.16%, respectively). However, exports were predominant in the GG (19.66%), while respiration held the highest proportion in the SCS (19.74%). Conversely, the lowest percentages were attributed to respiration in the GG (13.48%) and exports in the SCS (3.69%).

The MMS is characterized by a significantly higher Total Primary Production/Total Respiration ratio than other ecosystems. It also has a relatively high Total Primary Production/Total Biomass (TPP/TB) ratio compared to other Mediterranean models. However, the Total Biomass/Total Throughput (TB/TST) ratios for the MMS are relatively similar to those of other ecosystems. The calculated Finn's cycling index shows the lowest value for the GG and the highest in the AS, while the average Finn's mean path shows similar values, the highest being observed in the SCS. Notably, the estimated value of ascendancy is highest in the MMS, while the system overhead is lowest. The connectance index is comparatively lower in the MMS

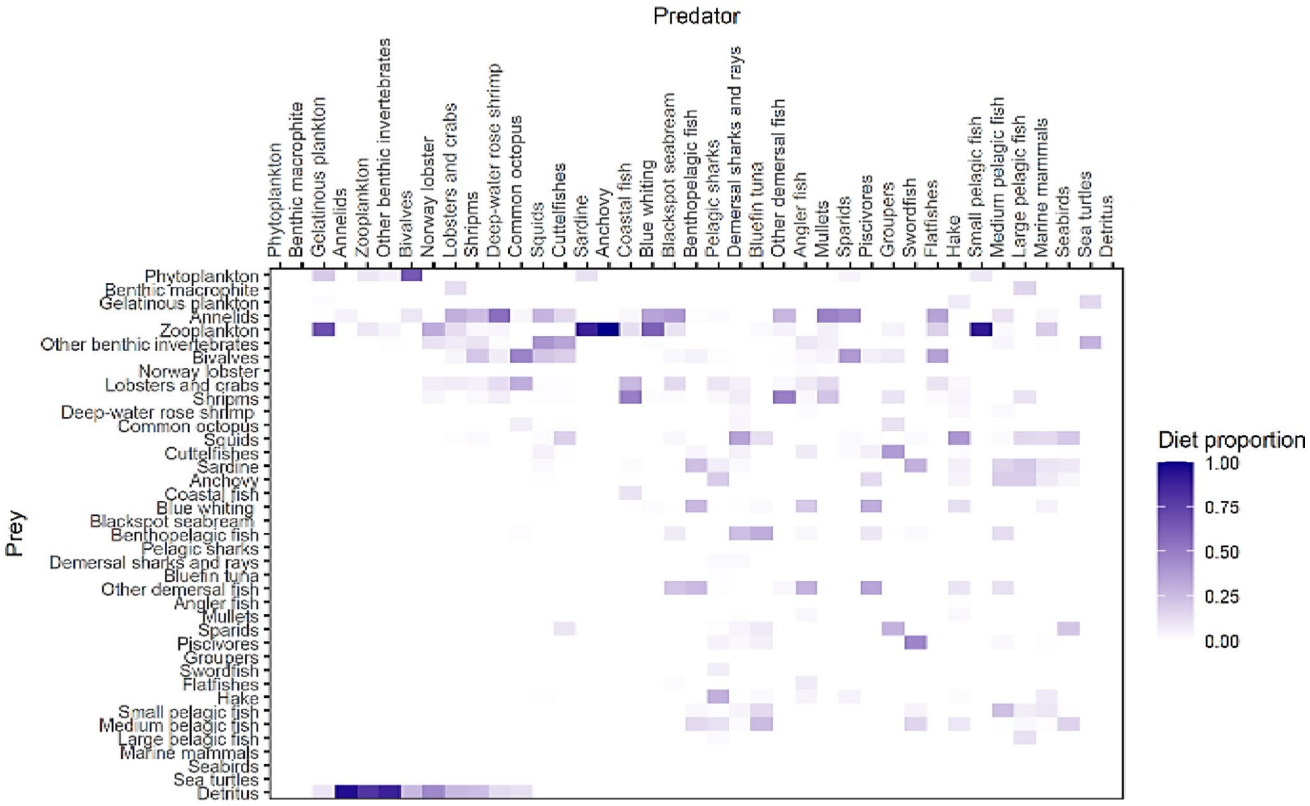


Fig. 2 Diet composition matrix for the Moroccan Mediterranean Sea model

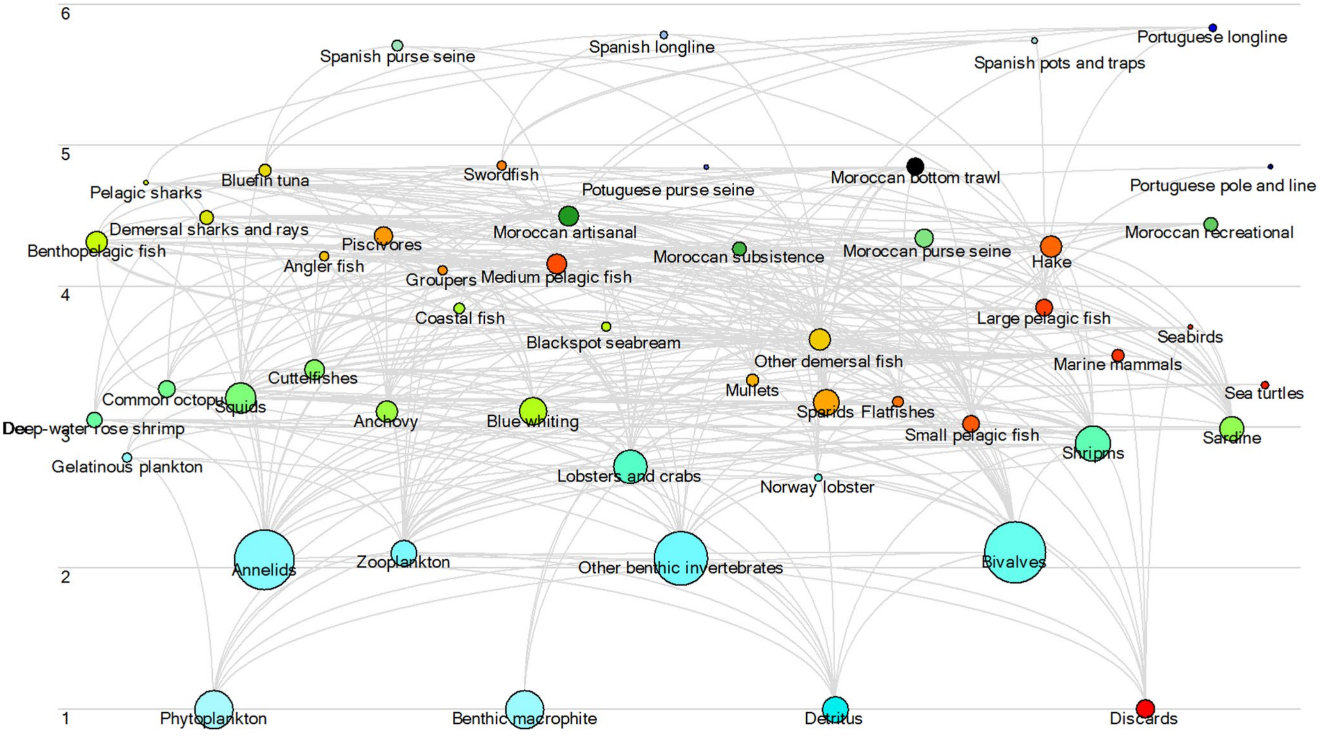


Fig. 3 Flow diagram of the MMS food web. The lines represent the energy flow and the trophic level of the group denoted on the y-axis

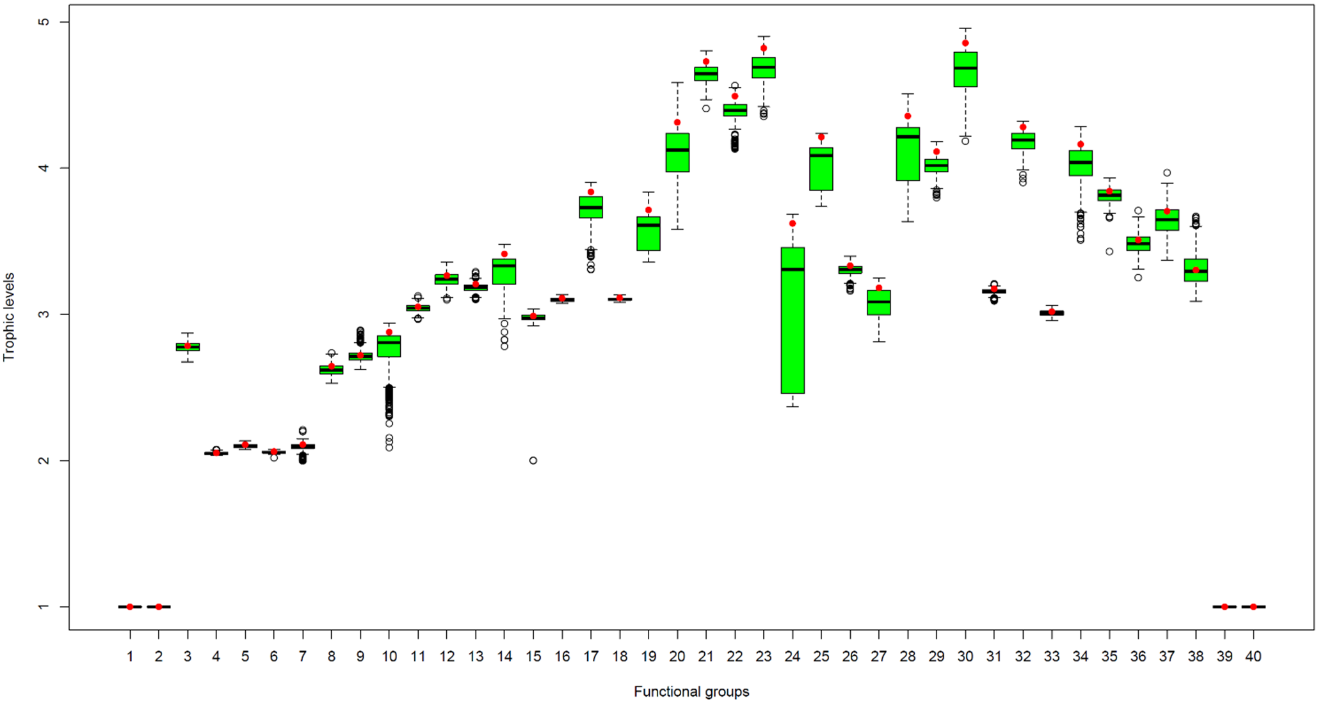


Fig. 4 Distribution of trophic levels across functional groups

ecosystem than in the other models. The pedigree index for the MMS is 0.42, with higher values observed for the GG (0.65), the AS (0.66), and the SCS (0.67). The GG in demonstrates the highest transfer efficiency at 19.10%, followed by the MMS at 14.89%, the SCS at 12.60%, and finally the AS at 11.70%.

The comparison of indicators considered useful for defining ecosystem health in terms of vigor, resilience and organization (Costanza and Mageau 1999) are shown in Fig. 7. Results show that expert-based balancing result are within the 1000 food webs developed with the iterative Monte Carlo approach. Notably, the GG model appears outside the cloud obtained from the iterative Monte Carlo food web developer.

Lindeman spine (Fig. 8) shows that the majority of the energy flows in the study area occurred in the first two levels, which together represent 54% of the TST. Trophic level I accounts for 44% of the total TST, while 10% is accounted for by trophic level II, which produce the highest flows to detritus of the ecosystem, and made up by groups that are very important in terms of biomass (Bivalves (23.38 t/km^2), other benthic invertebrates (14.46 t/km^2), and Annelida (33.65 t/km^2). Those groups represent 76% of the total biomass excluding detritus.

Discussion

Ecological interpretation of the results

The Moroccan Mediterranean region has experienced significant development in recent decades, particularly in the tourism, fishing, industry, agriculture and construction sectors (Nakhli 2010).Yet, the trophic functioning of this system and its sensitivity to these impacts have not been documented and studied before. This work presents the first food web model developed for the Moroccan Mediterranean Sea (MMS), contributing new insights into its trophic structure and functioning.

Ecosystem structure, biomass, and productivity

Biomass in the MMS varies considerably across functional groups, from 8.09E-05 t/km^2 for pelagic sharks to 33.65t/km^2 for Annelida (Table 1). Annelids occupy lower trophic levels, where energy availability is higher, explaining their greater biomass (see also Fig. 3). The Lindeman Spine (Fig. 6) demonstrated the importance of TL II and III in the MMS ecosystem. In fact, 88.53% of total system biomass (excluding detritus) is within TLs II and III. The first two trophic levels, accounting for 54% of the total system flow (TST), accommodate the majority of energy flows, consistent with ecological theory (Lalli and Parsons 1997), as trophic levels increase, the total system throughput decrease.

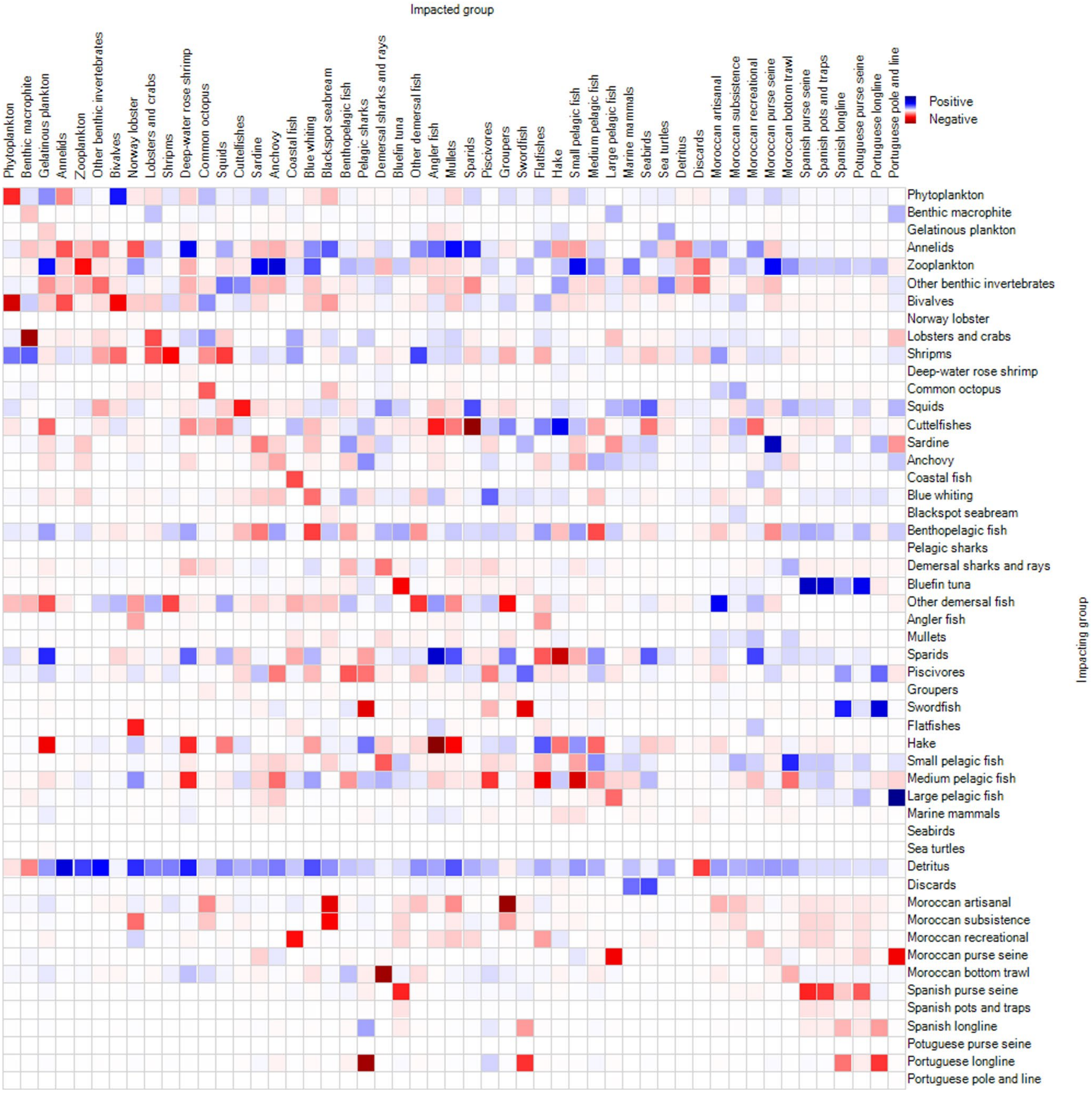


Fig. 5 Mixed Trophic Impact for the MMS model: the boxes indicate positive (blue) or negative (red) impacts, with the intensity proportional to the degree of these impacts

The third trophic level had higher export flows than other trophic levels due to fishing exports.

The ecotrophic efficiencies were taken to be 0.95 in the expert-balanced MMS model based on Ricker (1968) because there was a lack of biomass data. However, the balanced model's estimation of the EE of the top predator groups (sea turtles, seabirds, and marine mammals; Table 1) was zero (Table 1), meaning that a sizable portion of those groups' production was not utilized in the system under study. Notably, the results from the iterative Monte Carlo approach are consistent with those of the expert-balanced approach. The phytoplankton and benthic macrophyte EEs are 0.073 and 0.329, respectively, suggesting while both groups are important producers in the ecosystem, benthic macrophytes serve as crucial habitat-forming species, offering food and shelter to numerous organisms and facilitating ecological interactions such as predation and competition. They also play a vital role in ecosystem functioning by contributing to biomass and oxygen production, nutrient cycling, and sediment stabilization (Cabral et al. 2025). In the Mediterranean Sea, however, anthropogenic pressures, including aquaculture, nutrient enrichment, and coastal pollution, can significantly disrupt macrophyte communities (Zachariadou et al. 2025). Similar pressures are increasingly observed along the Moroccan Mediterranean Coast, indicating that local macrophyte assemblages may face comparable threats (Er-Ramy et al. 2025).

Mixed trophic impacts and keystone species

Mixed trophic impact analysis reveals the complex interplay between different functional groups within the ecosystem (Fig. 3). In general, most groups had a negative or positive impact on the others. Zooplankton have a substantial positive impact on gelatinous plankton, sardine, anchovy, blue whiting, small pelagic fish and marine mammals. Nevertheless, they also have a negative impact on annelids, demersal sharks and rays and on themselves, indicating potential predation pressure or competition from this group. However, seabirds, sea turtles, groupers, anglerfish, pelagic sharks, norway lobster, and gelatinous plankton had little or no impact on other groups in the ecosystem, probably because these groups present low levels of biomass and that in some cases their prey are considered mostly imported. The Moroccan artisanal fleet (Fig. 3) stands out for its predominant negative impact on various groups, including coastal fish, blackspot seabream, groupers and bluefin tuna, as well as on its own fleet. This negative impact on itself can stem from a variety of factors, such as overfishing or bycatch of non-target species. A keystone group has a disproportionate impact on other groups in the system, despite relatively low biomass (Paine 1995). These groups are pelagic sharks, large pelagic fish and bluefin tuna (Fig. 4). This pattern is consistent across the different Mediterranean models. For example, sharks are highlighted in numerous other studies carried out in different regions such as the lower continental slope of the Catalan Sea (Tecchio et al. 2013), the Gulf of Gabes (Hattab et al. 2013) and the Greek Ionian Sea (Moutopoulos et al. 2013). Similarly, large pelagic fish are highlighted in many models, including those conducted in the northern Aegean Sea (Tsagarakis et al. 2010) and the northwestern Mediterranean Sea (Corrales et al. 2015). The MMS is a crucial breeding ground for many elasmobranchs, including sharks. This underlines the ecological importance of sharks in this region (Keznine et al. 2024).

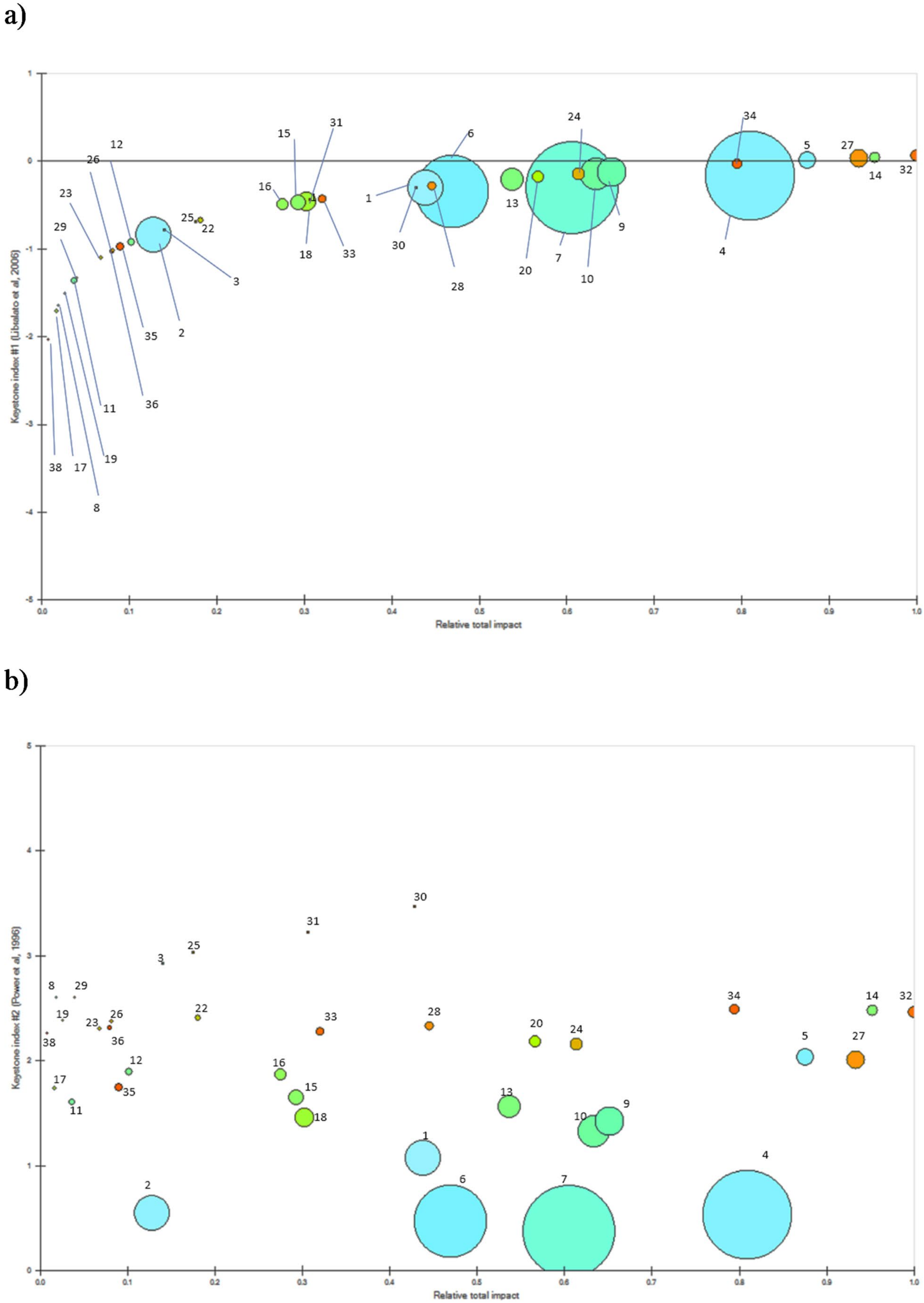
System indicators and ecosystem maturity

The estimated TST value for the MMS was higher compared to the other Mediterranean ecosystems (Table 2) which can be attributed to the higher number of compartments present. This increase in TST is in line with general observations on ecosystem network indicators, which tend to rise as systems progress toward more mature stages (Scotti et al. 2022). Total net primary production (NPP) is generally higher in ecosystems characterized by eutrophic conditions and upwelling (Christensen and Walters 2004).

In immature ecosystems, the ratio of total primary production (PP) to total respiration is often greater than 1. Over time, this ratio tends to decrease as ecosystems mature (Odum 1971). It is remarkable that the MMS and the other ecosystems have a ratio of total primary production to total respiration greater than 1, indicating high productivity. However, the ratio between total primary production to total biomass varies from one ecosystem to another. In particular, the MMS has lower PPT/TB values than other systems, suggesting that it is less mature than the others (Odum 1971).

Finn's cycle index is higher in systems with the capacity to reuse energy and matter (Finn 1976). However, it should be noted that the MMS has the lowest value among the Mediterranean ecosystems studied, indicating potential limits in its capacity to recycle energy and matter compared with other ecosystems. The connectance index tends to be higher in ecosystems characterized by a greater number of functional groups (Nee 1990). However, in the case of the MMS ecosystem, the connectance index is lower than in other ecosystems, reflecting the structure of the network and the number of functional groups. The system omnivory index generally exceeds 0 in ecosystems where functional groups exhibit feeding behaviors at multiple trophic levels (Pauly et al. 1993). Although this index is above 0 in all the ecosystems studied, it has a significantly higher value in the MMS than in other ecosystems. This suggests a pronounced prevalence of omnivory and complex trophic interactions within the MMS ecosystem. The ascendancy tends to decrease in systems with low internal constraints, indicating high resilience, while it increases with energy transfer efficiency, as illustrated by general studies of flow network indices (Scotti et al. 2022). Interestingly, the MMS exhibits the highest value of ascendancy compared to the other ecosystems studied, suggesting a potentially greater degree of energy transfer efficiency within the MMS ecosystem. Out of the three ecosystems evaluated, the MMS's system overhead was the lowest, suggesting that it had the least amount of redundancy for potential usage against disturbances (Ulanowicz 1986).

According to Odum (1971) and Pauly and Christensen (1995), the transfer efficiencies (TE) of the MMS model were within the range of typical values found in other aquatic ecosystems. These values were nevertheless higher than the reported world average (10%), as well as values found in other Mediterranean ecosystems, except the AS


a)
Keystone index #1 (Libralato et al, 2006)
Relative total impact
1
0
-1
-2
-3
-4
-5
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
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25
26
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32
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34
35
36
38
b)
Keystone index #2 (Power et al, 1996)
Relative total impact
5
4
3
2
1
0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
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◀ **Fig. 6** Keystone Index analysis of the MMS web. The diameter of each circle corresponds to the biomass of the functional groups, as indicated in **a** according to Libralato et al. (2006), and **b** according to Power et al. (1996). The numbers correspond to the functional groups within the MMS model (see Table 1)

ecosystem. This indicates that the Mediterranean Sea is oligotrophic, as opposed to more eutrophic ecosystems (Coll et al. 2006a, b; Shannon et al. 2003).

The statistics mentioned before generally point to the MMS as a stressed ecosystem that can be considered in a developmental stage, and relatively immature (Odum 1969; Finn 1976; Ulanowicz 1986). The primary production to total respiration ratio (Pp/R) is close to, but not exactly 1, indicating that production slightly exceeds respiration, characteristic of a system that is productive but not fully mature. Finn's cycling index is moderate, showing that energy recycling occurs but is not as extensive as in mature ecosystems. Similarly, the connectance and omnivory indices reflect some food web complexity without reaching maximal structural organization. Together, these metrics suggest that the MMS ecosystem exhibits established trophic structure and functioning, yet has not attained the highest maturity or complexity typical of fully developed systems. This can be partly attributed to intensive exploitation by domestic and foreign vessels (Ariz 1985; Baddyr and Guénette 2001; Belhabib et al. 2013), coupled with a lack of control and enforcement due to economic difficulties (Kaczynski 1989; Belhabib et al. 2013), leading to overexploitation of significant stocks (Balguerías et al. 2000; Pitcher et al. 2002; Anon 2005a; Belhabib et al. 2013). Furthermore, the focus has been on short-term profits rather than long-term sustainable profits, thereby contributing to an increase in illegal, unreported and unregulated fishing (Anon, 2005b). These historical and contemporary fishing practices likely influenced the state of the MMS ecosystem during the period 2000–2003, highlighting the urgent need for sustainable management measures to ensure its long-term health and resilience.

Methodological contribution

Monte carlo approach and uncertainty assessment

The iterative Monte Carlo approach provides a structured way to integrate parameter uncertainty into the MMS food web model. In this framework, uncertainty ranges were assigned to all input parameters: 10% for the biomass of primary producers, seabirds, and turtles; 80% for the biomass of all other groups; 50% for P/B and Q/B values across all groups; 30% for catch data; and 20% for diet proportions (80% for turtles). Using uniform distributions within these ranges, the iterative random food-web developer reconstructed 1000 valid food webs, producing distributions for both inputs and outputs rather than fixed values.

Comparison with the expert-balanced MMS model shows strong agreement. For system-level indicators, median values from the 1000 Monte Carlo realizations closely match those of the reference model (Table 2). At the same time, the interquartile ranges generated by the iterative approach quantify the uncertainty around each indicator, providing essential information when comparing MMS with other Mediterranean ecosystems (Fig. 5). This added dimension of uncertainty is also evident in the reconstructed diets: the dispersion across the 1000 food webs reveals relatively narrow variability for most diet proportions, indicating consistency with the balanced model (Fig. 2).

The Monte Carlo simulations also highlight the variability associated with trophic level estimates (Fig. 3). While both modeling approaches exhibit strong correspondence, the expert-balanced trophic levels tend to fall in the upper portion of the interquartile ranges obtained from the 1000 realizations. This shows that deterministic expert balancing represents a single plausible configuration within a broader envelope of solutions that satisfy all input constraints. Given the general variability of biological and ecological data and the difficulties in gathering coherent (in time, space, in resolution) information for all levels of the ecosystem, the ecosystem-level uncertainty might be considered a promising measure of the quality of the model given the quality of the input data.

Ecosystem indicators related to vigor, resilience, and organization (following Costanza and Mageau 1999) also fall within the cloud of values obtained from the Monte Carlo simulations (Fig. 7). This confirms the internal coherence between the two modeling approaches and demonstrates the advantage of having entire distributions, rather than just single deterministic outputs when positioning MMS relative to ecosystems such as the Gulf of Gabes, Southern Catalonia Sea, and Adriatic Sea.

Finally, the Monte Carlo-derived ecotrophic efficiencies offer an additional perspective on biomass utilization. While EE values in the expert-balanced model were set at 0.95 due to limited biomass data, the distributions obtained from the iterative approach confirm consistency with the reference model and reveal which functional groups show narrower or wider uncertainty. For instance, phytoplankton and benthic macrophytes display EEs of 0.073 and 0.329, respectively, reflecting their ecological roles and sensitivities to pressures already reported for Mediterranean macrophyte communities.

Table 2 Summary statistics for the MMS food web model (expert-based MMS and iterative MMS*) compared with three other Mediterranean models: GG (Hattab et al. 2013), SCS (Coll et al. 2006a, 2006b) and AS (Coll et al. 2007)

Parameter	MMS	MMS*	GG	SCS	AS	Units
Ecosystem properties						
Sum of all consumption (TC)	829.55	820.14 (294.31)	1402.88	852.11	1305.04	$t/km^2/y$
Sum of all exports (TE)	2.96	31.91 (177.18)	747.08	61.27	730.15	$t/km^2/y$
Sum of all respiratory flows (TR)	495.32	467.52 (203.22)	512.15	327.16	421.09	$t/km^2/y$
Sum of all flows into detritus (TD)	443.16	506.57 (233.77)	1136.87	416.91	1387.46	$t/km^2/y$
Total system throughput (TST)	1770.99	1983.21 (522.92)	3798.99	1657.00	3844.00	$t/km^2/y$
Sum of all production (TP)	663.42	685.27 (236.46)	1791.7	658.00	1566.00	$t/km^2/y$
Total net primary production (NPP)	495.11	498.24 (234.02)	1258.35	386.68	1149.85	$t/km^2/y$
Net system production (NSP)	1956.09	1983.21 (522.92)	746.2	59.52	728.76	$t/km^2/y$
Total biomass (excluding detritus) (TB)	99.96	105.03 (27.51)	73.75	58.99	130.30	t/km^2
Ecosystem maturity						
Total primary production/total respiration PPT/TR	1.00	1.03 (0.59)	2.46	1.18	2.73	
Total primary production/total biomass PPT/TB	4.95	4.74 (2.35)	17.06	6.55	8.82	
Total biomass/total throughput TB/TST	0.06	0.05 (0.01)	0.02	0.04	0.03	y–1
Food web structure						
Connectance Index (CI)	0.19	0.19	–	0.20	–	
System omnivory Index (SOI)	0.25	1.00 (0.25)	–	0.19	0.19	
Finn's cycling Index (FCI)	9.590	13.58 (3.98)	7.35	–	14.70	%TST
Finn's mean path length (FML)	2.891	3.3 (0.42)	3.02	4.27	3.34	
Ascendancy (AS)	25.80	26.29 (3.3)	17.03	25.50	27.00	%
System overhead (SO)	74.20	73.7 (3.3)	72.80	74.50	73.00	%
Model reliability						
Ecopath pedigree index	0.42		0.65	0.67	0.66	
Transfer efficiency total	14.89		19.10	12.60	10.00	%

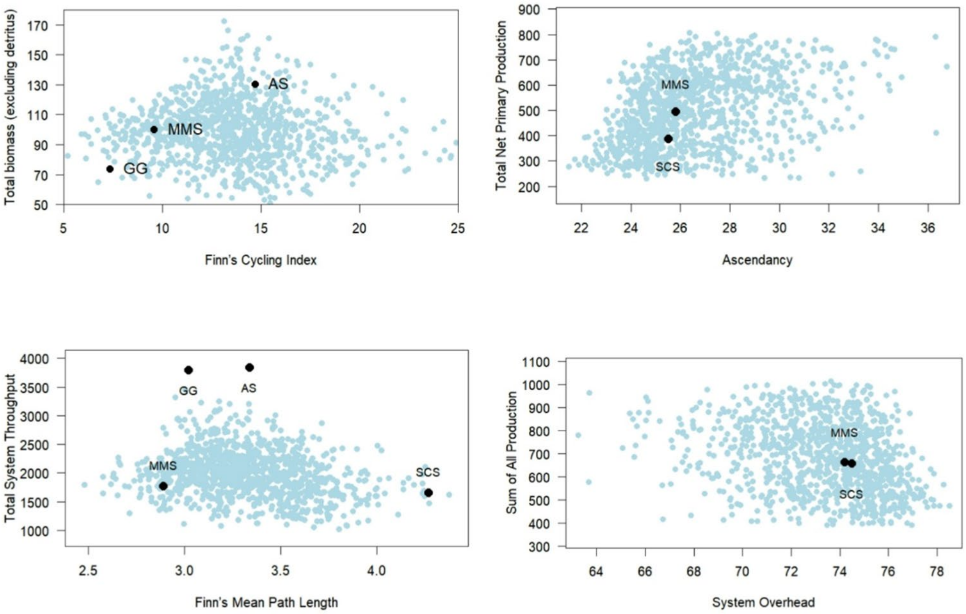

Fig. 7 Histograms of ecosystem indicators (Finn's mean path length, system overhead, ascendancy, Finn's cycling index) for four Ecopath models: MMS, GG, SCS, and AS. Some models are not displayed in certain panels when their values lie far outside the main range of the data cloud

Conclusion

This study presents the first mass-balance food web model of the Moroccan Mediterranean Sea (MMS) for the period 2000–2003, providing a comprehensive understanding of its trophic structure and functioning. By combining classical expert-based balancing with an iterative Monte Carlo approach, the model not only estimates ecosystem indicators but also quantifies uncertainty, offering ranges of inputs, outputs, and key metrics that are particularly useful when comparing the MMS to other Mediterranean ecosystems.

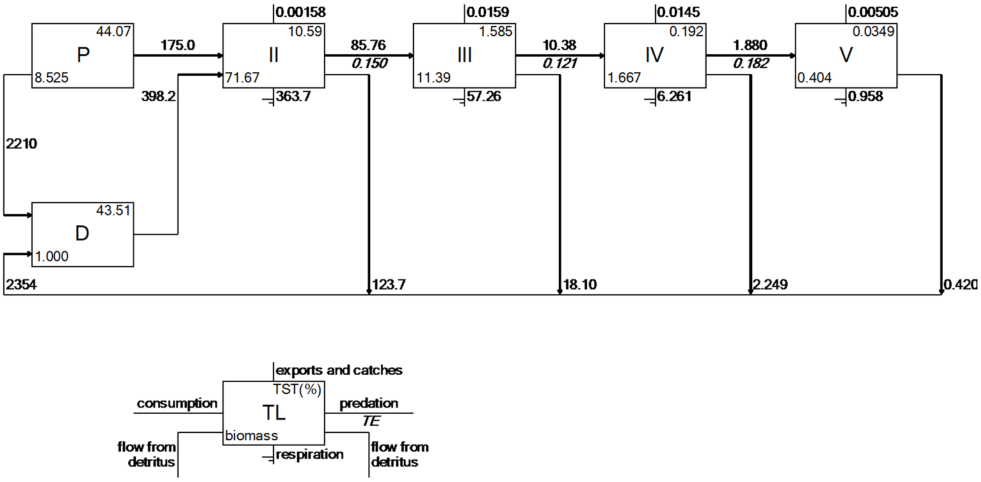

Fig. 8 Lindeman spine representation of trophic flows of MMS model

From an ecological perspective, the model identifies five trophic levels, with swordfish and bluefin tuna occupying the top positions. Certain functional groups, such as pelagic sharks, large pelagic fishes, and bluefin tuna, emerge as keystone species, exerting disproportionate influence on other groups despite relatively low biomass. Mixed trophic impact analysis demonstrates that piscivores affect most groups in the ecosystem, while the Moroccan artisanal fleet has clear negative impacts on several commercially important species, highlighting pressures from overfishing and habitat disruption. System-level indicators, including Primary Production/Total Respiration (PP/R), Connectance Index, Finn's Cycling Index, Omnivory Index, Ascendency, and system overhead, suggest that the MMS is productive but relatively immature and stressed, with limited redundancy to buffer disturbances. These findings highlight the MMS as a highly dynamic, yet vulnerable ecosystem, providing a baseline for assessing its resilience and guiding conservation priorities. The integration of iterative Monte Carlo simulations with EwE modeling represents a significant advancement for the study of data-limited ecosystems. This approach enables robust evaluation of uncertainty in biomass estimates, trophic interactions, and network indicators, complementing deterministic expert-based models. By providing probabilistic ranges for key metrics, the model strengthens confidence in ecological interpretations and supports comparative analyses with other Mediterranean systems, offering a framework for assessing ecosystem health under different scenarios.

Overall, this mass-balance model is a powerful tool for ecosystem-based management, offering a detailed snapshot of species interactions, energy flows, and system functioning. It establishes a foundation for future research, including temporal and spatial simulations to explore environmental, climatic, and anthropogenic impacts. The insights gained from this work will be essential for informing sustainable fisheries management, conservation strategies, and policy decisions in the MMS, ultimately contributing to the long-term resilience and health of this critical marine ecosystem.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42974-026-00301-9.

Acknowledgements We thank Matteo Loschi for his assistance in implementing the method used to generate the 1000 model replicates. The present work was conducted as part of Salma Aboussalam's PhD thesis.

Funding No funds, grants, or other support was received.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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