



## Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea

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### Abstract

Ecological modelling tools are applied worldwide to support the ecosystem-based approach of marine resources (EAM). In the last decades, numerous applications were attempted in the Mediterranean Sea, mainly using the *Ecopath with Ecosim* (*EwE*) tool. These models were used to analyse a variety of complex environmental problems. Many applications analysed the ecosystem impacts of fishing and assessed management options. Other studies dealt with the accumulation of pollution through the food web, the impact of aquaculture or the ecosystem effects of climate change. They contributed to the scientific aspects of an ecosystem-based approach in the region because they integrated human activities within an ecosystem context and evaluated their impact on the marine food web, including environmental factors. These studies also gathered a significant amount of information at an ecosystem level. Thus, in the second part of this review, we used this information to quantify structural and functional traits of Mediterranean marine ecosystems at regional scales as the illustration of further potentialities of *EwE* for an EAM. Results highlighted differential traits between ecosystem types and a few between basins, which illustrate the environmental heterogeneity of the Mediterranean Sea. Moreover, our analysis evidenced the importance of top predators and small pelagic fish in Mediterranean ecosystems, in addition to the structural role of benthos and plankton organisms. The impact of fishing was high and of a similar intensity in the western, central and eastern regions and showed differences between ecosystem types. The keystone role of species was more prominent in protected environments.

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## Introduction

Marine ecosystems are impacted by a diversified number of anthropogenic stressors including fishing (e.g. Pauly *et al.* 2002), aquaculture (e.g. Naylor *et al.* 2000), chemical pollution (e.g. Ueno *et al.* 2004) and eutrophication (e.g. Vitousek *et al.* 1997), which act simultaneously and sometimes synergistically (e.g. Jackson *et al.* 2001; Pandolfi *et al.* 2003; Lotze *et al.* 2006). As target and non-target species of above stressors interact by establishing complex relationships (e.g. Jennings and Kaiser 1998; Jackson *et al.* 2001), human activities have direct and indirect impacts whose analysis is notably challenging. Marine ecosystems are also influenced by environmental natural fluctuations and variability (Cury *et al.* 2008; Link *et al.* 2010). Thus, the ability to understand how these human activities, environmental factors and ecological components interact and influence each others, and eventually how the services and products provided to humans are affected, is a key issue that is of growing importance. Understanding these interactions and influences requires adoption of an ecosystem approach to the management of marine resources.

The need to consider natural changes and human activities when analysing and managing marine resources evidences the urge to adopt an integrated view of complex systems, which would make it possible to consider not only the dynamics of target species but also non-target organisms, trophic relationships and flows, and environmental factors (Botsford *et al.* 1997; Duda and Sherman 2002; Sherman and Duda 2002; Cury *et al.* 2003). This

implies a progress towards what is called the ecosystem-based approach to marine resources management (EAM), and when dealing specifically with fishing activities, the ecosystem-based approach to fisheries (EAF) (Botsford *et al.* 1997; Costanza *et al.* 1998; FAO, 2003, Garcia *et al.* 2003; Pikitch *et al.* 2004).

For the EAM, adaptations to the scientific method are required, in parallel with changes in the way ecological, social and economic issues are integrated to manage marine resources (Browman *et al.* 2005a,b). New methodological tools have been developed that contribute to an EAM, such as a selection of ecosystem indicators (e.g. Pauly and Christensen 1995; Cury *et al.* 2005; Jennings 2005; Shin and Shannon 2010) and ecological models (e.g. Walters *et al.* 1997; Christensen and Walters 2004; Fulton and Smith 2004; Shin *et al.* 2004; Plagányi 2007; Fulton 2010).

At present, the software package *Ecopath with Ecosim* (*EwE*, Pauly *et al.* 2000; Christensen and Walters 2004; <http://www.ecopath.org>) is applied worldwide and used for building ecological models under the context of EAM (Christensen and Pauly 2004; Christensen *et al.* 2009; Palomares *et al.* 2009). Some studies have questioned the potential of *EwE* models to contribute to EAM (Longhurst 2006). However, the *EwE* models have been widely used to study the structure and functioning of marine ecosystems (e.g. Lin *et al.* 2001; Heymans *et al.* 2004), perform ecosystem comparisons (e.g. Heymans *et al.* 2004; Moloney *et al.* 2005), derive emergent properties (e.g. Christensen 1995; Pauly and Christensen 1995), assess the impacts of human activities (e.g. Manickchand-Heileman *et al.*

2004; Shannon *et al.* 2008; Mackinson *et al.* 2009), analyse management options for marine resources (e.g. Pitcher 2001; Criales-Hernandez *et al.* 2006; Araújo *et al.* 2008) and describe bioaccumulation of toxins in the food web (e.g. Booth and Zeller 2005). Recently, the Institute for European Environmental Policy concluded that, among the available models of marine ecosystems, *EwE* was the most suitable for the development of scenarios for exploring future trends of marine biodiversity and changes in ecosystem services (Sukhdev 2008). *EwE* currently allows to integrate a large body of information from the ecosystem in a coherent description of aquatic food webs and makes it possible to place human activities in an ecosystem context which accounts also for environmental changes (Christensen and Walters 2004). A summary of the main equations and assumptions of the *EwE* is reported in Appendix S1 (in online Supporting Information), and critical overviews are available in the literature (Christensen and Walters 2004; Plagányi 2007; Coll *et al.* 2008b).

Several *EwE* applications have been developed for ecosystems in the Mediterranean and Black Sea. The Mediterranean basin is a complex and fascinating region with high biological diversity and much human activity extending over a long period of time (Bianchi and Morri 2000; Blondel and Aronson 2005). The landmass surrounding the sea has been inhabited for millennia and it is now heavily populated. The basin includes more than 20 countries with very different socioeconomic traits and some of the most renowned marine tourist destinations in the world. As a result of this complex socioeconomic and ecological context, the management of Mediterranean resources is seldom proactive with respect to environmental problems and actions are usually taken only after problems have appeared.

Recently, there has been an increase in public awareness, leading to a demand for better management of marine resources in the Mediterranean area (e.g. WWF/IUCN, 2004, UNEP, 2009) and to progress towards the development of an ecosystem-based approach (e.g. Nicholls and Hoozemans 1996; Pavasovic 1996; Van der Meulen and Salman 1996; EU, 2001, Massoud *et al.* 2003; GFCM-SAC, 2005). Several countries around the Mediterranean Sea have signed international treaties and agreements, such as the Convention on Biological Diversity (CBD) or the UN Framework Convention on Climate Change (UNFCCC), which

require the adoption of a more holistic ecosystem approach to the management of resources. Thus, contributions to the implementation of an EAM process have been increasing and are especially abundant in the context of conservation and fisheries (e.g. CIESM, 1999, 2000, 2008, Cori 1999; Goñi *et al.* 2000; Fraschetti *et al.* 2002; Pinnegar *et al.* 2003; Danovaro *et al.* 2004; Tudela 2004; WWF/IUCN, 2004; Karakassis *et al.* 2005; GFCM, 2007, IUCN, 2007; Tsikliras *et al.* 2007; Cochrane and de Young 2008; Abdulla *et al.* 2009; Stergiou *et al.* 2009; Linares *et al.* 2010). The scientific community around the Mediterranean has shown a growing interest on ecosystem-based studies, with an increase in research on ecosystem indicators (e.g. Pinnegar *et al.* 2003; Tudela *et al.* 2005; Sardà *et al.* 2009) and in the development of ecological models such as *EwE* (Table 1) and economic models. An example of this type of model is the MEFISTO bioeconomic model, e.g. Merino *et al.* (2007). Other multispecies models are poorly applied in the Mediterranean Sea: size-based models such as OSMOSE are being used in studies of the Gulf of Lion and age-structured models are only applied to single species (e.g. Santojanni *et al.* 2005). Moreover, at present, there are no applications of other ecosystem models such as Atlantis (Fulton *et al.* 2005) or multispecies virtual population analysis, and few other models were specially built for a specific context and therefore are non-standardized and difficult to use for comparison. Therefore, available ecosystem modelling applications are mainly *EwE* models that are based on a large amount of information collected in the last 30 years.

As the Mediterranean has east–west and north–south gradients of physical, ecological and socioeconomic factors, this region can be used as a model of the world's oceans. The comparison of modelling contributions to EAM in such a broad, complex and heterogeneous region as the Mediterranean Sea can provide insights into the ecosystem-based processes in other regions. Therefore, the aims of this contribution are threefold:

1. To investigate the contribution of existing applications of *EwE* models towards an EAM in the Mediterranean Sea;
2. To quantify ecological traits of Mediterranean ecosystems taking advantage of information standardized in available *EwE* models; and

**Table 1** *Ecopath* models developed in the Mediterranean Sea. Location of these models is represented in Figure 1 (Model No).

Model No	Model code	Model name	FG	Ecosystem Type	Fishing	Basin	Depth	Area km <sup>2</sup>	References
1 <sup>1</sup>	ARAN_94	Aranci Bay, Sardinia 1994	12	Coastal	Non-/light fishing	NW	0–50	16	(Diaz López <i>et al.</i> 2008)
2	ARAN_06	Aranci Bay, Sardinia 2006	12	Coastal	Fishing	NW	0–50	16	(Diaz López <i>et al.</i> 2008)
3	BAY_C	Bay of Calvi 1998	27	Coastal	Non-/light fishing	NW	0–18	22	(Pinnegar 2000; Pinnegar and Polunin 2004)
4	BONI_00	Bonifacio Straits Natural Reserve, Corsica 2000–2001	32	Coastal	Non-/light fishing	NW	0–15	800	(Albouy <i>et al.</i> 2009, 2010)
5	LAG_THAU	Etan the Thau lagoon 1980s	11	Lagoon	Fishing	NW	0–10	88	(Palomares <i>et al.</i> 1993)
6	MEDES	Medes Islands Reserve 1970s–90s	55	Coastal	Non-/light fishing	NW	0–15	0.20	(Meliado 2006)
7	ORBE_95	Orbetello lagoon 1995	16	Lagoon	Fishing	NW	0–1	25	(Auteri <i>et al.</i> 1993; Brando <i>et al.</i> 2004)
8	ORBE_96	Orbetello lagoon 1996	16	Lagoon	Fishing	NW	0–1	25	(Auteri <i>et al.</i> 1993; Brando <i>et al.</i> 2004)
9	PCROS	Port-Cros National Park 1998–2008	41	Coastal	Non-/light fishing	NW	0–50	13	(Valls 2009)
10	CAT_78	Southern Catalan Sea 1978–79	40	Shelf and slope	Fishing	NW	50–400	4500	(Coll <i>et al.</i> 2008e, 2009a)
11	CAT_94	Southern Catalan Sea 1990s	40	Shelf and slope	Fishing	NW	50–400	4500	(Coll <i>et al.</i> 2006a,b)
12	CAT_03	Southern Catalan Sea 2003	40	Shelf and slope	Fishing	NW	50–400	4500	(Coll <i>et al.</i> 2008a, 2009a)
13	CAT_NF	Southern Catalan Sea No fishing	40	Shelf and slope	Non-/light fishing	NW	50–400	4500	(Coll <i>et al.</i> 2009a)
14	MIRA_1	Miramare Natural Marine Reserve 2000–2003	19	Coastal	Non-/light fishing	NC	0–18	0.12	(Libralato <i>et al.</i> 2006b)
15	MIRA_2	Miramare Natural Marine Reserve 2000–2003	16	Coastal	Non-/light fishing	NC	0–18	0.12	(Libralato <i>et al.</i> 2010b)
16	NADRI_90	N Adriatic Sea 1990s	34	Shelf	Fishing	NC	0–50	32000	(Barausse <i>et al.</i> 2009)
17	NADRI_S	N Adriatic Sea 1997–2000	20	Shelf	Fishing	NC	0–50	9900	(Zucchetto <i>et al.</i> 2003)
18	NADRI_00	N Adriatic Sea 1997–2000 updated	20	Shelf	Fishing	NC	0–35	14178	(Pranovi and Link 2009)
19	ADRI_75	NC Adriatic Sea 1975–1980	40	Shelf	Fishing	NC	10–200	55500	(Coll <i>et al.</i> 2008d, 2009c)
20	ADRI_90	NC Adriatic Sea 1990s	40	Shelf	Fishing	NC	10–200	55500	(Coll <i>et al.</i> 2007, 2008d)
21	ADRI_02	NC Adriatic Sea 2002	40	Shelf	Fishing	NC	10–200	55500	(Coll <i>et al.</i> 2009c)
22	ADRI_NF	NC Adriatic Sea No fishing	40	Shelf	Non-/light fishing	NC	10–200	55500	(Coll 2006)
23	VEN_88/91	Venice lagoon - muddy habitat 1980s	27	Lagoon	Fishing	NC	0–4	134	(Pranovi <i>et al.</i> 2003)

**Table 1** Continued.

Model No	Model code	Model name	FG	Ecosystem Type	Fishing	Basin	Depth	Area km <sup>2</sup>	References
24	VEN_C	Venice lagoon - muddy habitat 1990s	21	Lagoon	Fishing	NC	0–4	134	(Libralato <i>et al.</i> 2002; Libralato 2004)
25	VEN_P	Venice lagoon - Palude della Rosa 1990s	16	Lagoon	Non-/light fishing	NC	0.5	35	(Carré and Opitz 1999; Carré <i>et al.</i> 2000)
26	VEN_S	Venice lagoon - seagrass 1990s	21	Lagoon	Fishing	NC	0–15	40	(Libralato <i>et al.</i> 2002; Libralato 2004)
27	VEN_ALL	Venice lagoon 1990s	27	Lagoon	Fishing	NC	0–15	450	(Libralato and Solidoro 2009; Libralato <i>et al.</i> 2010a)
28	VEN_98	Venice lagoon 1998	27	Lagoon	Fishing	NC	0–15	450	(Pranovi <i>et al.</i> 2003)
29	VEN_08	Venice lagoon 2008	27	Lagoon	Fishing	NC	0–16	450	(Pranovi <i>et al.</i> 2003)
30	BLACK_S3.2	Black Sea 1989–1991 (jellyfish)	16	Shelf and slope	Fishing	NE	0–2000	423000	(Örek 2000)
31	BLACK_S1.1	Black Sea 1960 pelagic web	15	Shelf and slope	Fishing	NE	0–200	423000	(Daskalov 2002)
32	BLACK_S1.2	Black Sea 1960 with eutrophication	15	Shelf and slope	Fishing	NE	0–200	423000	(Daskalov 2002)
33	BLACK_S2.1	Black Sea 1960–1970	7	Shelf and slope	Fishing	NE	0–2000	423000	(Gucu 2002)
34	BLACK_S2.2	Black Sea 1980	7	Shelf and slope	Fishing	NE	0–2000	423000	(Gucu 2002)
35	BLACK_S3.1	Black Sea 1989–1991	16	Shelf and slope	Fishing	NE	0–2000	423000	(Örek 2000)
36	BLACK_S2.3	Black Sea 1990	7	Shelf and slope	Fishing	NE	0–2000	423000	(Gucu 2002)
37	ION_07	NE Ionian Sea 2007	19	Shelf	Fishing	NE	0–200	4500	(Piroddi 2008)
38	ION_60	NE Ionian Sea 1960	22	Shelf	Fishing	NE	0–200	1021	(Piroddi 2008; Piroddi <i>et al.</i> 2010)
39	AEG_03	N Aegean Sea 2003–2006	40	Shelf	Fishing	NE	20–300	8374	(Tsagarakis <i>et al.</i> 2010)
40 <sup>2</sup>	GTUNIS	Gulf of Tunis 2000–2007	26	Shelf	Fishing	SC	0–200	2100	(Errais 2010)

NW, north-western; NC, north-central; NE, north-eastern; SC, south-central.

<sup>1</sup>Model not included in the analyses because of limit accessibility.

<sup>2</sup>Model not included in the analyses because of models availability in Southern areas of the Mediterranean Sea.

- To assess the ecosystem impacts of fishing at a basin scale as an illustration of modelling potentialities for an EAM.

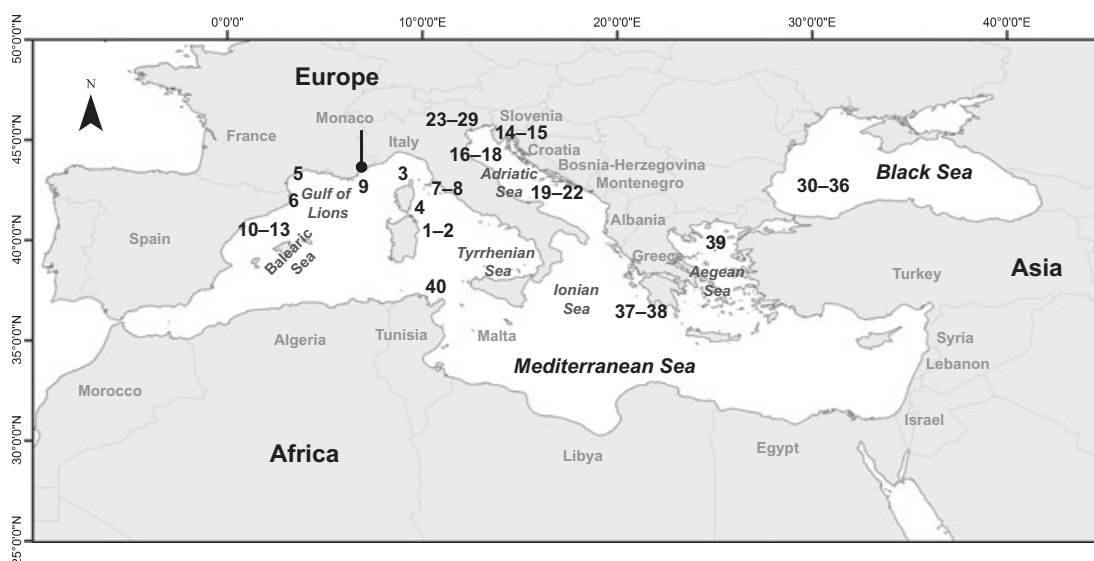
This work represents the first contribution of its kind to our understanding of the Mediterranean Sea. It concludes with a discussion on the available contributions of ecosystem modelling to an EAM process and reflects on future directions for research.

### The Mediterranean Sea and the Ecosystem Approach

The Mediterranean Sea, including the Black Sea basin, is the largest (3 405 400 km<sup>2</sup>) and deepest (average 1460 m, maximum 5267 m) enclosed sea on Earth (Fig. 1). It is located between Africa, Europe and Asia, and it is connected through the Strait of Gibraltar to the Atlantic Ocean in the west and through the Suez Canal to the Red Sea and the Indian Ocean in the south-east. In the Strait of Sicily, a shallow ridge at 400 m depth separates the island of Sicily from the coast of Tunisia. This ridge divides the sea into the western (area = 0.85 million km<sup>2</sup>) and the eastern (area = 1.65 million km<sup>2</sup>) regions. The Mediterranean and Black Seas have, generally, narrow continental shelves and a large area of open sea. The widest continental shelves are located in the Adriatic Sea, in the Gulf of Gabes and in the north-western side of the Black Sea.

General oceanographic conditions in the Mediterranean have been previously described in detail (e.g. Bethoux 1979; Hopkins 1985; Pinardi *et al.* 2006; Bas 2009). The annual mean sea surface temperature shows a high seasonality and important gradients from west to east and from north to south (Hopkins 1985). The basin is generally oligotrophic, but local and regional features such as river discharges, municipal sewage, local upwelling because of winds and currents result in locally enriched coastal areas (Estrada 1996; Bosc *et al.* 2004). The biological production decreases from north to south and from west to east and it is inversely related to temperature and salinity. The Black Sea presents peculiar features being eutrophic because of the high influence of the nutrient discharge from big rivers and characterized by a permanent deep anoxic layer rich in hydrogen sulphides (Özsoy and Ünlüata 1997).

The Mediterranean Sea is also a hot spot of biodiversity and hosts approximately 7–10% of the world's marine species with high percentages of endemic species (Tortonese 1985; Bianchi and Morri 2000; Boudouresque 2004; Coll *et al.* 2010a). This sea has emblematic species of conservation concern, such as the Bluefin tuna (*Thunnus thynnus*, Scombridae) and the Mediterranean monk seal (*Monachus monachus*, Phocidae) (e.g. Groombridge 1990; Reijnders *et al.* 1997; Bearzi *et al.* 2004; MacKenzie *et al.* 2009). There are as well several unique, endangered and sensitive



**Figure 1** EwE models developed within the Mediterranean basin. Model details are provided in Table 1.



habitats such as the seagrass meadows of the endemic *Posidonia oceanica* (Posidoniaceae), the coralligenous assemblages, the rocky outcrops or biogenic reefs and deep-sea habitats (Bellan-Santini *et al.* 1994; Ballesteros 2006; IUCN-MED, 2009, Sardà *et al.* 2009).

Given the demographic density generally high on its shores, the long history and diversity of human impacts and the enclosed feature of this sea, the Mediterranean have been altered in many ways since historical periods (Blondel and Aronson 2005; Lotze *et al.* 2006; Costello *et al.* 2010). At present, habitat loss and degradation, fishing impacts, pollution, climate change, eutrophication and the introduction of alien species are the most important threats (Coll *et al.* 2010a). A large amount of studies exists on threats to marine biodiversity and marine resources in the Mediterranean Sea (e.g. Galil 2000; Danovaro 2003; Abdulla 2004; Bianchi 2007; Tsounis *et al.* 2007; Ben Rais Lasram *et al.* 2010; Lejeune *et al.* 2010). However, there is still the need to investigate how human and natural drivers interact and how they affect communities and ecosystems as a whole. In this context, the need to move towards an EAM is evident. Ecosystem models are an essential tool in this direction, both for accounting of the complexity of ecosystem effects and for producing quantitative future scenarios.

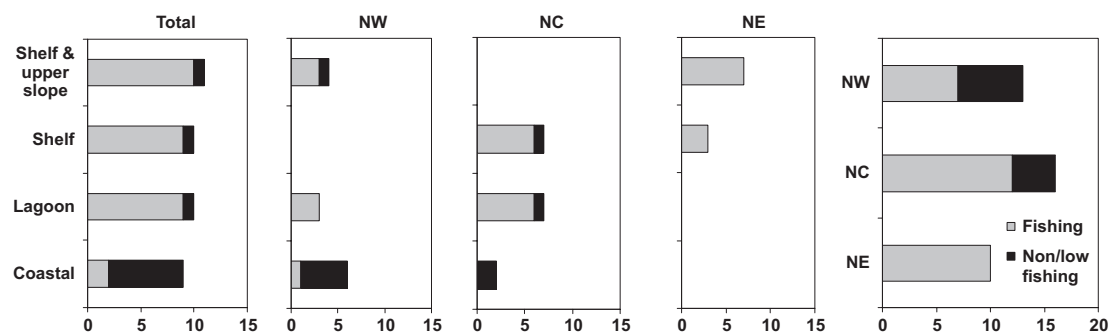
### Contributions of existing applications of *EwE* models towards an EAM in the Mediterranean

A total of 40 *Ecopath* models describing Mediterranean ecosystems have been fully developed and documented (Fig. 1 and Table 1). Trophic models were composed of a mean of  $25 \pm 1.9$  (standard deviation, sd) functional groups or ecological compartments, with a maximum of 55 and a minimum

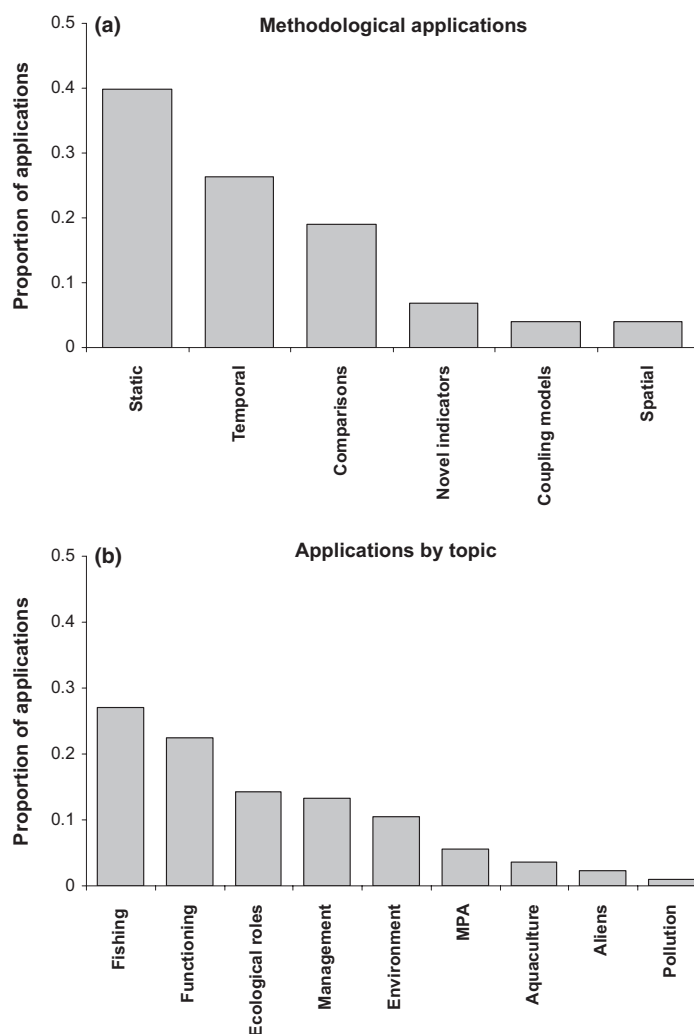
of seven groups. The models covered depths from 0 m to 2000 m and represented several ecosystems, from past states beginning in the 1960s to the present. Some of these available models were also used to project ecological scenarios into the future by developing dynamic simulations.

In terms of ecosystem types, the modelling applications were mainly developed to describe continental shelf and upper slopes, followed by lagoons and coastal areas (Table 1 and Fig. 2). There were several applications that covered more than one ecosystem type, including, for example, shelves and slopes together. The applications were located in the north-western Mediterranean and north-central Mediterranean (mainly in the Adriatic Sea), followed by applications including the north-eastern basin and the Black Sea (Fig. 2). Most of the models available were developed to represent exploited ecosystems (75%), but some studies represented protected or slightly exploited ecosystems (25%). No applications were found for the southern areas, except for one recent model developed for the Gulf of Tunis (Fig. 1 and Table 1).

Most of *EwE* applications used the static tool *Ecopath*, the dynamics of which are then explored using *Ecosim* followed by a comparative study of models (Fig. 3a). *EwE* was also used to develop new indicators, to couple different types of models and to perform spatial analysis with the module *Ecospace*. Several applications aimed at assessing fishing impacts on Mediterranean ecosystems through the description of ecosystem structural and functional traits and the examination of positive and negative impacts under different fisheries management regimes. These included changes in fishing effort and the establishment of marine protected areas (Fig. 3b). Common topics for the application of *EwE* were the analysis of the ecological roles of species



**Figure 2** Ecosystem models developed within the Mediterranean Sea ( $n = 39$ , excluding the Gulf of Tunis in the Southern-Central Mediterranean) by ecosystem type, sub-basins and fishing activities.



**Figure 3** Applications (%) of *EwE* models in the Mediterranean Sea by (a) methodology, and (b) topic (total number of applications = 79).

within food webs and the role of the environment in shaping ecosystem properties and dynamics. In the following subsections, the main *EwE* application in the Mediterranean (Table 1) is presented by topic to highlight modelling potentialities for an EAM.

#### Habitat loss and degradation

The first models developed in the Mediterranean Sea represented coastal areas and lagoons of the north-western and central Mediterranean Sea (e.g. Auteri *et al.* 1993; Palomares *et al.* 1993). Several models were developed in the Venice Lagoon (northern Adriatic Sea, Italy) to describe the trophic structure of different sites (Carrer and Opitz 1999; Granzotto *et al.* 2003) and to analyse two different lagoon habitats, the seagrass meadows of *Zostera spp.* (*Zosteraceae*) and *Cymodocea sp.* (*Cymodoceaceae*)

and the fishing grounds of the Manila clam (*Tapes philippinarum*, *Veneridae*) (Libralato *et al.* 2002). These two models highlighted the potential regression of seagrass meadows because of the stress induced by the new fishery targeting the Manila clam and evidenced higher species diversity and complexity in the seagrass meadows, which appeared to represent an ecosystem at a higher stage in the ecological succession.

#### Introduction of alien species

Applying *EwE*, Pranovi *et al.* (2003) constructed two models comparing the Venice Lagoon in 1988–1991 and 1998, i.e., the period before the introduction of the Manila clam into the lagoon (1983) and the period after its spreading that was followed by the expansion of a new intensive exploitation



using mechanical dredges. This study described the complex impacts of clam mechanical harvesting in the area and highlighted how Manila clam population benefited from the dredging activity because of the nutritional advantages from the re-suspended organic matter.

At the same time, models from the Black Sea (Örek 2000; Daskalov 2002; Gucu 2002) facilitated the study of the structure and functioning properties of this peculiar ecosystem, the description of a trophic cascade because of fishing impacts and, in particular, the analysis of the ecological role of the invasive comb jellyfish *Mnemiopsis leidy* (Bolinopsidae). Afterwards, the analysis of the jellyfish blooms in relation to environmental and exploitation changes in the Mediterranean Sea had been also highlighted using *Ecosim* simulations and the meta-analysis of model outputs (Pauly *et al.* 2009).

#### Eutrophication effects

Another application of *EwE* to shallow waters was the construction of two models to describe the coastal ecosystem of Orbetello Lagoon (central western Italy) for 1995 and 1996 (Brando *et al.* 2004). In this case, the application analysed the effectiveness of management activities to control eutrophication. The Orbetello Lagoon is characterized by limited exchange with the sea and a high availability of nutrients, and it had shown increasing eutrophication since 1975. From 1993, a series of management activities were carried out to reduce nutrient loading, increase water circulation and carry out selective harvesting of macroalgae. Results obtained with *EwE* modelling revealed the positive effects of management activities at the ecosystem level as well as the potential indirect effects with fisheries and seabirds.

#### Fishing effects and assessments of management options

Moving to ecosystems located at deeper depths in the Mediterranean Sea, later *EwE* applications focussed on continental shelves and slopes of various areas (such as the South Catalan, north and north-central Adriatic, North Aegean and North Ionian seas, Coll *et al.* 2006a, 2007; Barausse *et al.* 2009; Piroddi *et al.* 2010; Tsagarakis *et al.* 2010). These applications aimed at describing the structure and functioning of shelf ecosystems as well as to quantify the effects of fishing, which has

the greatest impact on the areas examined. Results highlighted the key role of benthic-pelagic coupling and the ecological importance of small pelagic fishes, such as anchovy (*Engraulis encrasicolus*, Engraulidae) and sardine (*Sardina pilchardus*, Clupeidae) in both the western and eastern Mediterranean ecosystems. They also indirectly underlined the importance of the microbial food web.

Meanwhile in coastal areas, Albouy *et al.* (2010) recently described the Bonifacio Straits Natural Reserve of Corsica and examined management options for recreational fisheries. Valls (2009) studied the impacts of recreational fisheries, and the ecological roles of coastal species in Port-Cross National Park MPA and Errais (2010) described the ecosystem impacts of fishing in the Gulf of Tunis.

Many *EwE* applications were also used to explore management strategies for exploited areas. Applications related to fishing management in the Adriatic Sea were designed to assess the effectiveness of MPAs of different sizes (Zucchetto *et al.* 2003; Fouzai 2010). In the Catalan Sea, spatial analyses were used to explore the options for recovery of important commercial species such as the European hake (*Merluccius merluccius*, Merlucciinae) (Vargiu *et al.* 2009) and temporal analysis was developed to explore the impact of aquacultural activities of Bluefin tuna (Forestal 2010). In the same area, *Ecosim* dynamic simulations were used to evaluate selectivity measures for trawling within an ecosystem context (Coll *et al.* 2008a).

#### Ecological analyses and comparisons of food web traits

Another interesting *EwE* application to an EAM process was the cross-system comparison of standardized models which made possible an examination of the differences within ecosystems in the Mediterranean Sea and between Mediterranean ecosystems and those elsewhere (e.g. Coll *et al.* 2006b, 2008d, 2009a,b; Mackinson *et al.* 2009; Shannon *et al.* 2009a,b; Tsagarakis *et al.* 2010). It was also possible to examine the ecosystem effects of protection (Libralato *et al.* 2006b, 2010b). Coll *et al.* (2006b) standardized an ecological model representing a north-western (NW) Mediterranean exploited ecosystem and compared it with four standardized models from coastal upwelling ecosystems described elsewhere (Moloney *et al.* 2005). The high fishing pressure in this Mediterranean ecosystem was highlighted relative to its low primary

production. The importance of pelagic-demersal coupling and the relevance of gelatinous zooplankton in the Namibian and Mediterranean case-studies were in remarkable contrast to the other ecosystem models examined. Results highlighted similarities between Mediterranean and Namibian ecosystems that may be related to effects induced by high fishing pressure.

Recently, Navarro *et al.* (2011) used both food web models and stable isotope analyses to describe in a comparative way the marine food web topology of the Southern Catalan Sea and the results showed several similarities among the two methodologies.

#### Food web effects of multiple stressors

Fewer studies have explored the additional effects of environmental forcing on Mediterranean ecosystem dynamics (Daskalov 2002; Coll *et al.* 2008e, 2009b,c; Piroddi *et al.* 2010) because of the general lack of long time series of biological data in the Mediterranean Sea. Results from available applications showed that Mediterranean ecosystems have gone through important changes in the last decades and that climate change and eutrophication were important drivers of marine resources, in addition to fishing. Models fitted to fishing and environmental data were also used to evidence that declines in the populations of many commercial species and top predators produced proliferation of lower trophic level organisms, such as invertebrates, jellyfish or benthic-pelagic fish because of trophic cascades (e.g. Daskalov 2002; Coll *et al.* 2008e, 2009c; Piroddi *et al.* 2010).

#### Climate change

Recent *EwE* applications dealt with the effects of climatic changes on the marine food web. First, they were studied by applying time series of environmental forcing to influence primary production directly in ecosystem models (e.g. Coll *et al.* 2008e, 2009c). However, more complicated downscaling has been produced recently by linking climatic model outputs to nutrient discharges to coastal areas, eventually used in an extended end-to-end food web model representing also the biogeochemical cycles (Libralato and Solidoro 2009; Libralato *et al.* 2010a). These downscaling approaches allowed inferring the potential changes in the food web of the Adriatic Sea in different scenarios of CO<sub>2</sub> emission, assuming that change in

run-off is the major climatic effect for coastal areas. Results showed substantial differences in the ecosystem dynamics under different scenarios, especially in the first years after changes in climatic conditions. These unexpected differences in the transient phases suggest short-term adaptive fisheries management being necessary to avoid critical situations.

#### Aquaculture, pollution and bioaccumulation

Other applications in western and central areas of the Mediterranean Sea dealt with human impacts such as aquaculture and pollution. Díaz López *et al.* (2008) used trophic models to study the ecosystem effects of aquaculture on the Aranci Bay ecosystem (Sardinia, Italy), and in particular, to estimate the potential effects of finfish aquaculture, to quantify the key role of the species within the ecosystem and to examine potential conflicts with top predators. Trophic flows estimated by *Ecopath* permitted the direct coupling with an ecotoxicological model and provided a representation of the bioaccumulation of organic pollutants in the food web of the Venice Lagoon (Carrer *et al.* 2000). Moreover, food web flows obtained from a model developed for the same ecosystem (Libralato *et al.* 2002) were used to evaluate uncertainty in the parameters of the bioaccumulation model and highlighted critical processes and functional groups (Ciavatta *et al.* 2009).

#### Quantification of ecological traits of Mediterranean ecosystems using *EwE* models

As illustrated above, existing *EwE* models were used to the study several topics that are relevant for the Mediterranean Sea in the EAM context. Moreover, they also contain an important amount of information at the ecosystem level that we used here to calculate structural and functional traits of Mediterranean and Black Sea marine ecosystems and to identify key species of the basin, aiming to further illustrate *EwE* potentialities for an EAM.

#### Ecosystem properties of the Mediterranean Sea

For each of the 39 available models, excluding the model for the Gulf of Tunis as it was the only application of the method in the southern Mediterranean Sea, we calculated a series of ecological indicators: total system throughput (TST,

t km<sup>-2</sup> year<sup>-1</sup>), total biomass (excluding detritus, TB, t km<sup>-2</sup>), total detritus (TD, t km<sup>-2</sup>), the sum of all flows into detritus (SD, km<sup>-2</sup> year<sup>-1</sup>), total primary production (PP, km<sup>-2</sup> year<sup>-1</sup>), the ratio of PP/TST, SD/TST, TB/TD, TB/TST (year<sup>-1</sup>), the System Omnivory Index (SOI), the Finn's Cycling Index (FCI), the total mean transfer efficiency (TE<sub>m</sub>, %), mean transfer efficiencies from primary producers (TE<sub>pp</sub>, %) and from detritus (TE<sub>d</sub>, %), and the mean trophic level of the whole community (mTL<sub>co1</sub>) and of the consumers only (with TL ≥ II, mTL<sub>co2</sub>) (Ulanowicz 1986; Christensen 1995; Pauly and Christensen 1995; Pauly *et al.* 1998; Christensen and Walters 2004; Christensen *et al.* 2005).

We used the non-parametric multivariate permutational analysis of variance (PERMANOVA, in PRIMER with PERMANOVA+ v. 6, PRIMER-E Ltd., Plymouth, UK) on the Euclidean distance matrix to investigate differences of indicators between factors. PERMANOVA calculates a pseudo-F-statistic that is directly analogous to the construction of the traditional F-statistic for multifactorial univariate ANOVA models, but uses permutation procedures (here 9999 permutations) to obtain *P*-values for each term in the model (Anderson *et al.* 2008). The following variables were considered: (i) ecosystem types, including four levels: lagoons, coastal areas, continental shelves and shelves-slopes, (ii) sub-basins with three levels: north-western, north-central and north-eastern, (iii) fishing at two levels: fishing and non- or light fishing, and (iv) years with three time periods: 1960s–1970s, 1980s–1990s and 2000s. Because of the lack of replication, and an unbalanced design among factors, we performed a one-way analysis with each variable using first all the indicators together and then each indicator separately. As the number of functional groups and aggregation used to represent food webs influence model outputs and analyses (e.g. Dunne *et al.* 2002; Pinnegar *et al.* 2004), we included the number of functional groups of each model as a covariate in the PERMANOVA analysis to directly take into account the robustness of indicators to changes in the model design. We used a Type I (or sequential) partition of the sum of squares (SS) because individual SS terms were not independent when including covariates. We developed the multivariate analysis with (39 models) and without the Black Sea (32 models) to evaluate the potential differences of including these unusual ecosystems in the comparison.

For each test, we first assessed skewness and individual correlations between food web properties by constructing a matrix of plots of each property against the others and examining the resulting Spearman rank correlations. Properties skewed to the right (TST, TB, TD, SD, PP, TB/TD, TB/TST, TC, mTL<sub>c</sub>, GE and Lindex) were log(*x*) or log(*x*+1) transformed. We removed one of each pair of properties that were significantly correlated ( $\rho \geq 0.95$ ); thereby reducing redundancy in the data. Because the properties represented different measures (e.g.: %, counts, etc.), they were normalized prior to the construction of the Euclidean distance matrix (Clarke and Gorley 2006).

When comparing all the indicators together, we found global differences between ecosystem types including and not including the Black Sea in the analysis (pseudo-*F* = 4.239, *P* = 0.001, and pseudo-*F* = 6.622, *P* = 0.001, respectively). The pair-wise test evidenced significant differences between all the ecosystem types (*P*-value < 0.05), except between shelves and shelves/slopes that presented similar ecosystem structural and functional traits when the Black Sea was included. We found significant differences between sub-basins (pseudo-*F* = 2.11, *P* = 0.017), but we did not find any difference when the Black Sea was excluded from the analysis. In fact, the pair-wise test provided evidence for significant differences between the north-western and the north-eastern Mediterranean only when the Black Sea data were considered (pseudo-*F* = 1.684, *P* = 0.009). The north-western and north-central Mediterranean and the north-central and north-eastern Mediterranean showed overall similar functional traits. The analysis between the two fishing levels showed significant results between exploited and non- to lightly exploited ecosystems, both including and excluding the Black Sea (pseudo-*F* = 6.023, *P* = 0.0001, and pseudo-*F* = 9.218, *P* = 0.001), giving evidence for the overall effects of fishing on the ecosystem traits of the Mediterranean Sea. Results including year as a factor did not show significant results. In addition, the analysis highlighted a strong and significant effect of the covariate (functional groups) with ecosystem type, basin and fishing factors. Nevertheless, even given the variation of the indicators because of the functional groups of the models, there was still a significant variability detected.

Univariate PERMANOVA of each of the indicators revealed differences on structural and functional

traits between Mediterranean ecosystems classified by using three of the four factors (Table 2). Several indicators showed significant differences between ecosystems types: TB decreased from lagoons to deeper areas significantly (Fig. 4a), as well as TD and TB/TST (Fig. 4b,e). On the contrary, PP/TST (total primary production/TST) and mTLco1 (the mean trophic level of the whole community) increased from lagoons to deeper areas (Fig. 4c,f). TB/TD and mTLco2 (mTL of the consumers, with  $TL \geq II$ ) showed higher values in the coastal areas (Fig. 4d). We also found significant differences between Mediterranean basins, such as an increase in SD/TST (Sum of all flows into detritus/TST) and mTLco1 from the north-western to the eastern side (Fig. 5a,e). We also observed a decrease in SOI (System Omnivory Index) from west to east, and the mTLco2 was lowest in the north-central basin and highest in the north-western (Fig. 5b,f). The efficiency in which the energy is transferred from lower to higher trophic levels was the lowest in the central areas (mainly Adriatic Sea, Fig. 5c,d), providing evidence for the higher production of the Adriatic basin, and the lower primary production of the east, in accordance with observed productivity patterns (Bosc *et al.* 2004). We found as well a decrease in TB from the west to the east (Table 2). These results highlight large differences on the structure and functioning of ecosystems with depth and between basins because of productivity and environmental gradients in the Mediterranean Sea. Exploited ecosystems showed lower TB/TD, while a decreasing marginally significant trend was also observed for TB, mTLco1 and mTLco2 and an increasing trend was observed for the TEpp (mean transfer efficiencies from primary producers) (Table 2). Year as a factor did not have significant effects. Interestingly as well, of the sixteen ecological indicators included in the analysis, six indicators showed a strong and significant effect of the covariate with the ecosystem type and fishing factors, five showed an effect with the basin factor and four showed an effect with the year factor (Table 2). However, there was still a significant variability detected among ecosystem type, basin and fishing. These results were similar when the models of the Black Sea were included, with the exception of mTLco2 and PP/TST, which did not show significant results between ecosystems and ecosystem-type factors, and TD was significantly different between basins (Appendix S2 in online Supporting Information).

### Key species of Mediterranean marine ecosystems

Key species are those with important roles in the food web and include keystone and structuring species (Power *et al.* 1996). Keystone species are defined as relatively low-biomass species with disproportionate high effects on the food web (Power *et al.* 1996; Libralato *et al.* 2006a), which need to be distinguished from structuring functional groups that have high effects because of their biomass (Piraino *et al.*, 2002). Results from *Ecopath* models were used to calculate the absolute overall effect of a species on the food web as the sum of all the direct and indirect effects quantified through the mixed trophic impact analysis (Ulanowicz and Puccia 1990). The absolute overall effect together with the biomass proportion of the functional group was used to identify key species (or groups of species) other than keystone indicator as proposed by Libralato *et al.* (2006a). Appendix S3 (in online Supporting Information) summarizes how keystone species are identified quantitatively using *Ecopath* results.

Results from the keystone indicator showed a high variety of functional groups acting as keystones in the Mediterranean Sea food webs (Table 3). Top predators such as large fishes, marine mammals and seabirds ranked high in several ecosystems, especially in food webs representing open sea areas such as the Adriatic Sea, Catalan Sea, Aegean Sea, Ionian Sea and Black Sea. Seabirds were also keystone species in coastal areas such as the Venice Lagoon and the Bay of Calvi, Corsica.

Interestingly, small pelagic fish played important roles in several models (Table 3), including the ones developed to represent the Black Sea and various open areas of the western, central and eastern Mediterranean, because of their high overall effect despite biomasses being not 'disproportionately low' (Power *et al.* 1996). Plankton and benthic invertebrates were also important in several case-studies, and jellyfish were important groups in all the Black Sea models, in line with time series of data documenting the impact of these organisms in this basin (Daskalov 2002; Gucu 2002; Kideys 2002).

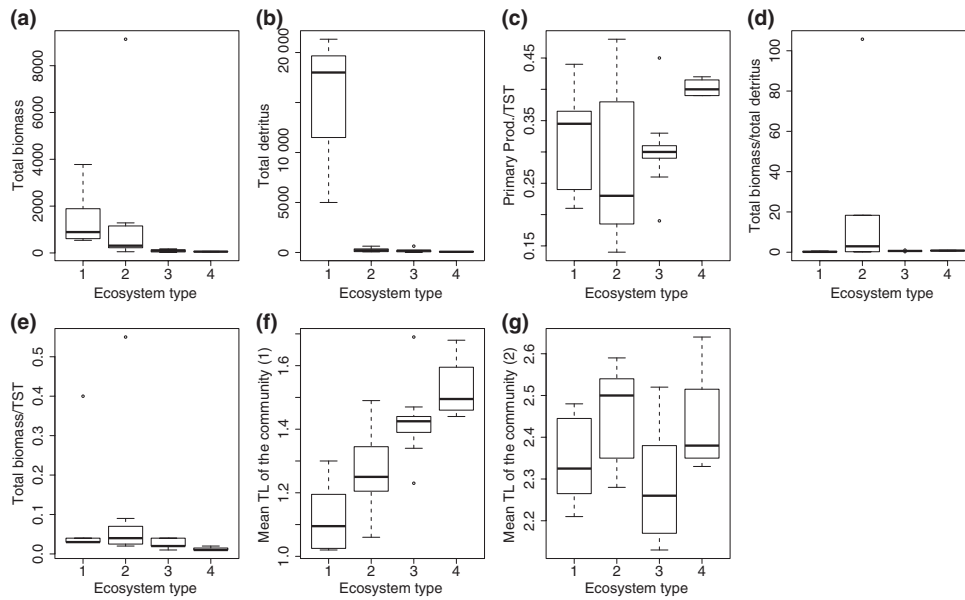
These results also highlighted potential problems in the weighting of biomass proportion in the index proposed by Libralato *et al.* (2006a) which measures the degree to which a species is a keystone species, labelled the 'index of keystone-ness'. The methodology, however, can be made useful by analysing estimates of absolute overall effects and

**Table 2** Ecosystem properties of the Mediterranean Sea ( $n = 32$  models, excluding the Black Sea and the Gulf of Tunis models from Table 1), sd = standard deviation. Results by year are not shown because of they were not significant. Results including Black Sea models are shown in Appendix S2 (in online Supporting Information).

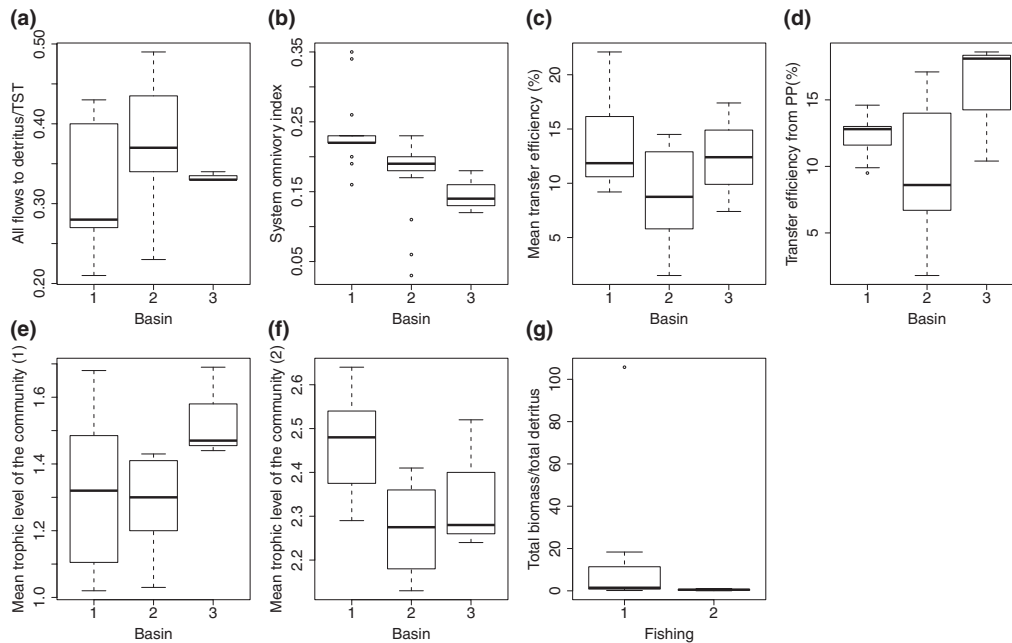
Indicators (mean ± sd)	Ecosystem type												Basin						Level of fishing								
	Lagoon			Coastal			Shelf			Shelf-slope			NW			NC			NE			Non-/low fishing			Fishing		
	Mean	sd	Sig.*	Mean	sd	Sig.*	Mean	sd	Sig.*	Mean	sd	Sig.*	Mean	sd	Sig.*	Mean	sd	Sig.*	Mean	sd	Sig.*	Mean	sd	Sig.*	Mean	sd	Sig.*
TST	39123.4	42215.2	15070.1	16496.1	4066.7	2980.1	3893.3	187.7	0.29	15639.3	16559.4	14858.8	31491.4	2076.4	323.4	0.29	12212.6	15407.0	14555.0	26771.6	0.67	1464.8	2910.1	467.0	966.0	0.08	
TB	1542.0	1361.9	1749.2	3287.6	94.1	49.1	56.6	9.3	<b>0.00</b>	1242.6	2555.0	553.7	1094.7	39.9	6.0	0.13	173.4	105.7	4041.4	7605.1	0.24	173.4	105.7	4041.4	7605.1	0.24	
TD	15582.3	7227.4	262.5	208.8	188.1	180.1	70.0	0.0	<b>0.00</b>	3554.6	6888.7	2881.3	7455.9	57.1	22.2	0.09	173.4	105.7	4041.4	7605.1	0.24	173.4	105.7	4041.4	7605.1	0.24	
SD	15192.6	19343.1	4621.4	4773.9	1385.5	999.2	1602.0	25.5	0.43	4780.6	5229.9	6284.8	14015.5	692.3	112.7	0.38	3847.4	4430.6	5526.5	11634.9	0.60	3847.4	4430.6	5526.5	11634.9	0.60	
PP	34613.7	56524.4	3703.2	3043.1	1146.0	630.6	1567.5	28.9	0.09	3908.6	3349.0	16880.5	42227.2	621.7	74.7	0.49	3103.8	2919.1	12411.2	34653.1	0.38	3103.8	2919.1	12411.2	34653.1	0.38	
PP/TST	0.32	0.08	0.47	0.53	0.3	0.06	0.4	0.01	<b>0.12</b>	0.41	0.41	0.33	0.09	0.3	0.01	0.77	0.44	0.47	0.32	0.08	0.33	0.44	0.47	0.32	0.08	0.33	
SD/TST	0.37	0.09	0.3	0.09	0.35	0.03	0.41	0.02	0.08	0.31	0.08	0.38	0.07	0.33	0	<b>0.04</b>	0.32	0.09	0.36	0.07	0.09	0.32	0.09	0.36	0.07	0.09	
TB/TD	0.26	0.23	20.2	38.3	0.62	0.2	0.81	0.13	<b>0.00</b>	11.05	28.97	0.56	0.35	0.76	0.25	0.18	17.85	36.08	0.49	0.28	<b>0.00</b>	17.85	36.08	0.49	0.28	<b>0.00</b>	
TB/TST	0.08	0.13	0.12	0.18	0.03	0.01	0.01	0	<b>0.04</b>	0.08	0.15	0.06	0.1	0.02	0	0.67	0.11	0.17	0.05	0.08	0.18	0.11	0.17	0.05	0.08	0.18	
SOI	0.2	0.09	0.21	0.08	0.18	0.03	0.21	0.01	0.66	0.24	0.06	0.17	0.06	0.15	0.03	<b>0.02</b>	0.19	0.09	0.2	0.05	0.77	0.19	0.09	0.2	0.05	0.77	
FCI	15.38	10.53	12.61	10.8	16.21	8.19	5.9	0.93	0.39	13.4	10.6	13.18	9.19	17.72	5.79	0.70	12.91	10.67	14.09	8.99	0.84	12.91	10.67	14.09	8.99	0.84	
TEI	9.03	4.24	13.49	6.74	11.22	3.13	11.85	1.22	0.51	13.47	4.01	9.09	4.03	12.4	5	<b>0.05</b>	10.37	5.95	11.64	3.79	0.27	10.37	5.95	11.64	3.79	0.27	
TEpp	9.09	4.78	10.87	4.19	12.66	4.21	12.15	0.86	0.72	12.27	1.55	9.36	4.67	15.7	4.6	<b>0.02</b>	9.72	4.47	11.87	3.96	0.08	9.72	4.47	11.87	3.96	0.08	
TEd	8.34	4.4	13.87	7.77	10.51	3.26	11.78	2.08	0.38	13.32	5.34	8.86	3.99	10.7	6.22	0.11	10.54	7.04	11.05	4.15	0.52	10.54	7.04	11.05	4.15	0.52	
mTLco1	1.12	0.11	1.27	0.14	1.42	0.11	1.53	0.11	<b>0.00</b>	1.31	0.22	1.28	0.14	1.53	0.14	<b>0.05</b>	1.34	0.18	1.31	0.19	0.99	1.34	0.18	1.31	0.19	0.99	
mTLco2	2.35	0.1	2.45	0.12	2.28	0.13	2.43	0.14	<b>0.04</b>	2.46	0.11	2.28	0.09	2.34	0.15	<b>0.00</b>	2.42	0.15	2.33	0.13	0.70	2.42	0.15	2.33	0.13	0.70	

NW, north-western; NC, north-central; NE, north-eastern; FCI, Finn's Cycling Index; SC, south-central; SOI, system omnivory index; TB, total biomass; TD, total detritus; TST, total system throughput. \*PERMANOVA test. In bold =  $P$ -value < 0.05, in bold and italics =  $P$ -value < 0.01, (c) = significant effect of the covariate.





**Figure 4** Boxplot of significant differences of ecosystem traits by ecosystem type. Ecosystem type (a–g): 1 = lagoon, 2 = coastal areas, 3 = continental shelf, 4 = continental shelf and slope. The smallest observation (sample minimum), lower quartile, median, upper quartile, largest observation (sample maximum) and outliers are indicated.



**Figure 5** Boxplot of significant differences of ecosystem traits by basin (a–f), and fishing indicators (g). Basin: 1 = North-Western, 2 = North-Central, 3 = North-Eastern. Fishing: 1 = non/low fishing, 2 = high fishing. The smallest observation (sample minimum), lower quartile, median, upper quartile, largest observation (sample maximum) and outliers are indicated.

biomass proportion. In fact, these estimates might be used to distinguish two kind of key species: (i) keystone that have high overall effect but low

biomass and (ii) structuring functional groups with high overall effects because of their high biomass (Power *et al.* 1996; Piraino *et al.* 2002). The



**Table 3** First four groups ranking the highest in terms of key species by ecosystem model of Table 1. In bold: marine mammals, top predators and birds, underlined: gelatinous organisms, and *underlined and italics*: small pelagic fish. In grey, the ecosystems with light or absent exploitation.

Model No	Model name	FG ranking 1	FG ranking 2	FG ranking 3	FG ranking 4
2	ARAN_06	Zooplankton (TL 2.09) KS = -0.164; td = 85%	<b><i>Tursiops truncatus</i> (TL 3.82)</b> KS = -0.278; td = 95%	<b>Piscivorous fish (TL 3.75)</b> KS = -0.301; td = 97%	<u><i>Zooplanktivorous fish</i> (TL 2.58)</u> KS = -0.313; td = 27%
3	BAY_C	Suspension feeders (TL 2.47) KS = -0.077; td = 10%	Invertebrate feeders 3 (TL 3.55) KS = -0.088; td = 95%	<b>Seabirds (TL 4.27)</b> KS = -0.117; td = 99%	<b>Piscivorous fish (TL 4.29)</b> KS = -0.147; td = 98%
4	BONI_00	<u><i>Epinephelus marginatus</i></u> (TL 4.32) KS = 0.057; td = 70%	Small pelagic feeders (TL 4.57) KS = -0.049; td = 95%	Phytoplankton (TL 1) KS = -0.075; td = 13%	<u><i>Zooplanktivorous fish</i> (TL 3.42)</u> KS = -0.096; td = 92%
5	LAG_THAU	<i>Anguilla anguilla</i> (TL 3.65) KS = -0.09; td = 97%	Benthos (TL 2.3) KS = -0.183; td = 98%	Zooplankton (TL 2.43) KS = -0.305; td = 87%	Young predators (TL 2.99) KS = -0.409; td = 52%
6	MEDES	Zooplankton (TL 2.74) KS = 0.099; td = 36%	Large Decapods (TL 3.44) KS = 0.065; td = 83%	<i>Diplodus puntazzo</i> (TL 3.22) KS = 0.031; td = 96%	Bivalves (TL 2.41) KS = 0.004; td = 36%
7	ORBE_95	Pleustophytes (TL 1) KS = -0.037; td = 60%	Zoobenthos (TL 2.47) KS = -0.1; td = 32%	<i>Forage fish</i> (TL 3.32) KS = -0.297; td = 15%	Phytoplankton (TL 1) KS = -0.369; td = 5%
8	ORBE_96	Zoobenthos (TL 2.47) KS = -0.08; td = 32%	Pleustophytes (TL 1) KS = -0.092; td = 61%	<i>Forage fish</i> (TL 3.32) KS = -0.302; td = 13%	<i>Dicentrarchus labrax</i> (TL 3.79) KS = -0.338; td = 99%
9	PCROS	<b><i>Amberjack &amp; dentex</i> (TL 4.08)</b> KS = 0.28; td = 65%	Cephalopods (TL 3.60) KS = 0.099; td = 76%	<b><i>Epinephelus marginatus</i> large</b> (TL 4.37) KS = 0.056; td = 78%	Shallow seaweeds (TL 1) KS = -0.055; td = 5%
10	CAT_78	<b><i>Sarda sarda</i> (TL 4.06)</b> KS = -0.047; td = 97%	Benthic invertebrates (TL 2.02) KS = -0.061; td = 16%	<i>Mullus</i> spp. (TL 3.16) KS = -0.091; td = 94%	<b><i>Merluccius merluccius</i> adult</b> (TL 4.11) KS = -0.093; td = 69%
11	CAT_03	<b><i>Larus audouinii</i> (TL 2.31)</b> KS = -0.038; td = 100%	<b><i>Sarda sarda</i> (TL 4.04)</b> KS = -0.061; td = 98%	<i>Sardina pilchardus</i> (TL 2.99) KS = -0.078; td = 74%	<i>Mullus</i> spp. (TL 3.22) KS = -0.114; td = 95%
12	CAT_94	<b><i>Larus audouinii</i> (TL 3.22)</b> KS = -0.016; td = 100%	Benthic invertebrates (TL 2.02) KS = -0.073; td = 17%	<b><i>Merluccius merluccius</i> adult</b> (TL 4.1) KS = -0.105; td = 61%	<u><i>Sardina pilchardus</i> (TL 2.97)</u> KS = -0.119; td = 81%
13	CAT_NF	<b>Dolphins (TL 4.52)</b> KS = 0.29; td = 51%	<b><i>Larus audouinii</i> (TL 3.98)</b> KS = 0.099; td = 100%	Benthopelagic cephalopods (TL 3.76) KS = 0.058; td = 68%	<b><i>Merluccius merluccius</i> adult</b> (TL 4.07) KS = 0.041; td = 68%
14	MIRA_1	<i>Sciaena umbra</i> (TL 3.21) KS = -0.021; td = 78%	Polychaetes (TL 2) KS = -0.048; td = 81%	Mesozooplankton (TL 2.05) KS = -0.095; td = 25%	Bivalves (TL 2.21) KS = -0.134; td = 55%
15	MIRA_2	<b>Top predators (TL 4.24)</b> KS = -0.009; td = 99%	Non piscivorous (TL 2.4) KS = -0.011; td = 91%	Benthic invertebrates (TL 2.2) KS = -0.059; td = 4%	<b>Seabirds (TL 3.79)</b> KS = -0.11; td = 37%
16	NADRI_90	Crustacea 1 (TL 2.63) KS = 0.033; td = 67%	Zooplankton (TL 2.25) KS = -0.081; td = 22%	Zooplanktivorous fish (TL 3.25) KS = -0.104; td = 40%	Bacteria (TL 2) KS = -0.125; td = 81%

**Table 3** Continued.

Model No	Model name	FG ranking 1	FG ranking 2	FG ranking 3	FG ranking 4
17	NADRI_S	Phytoplankton (TL 1) KS = -0.136; td = 2%	Macrobenthos omnivorous (TL 2.77) KS = -0.201; td = 98%	Meiobenthos (TL 2.01) KS = -0.25; td = 99%	Macrobenthos predator (TL 2.78) KS = -0.256; td = 82%
18	NADRI_00	Phytoplankton (TL 1) KS = -0.111; td = 5%	Macrobenthos predators (TL 2.78) KS = -0.143; td = 87%	Macrobenthos detritivorous (TL 2.2) KS = -0.23; td = 59%	Macrobenthos omnivorous (TL 2.77) KS = -0.234; td = 98%
19	ADRI_02	Suprabenthos (TL 2.08) KS = 0.014; td = 44%	Micro and mesozooplankton (TL 2.05) KS = -0.021; td = 38%	<b>Dolphins (TL 4.21)</b> <b>KS = -0.032; td = 95%</b>	<u>Engraulis encrasicolus (TL 3.05)</u> <u>KS = -0.052; td = 21%</u>
20	ADRI_75	Suprabenthos (TL 2.11) KS = -0.006; td = 48%	<b>Dolphins (TL 4.27)</b> <b>KS = -0.04; td = 97%</b>	Micro- and mesozooplankton (TL 2.05) KS = -0.058; td = 34%	<u>Engraulis encrasicolus (TL 3.05)</u> <u>KS = -0.145; td = 25%</u>
21	ADRI_90	Suprabenthos (TL 2.11) KS = -0.006; td = 51%	<b>Dolphins (TL 4.31)</b> <b>KS = -0.039; td = 96%</b>	Micro- and mesozooplankton (TL 2.05) KS = -0.052; td = 34%	<u>Engraulis encrasicolus (TL 3.05)</u> <u>KS = -0.121; td = 24%</u>
22	ADRI_NF	<b>Seabirds (TL 4.52)</b> <b>KS = 0.087; td = 63%</b>	<b>Dolphins (TL 4.39)</b> <b>KS = 0.079; td = 90%</b>	<b>Lophius spp. (TL 4.48)</b> <b>KS = -0.049; td = 73%</b>	Micro- and mesozooplankton (TL 2.05) KS = -0.08; td = 36%
23	VEN_8891	Macrobenthos omnivorous mixed-feeders (TL 2.51) KS = 0.124; td = 88%	Macrobenthos omnivorous predators (TL 3.26) KS = 0.004; td = 95%	Zooplankton (TL 2.43) KS = -0.027; td = 41%	<i>Zosterisessor ophiocephalus</i> (TL 3.61) KS = -0.069; td = 95%
24	VEN_C	Macrobenthos omnivorous mixed-feeders (TL 2.46) KS = 0.101; td = 85%	Macrobenthos-herbivorous detritivorous (TL 2) KS = -0.025; td = 100%	Zooplankton (TL 2.34) KS = -0.152; td = 39%	Micro- and meiobenthos (TL 2.01) KS = -0.286; td = 60%
25	VEN_P	Nekton carnivorous nekton feeders (TL 3.86) KS = 0.058; td = 69%	Nekton carnivorous benthic feeders (TL 3.05) KS = -0.035; td = 55%	Nekton carnivorous fish (TL 2.9) KS = -0.095; td = 73%	Macrobenthos omnivorous-filter feeders (TL 2) KS = -0.185; td = 86%
26	VEN_S	<i>Atherina boyeri</i> (TL 3.34) KS = -0.032; td = 71%	Epiphytes (TL 1) KS = -0.082; td = 60%	Macrobenthos omnivorous mixed-feeders (TL 2.41) KS = -0.099; td = 95%	Macrobenthos herbivorous-detritivorous (TL 2) KS = -0.103; td = 99%
27	VEN_ALL	<b>Seabirds (TL 4.32)</b> <b>KS = 0.107; td = 99%</b>	Macrobenthos omnivorous mixed-feeders (TL 2.39) KS = -0.053; td = 84%	<i>Atherina boyeri</i> (TL 3.35) KS = -0.064; td = 68%	Macrobenthos-herbivorous-detritivorous (TL 2) KS = -0.067; td = 100%
28	VEN_98	<b>Seabirds (TL 4.4)</b> <b>KS = 0.129; td = 100%</b>	Macrobenthos mixed-feeders (TL 2.5) KS = 0.108; td = 83%	Macrobenthos herbivorous (TL 2) KS = -0.025; td = 100%	Zooplankton (TL 2.3) KS = -0.106; td = 32%

**Table 3** Continued.

Model No	Model name	FG ranking 1	FG ranking 2	FG ranking 3	FG ranking 4
29	VEN_08	Macrobenthos omnivorous mixed-feeders (TL 2.45) KS = 0.137; td = 86%	<b>Seabirds (TL 4.49)</b> <b>KS = 0.134; td = 100%</b>	Macrobenthos omnivorous predators (TL 3.3) KS = -0.015; td = 62%	Macrobenthos herbivorous-detritivorous (TL 2) KS = -0.025; td = 100%
30	BLACK_S3.2	<u>Small pelagics (TL 3.2)</u> KS = -0.046; td = 75%	<i>Merlangius merlangus</i> (TL 3.77) KS = -0.098; td = 61%	Mesozooplankton (TL 2) KS = -0.107; td = 65%	Phytoplankton (TL 1) KS = -0.192; td = 7%
31	BLACK_S1.1	<u>Aurelia aurita (TL 3.2)</u> KS = -0.008; td = 100%	<b>Dolphins (TL 4.3)</b> <b>KS = -0.05; td = 93%</b>	<u>Planktivorous fish (TL 3.26)</u> KS = -0.135; td = 58%	Large zooplankton (TL 2.13) KS = -0.199; td = 65%
32	BLACK_S1.2	<u>Aurelia aurita (TL 3.2)</u> KS = -0.006; td = 100%	<b>Dolphins (TL 4.3)</b> <b>KS = -0.057; td = 94%</b>	<u>Planktivorous fish (TL 3.26)</u> KS = -0.152; td = 56%	Large zooplankton (TL 2.13) KS = -0.212; td = 63%
33	BLACK_S2.1	Gelatinous organisms (TL 2.5) KS = -0.235; td = 48%	Phytoplankton (TL 1) KS = -0.569; td = 33%	Demersal fish (TL 3.11) KS = -0.577; td = 96%	<i>Small pelagic fish (TL 3)</i> KS = -0.613; td = 38%
34	BLACK_S2.2	Mesozooplankton (TL 2) KS = -0.312; td = 75%	Gelatinous organisms (TL 2.5) KS = -0.381; td = 64%	<i>Small pelagic fish (TL 3)</i> KS = -0.562; td = 86%	Phytoplankton (TL 1) KS = -0.565; td = 32%
35	BLACK_S3.1	<u>Small pelagics (TL 2.87)</u> KS = -0.036; td = 51%	Zooplankton (TL 2.1) KS = -0.236; td = 75%	<u>Aurelia aurita (TL 2.54)</u> KS = -0.306; td = 76%	Phytoplankton (TL 1) KS = -0.353; td = 19%
36	BLACK_S2.3	Mesozooplankton (TL 2) KS = -0.216; td = 65%	Gelatinous organisms (TL 2.5) KS = -0.232; td = 69%	Demersal fish (TL 3.11) KS = -0.414; td = 100%	Phytoplankton (TL 1) KS = -0.752; td = 27%
37	ION_07	<b>Sea birds (TL 3.43)</b> <b>KS = -0.117; td = 100%</b>	Phytoplankton (TL 1) KS = -0.147; td = 5%	Zooplankton (TL 2.11) KS = -0.205; td = 33%	<i>Sardines (TL 2.89)</i> KS = -0.219; td = 20%
38	ION_60	<b>Tursiops truncatus (TL 4.4)</b> <b>KS = -0.07; td = 93%</b>	<b>Seabirds (TL 3.43)</b> <b>KS = -0.131; td = 100%</b>	Phytoplankton (TL 1) KS = -0.176; td = 4%	Zooplankton (TL 2.11) KS = -0.223; td = 36%
39	AEG_03	Mesozooplankton (TL 2.33) KS = 0.068; td = 9%	<b>Seabirds (TL 3.10)</b> <b>KS = 0.041; td = 11%</b>	Suprabenthos (TL 2.22) KS = -0.152; td = 75%	Phytoplankton (TL 1) KS = -0.221; td = 8%

In bold: marine mammals, top predators and birds, underlined: gelatinous organisms, and underlined and italics: small pelagic fish. In grey the ecosystems with light or absent exploitation.

analysis of biomass proportion and overall effect helped distinguishing these key groups in the Mediterranean Sea (Figure 6a; black diamonds, grey squares and open circles are indicating keystone, structuring and non-key species, respectively) that might be difficult to disentangle in terms of keystone index (Figure 6b). Ranking the functional groups of the models that represent Mediterranean marine ecosystems in terms of overall effects (Figure 6c) highlighted that many key groups were keystones having a low proportion of the biomass (black diamonds and bars), whereas benthic producers, such as *Pleustophytes* in Orbetello Lagoon, (Brando *et al.* 2004) and benthic organisms, such as in the Orbetello Lagoon and the Adriatic Sea, (Brando *et al.* 2004; Coll *et al.* 2007) were mainly key structuring species having a high proportion of the biomass (grey squares and bars).

Overall, of the 627 analysed functional groups of the ecosystem models that include fishing, 14 (2%) were identified to be keystone groups following Libralato *et al.* (2006a) and 23 (4%) were structuring functional groups. Interestingly, in the 188 functional groups of non-fished (or slightly fished) ecosystems, 11 (6%) emerged as keystones and 7 (4%) were structuring functional groups. These proportions are in line with those that can obtain from Figure 6c with the first 60 functional groups of the models. Thus, we found a higher proportion of keystone functional groups in non-fished or slightly fished ecosystems in comparison with exploited areas, despite a consistently stable proportion of structuring species. This result is of particular interest and may indicate that fishing negatively affects keystone species and/or that the keystone role is more prominent and distributed among different functional groups in protected environments. This insightful result merits further study to verify its generality.

### Ecosystem impacts of fishing at a basin scale

Many of the *EwE* applications on the Mediterranean Sea were developed to study and quantify the ecosystem impacts of fishing. These studies confirmed that the Mediterranean Sea has been under a high fishing impact (e.g. Libralato *et al.* 2002, 2008; Coll *et al.* 2006a,b, 2007, 2008d, 2009a,c, 2010b; Piroddi *et al.* 2010; Tsagarakis *et al.* 2010).

Taking advantage of the fact that *EwE* models contained standardized information, we also analysed some indicators measuring fishing intensity

and impacts on the ecosystems in relation to the above reported four factors: ecosystem type, basin, fishing level and year. These indicators were as follows: the mean trophic level of the catch (mTLc), the gross efficiency (GE, catch/net p.p.), the primary production required to sustain the catch (PPR%) and the probability of an ecosystem being sustainably fished ( $P_{sust}$ ) (Christensen 1995; Pauly and Christensen 1995; Pauly *et al.* 1998; Christensen and Walters 2004; Christensen *et al.* 2005; Cury *et al.* 2005; Libralato *et al.* 2008). We also included total catch (TC,  $t\ km^{-2}\ year^{-1}$ ) as an indicator of fishing pressure, and we followed the procedure described above to perform the analysis with PERMANOVA, including the total number of functional groups as a covariate.

The analysis testing for differences of factors using all fishing indicators together showed an overall difference between ecosystem types including or not including the Black Sea in the analysis (pseudo- $F = 4.154$ ,  $P = 0.0003$ , pseudo- $F = 4.4003$ , and  $P = 0.001$ , respectively). The pair-wise test evidenced significant differences between coastal areas and continental shelves (pseudo- $F = 2.279$ ,  $P = 0.026$ , and pseudo- $F = 2.297$ ,  $P = 0.032$ ). Significant differences between lagoons and shelves/slope ecosystems, between coastal areas and continental shelves, and between coastal areas and shelves/slopes were shown including the Black Sea (pseudo- $F = 1.928$ ,  $P = 0.024$ , pseudo- $F = 2.789$ ,  $P = 0.001$ , and pseudo- $F = 1.799$ ,  $P = 0.041$ , respectively). When we excluded this area from the analysis, only the difference between coastal areas and continental shelves was still significant (pseudo- $F = 2.789$ ,  $P = 0.0002$ ). The analysis testing for differences of fishing impacts by basins showed overall significant differences between basins only when the Black Sea was included (pseudo- $F = 2.643$ ,  $P = 0.034$ ). The pair-wise tests showed that these differences were observed between the north-central and the north-eastern Mediterranean (pseudo- $F = 1.805$ ,  $P = 0.036$ ). The analysis testing for differences on fishing impacts by exploited or non/lightly exploited ecosystems showed differences both when including and excluding the Black Sea (pseudo- $F = 6.033$ ,  $P = 0.003$ , and pseudo- $F = 10.51$ ,  $P = 0.0001$ , respectively). When the Black Sea was included, we found significant results between year levels (pseudo- $F = 3.119$ ,  $P = 0.014$ ) suggesting that, overall, fishing indicators have changed with time. Results showed again a strong and significant effect of the covariate (functional groups) with ecosystem type,

**Table 4** Ecosystem impacts of fishing ( $n = 32$  models, excluding the Black Sea and the Gulf of Tunis models from Table 1). sd = standard deviation. Results by year are not shown because of they were not significant. Results including Black Sea models are shown in Appendix S4 (in online Supporting Information).

Indicators (mean $\pm$ sd)	Ecosystem type										Basin						Level of fishing					
	Lagoon		Coastal		Shelf		Shelf-slope		NW		NC		NE		Non-/low fishing		Fishing					
	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Mean	sd	Sig.*	
mTLC	2.43	0.9	3.29	0.88	3.06	0.32	3.1	0.03	0.43	3.08	0.61	2.63	0.81	3.25	0.19	0.17	3.72**	0.25	2.78**	0.67	0.14	
GE	0.09	0.17	0.01	0.02	0	0	0	0	0.30	0.01	0.02	0.05	0.14	0	0	0.53	0	0	0.04	0.12	0.26	
PPR%	8.36	5.33	1.81	3.82	10.5	5.58	6.22	4.5	<b>0.02</b>	5.07	4.39	8.33	6.91	10.7	2.53	0.18	1.27	3.24	10.4	4.21	0.00	
Lindex	1.04	2.75	0.01	0.02	0.06	0.03	0.04	0.03	0.76	0.05	0.1	0.59	2.09	0.05	0.03	0.86	0.01	0.02	0.47	1.78	0.41	
Psust	59.8	37.9	88.3	26	49	28.3	64.6	25.4	0.17	67.5	32.5	61.7	33.2	50.4	37.9	0.78	92.2	21.4	48.8	27.2	0.00	
TC	6.95	6.04	5.09	13.4	2.46	2.01	3.62	2.49	<b>0.02</b>	6.34	10.8	1.93	2.35	1.75	0.66	0.58	0.25	0.61	6.55	9.29	0.00	

\*PERMANOVA test. In bold =  $P$ -value  $< 0.05$ , in bold and italics =  $P$ -value  $< 0.01$ , \*\* only includes the cells with fishing (mTLC = 0 excluded), (c) = significant effect of the covariate. PPR, primary production required; NW, north-western, NC: north-central, NE: north-eastern, SC: south-central, TC, total catch.

basin, fishing factors and year. Nevertheless, even given the variation of the indicators because of the functional groups of the models, there was still a significant variability detected.

Univariate PERMANOVA of each of the indicators revealed few differences of Mediterranean sites between ecosystem types regarding fishing indicators (Table 4). Ecosystem types showed different PPR% (Figure 7a), which was the lowest in coastal areas because of inclusion of protected sites and the highest in shelf ecosystems, and TC decreased from lagoons to deeper areas (Figure 7b). These results evidence the high catch of primary producers from some of our models representing lagoon ecosystem with intense algal harvesting, such as Orbetello Lagoon (Brando *et al.* 2004), and coastal areas with aquaculture activities, such as Aranci Bay (Díaz López *et al.* 2008). Differences in fishing indicators between exploited and non- to lightly exploited ecosystems were evident for PPR%, Psust and TC (Figure 7c,d,e), with high PPR% and catch and low sustainability in highly exploited ecosystems. In addition, the mTLC was notably higher in non/ lightly exploited ecosystems ( $mTLC = 3.72 \pm 0.25$ ) in comparison with highly exploited ones ( $mTLC = 2.78 \pm 0.67$ ) (Figure 7f), as has been previously documented by Pauly *et al.* (1998). We did not find significant differences between basins and between years regarding fishing indicators, and fishing indicators were robust to model configurations because the covariate did not influence results significantly (Table 4). Similar results were observed when the models of the Black Sea were included in the analysis, with the exception of mTLC and TC, which showed significant differences between basins (Appendix S4 in online Supporting Information).

### Challenges and future research

There is an important set of modelling applications in the Mediterranean Sea using *EwE* tools. Although applications for the study of the effects of fishing are prominent, they varied notably on the scope and regional coverage and were applied to assess different scientific questions at different scales.

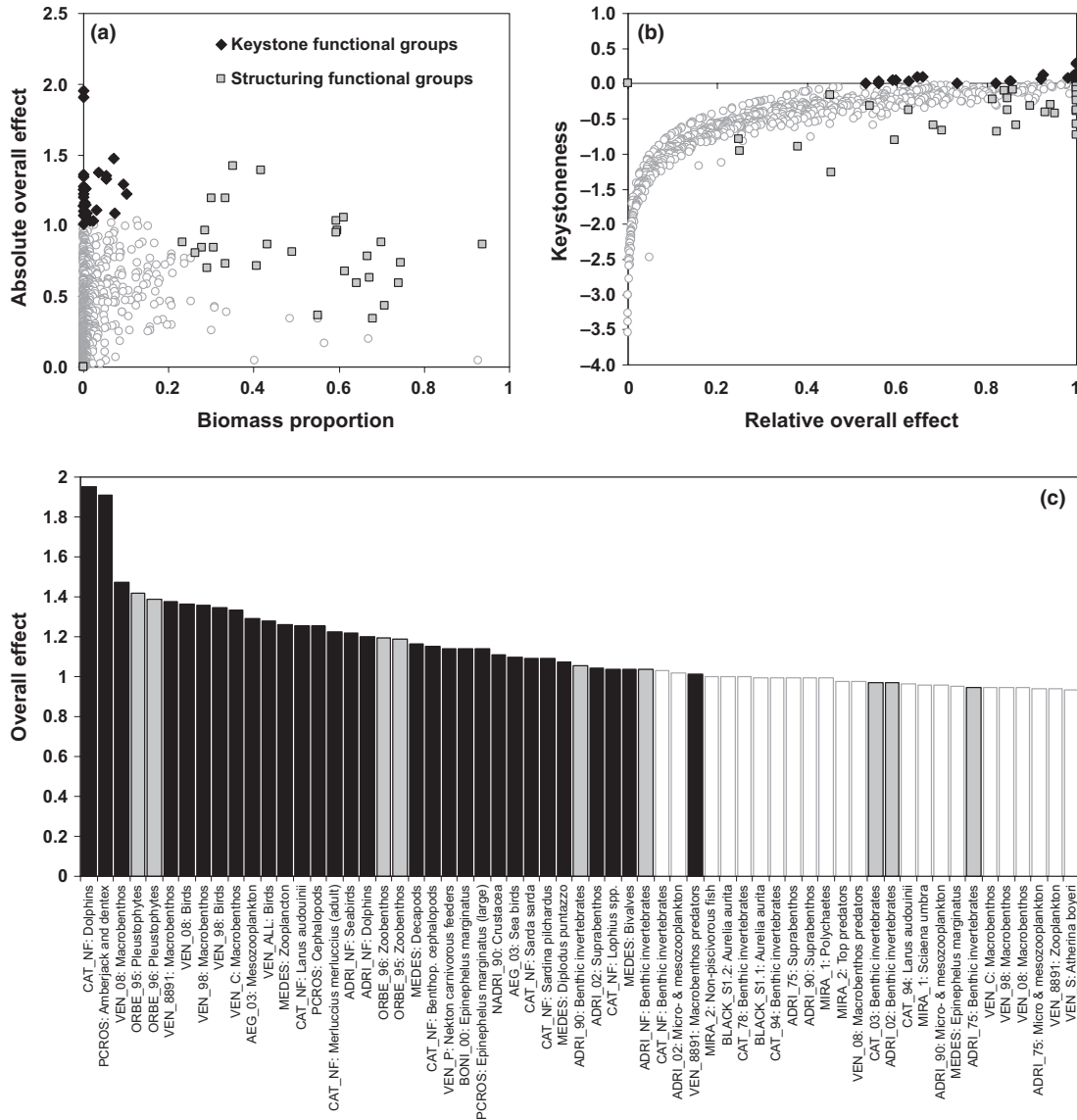
*EwE* applications started in the early 1990s in lagoons and coastal areas to tackle important environmental problems such as the introduction of alien species, eutrophication, pollution and the impacts of fishing and of aquaculture. Afterwards,

applications moved towards deeper areas, mainly to assess the ecosystem impacts of fishing and alternative management options including the establishment of marine protected areas, and taking into account climatic changes. These applications demonstrated the utility of *EwE* models to advance towards an ecosystem-based approach to marine resources (EAM) in the Mediterranean Sea because they covered essential topics and integrate human activities within the ecosystem context, evaluating their impact along the food web and including commercial and non-commercial organisms. This is required not only to evaluate comprehensively the effects of a stressor on ecosystems including indirect effects but also when the effects of different stressors and environmental variability have to be evaluated simultaneously.

Therefore, existing applications of the *EwE* model can provide insights about Mediterranean ecosystems that may be important for management, especially regarding fishing activities (Cochrane and de Young 2008). For example, ecological indicators highlighted that apex predators such as seabirds and cetaceans may be keystone species in the Mediterranean Sea, and thus important population declines of these groups (e.g. Cooper *et al.* 2003; Bearzi *et al.* 2008) may be unsustainable at an ecosystem level. Small pelagic fish were identified as key species at mid-trophic levels, and models illustrated how food web features such as flow control and trophic interactions, fishing activity and environmental factors played significant roles in driving small pelagic fish dynamics over time (Coll *et al.* 2008e, 2009c; Piroddi *et al.* 2010). Therefore, the high exploitation rates on these groups (Palomera *et al.* 2007) can cause important impacts on the structure and functioning of Mediterranean marine ecosystem. In addition, model results regarding fishing showed the important impacts of this activity in all Mediterranean areas. Fishing can cause important changes in the food web traits and may be translated into proliferation of species that are not as commercially valuable as the ones that were depleted or that can have important socioeconomic impacts, such as jellyfish. Existing models can be easily used in the near future to develop applications dedicated to tackle specific conservation issues of ecologically important species and to perform comparisons of subsets of models.

Available *EwE* models also provided an important set of coherently organized information on ecosystems that can be further used to investigate

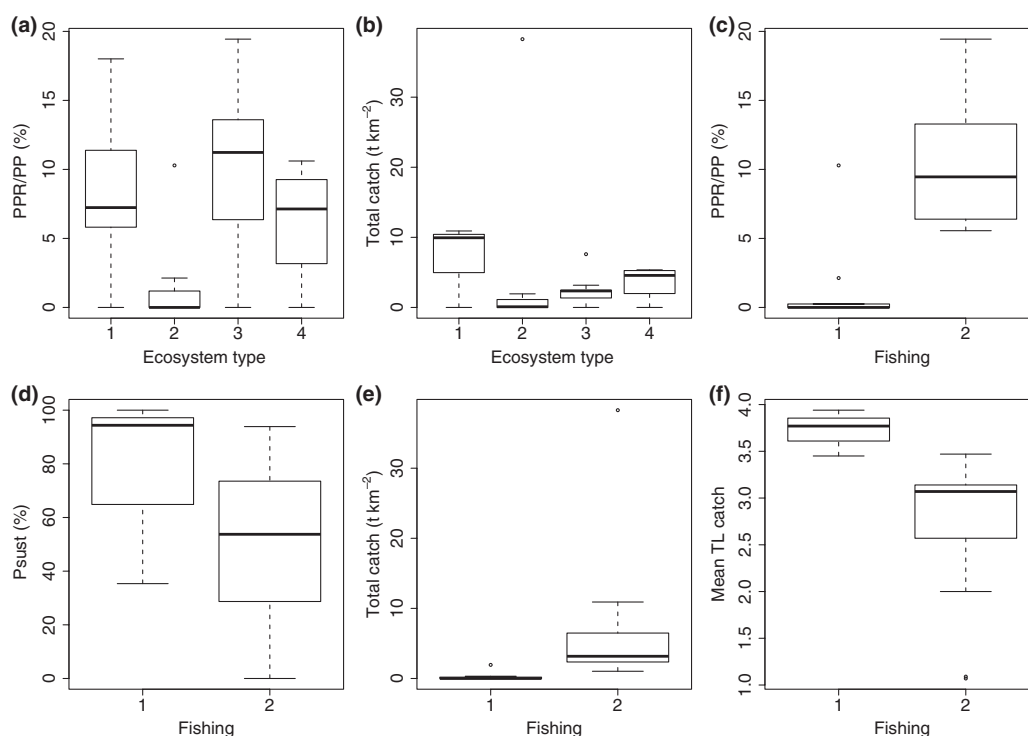




**Figure 6** Functional groups of the Mediterranean models in terms of (a) absolute overall effects versus biomass proportion, and (b) and (c) keystone versus relative overall effect. In (c) the first 60 groups ranking high in terms of overall effect are represented (Note that some models might have more than one FG and some models have none). Clearly identified keystones (with high overall effect and low biomass) are in black diamonds and bars, structuring species (with high overall effect due to high biomass) are in grey squares and bars.

ecosystem properties of the Mediterranean Sea. We illustrated how this information may be useful to generate further knowledge. For example, we found notable differences in ecosystem structure and functioning between ecosystem types, and some ecological differences were observed between western and eastern basins. These results are important in the EAM context because different ecosystems may respond differently to management

initiatives and regulations. Moreover, ecosystem traits were different overall between non- or slightly exploited and highly exploited ecosystems demonstrating the ecosystem effects of protection, although we did not find significant differences with time, which may be a response to the important changes that have taken place in Mediterranean ecosystems before the 1960s (e.g. Lotze *et al.* 2011).



**Figure 7** Boxplot of significant differences of fishing indicators by ecosystem type (a–b) and fishing (c–f). Ecosystem type: 1 = lagoon, 2 = coastal areas, 3 = continental shelf, 4 = continental shelf and slope; Fishing: 1 = non/low fishing, 2 = high fishing. The smallest observation (sample minimum), lower quartile, median, upper quartile, largest observation (sample maximum) and outliers are indicated.

Our results also showed the existence of important limitations of Mediterranean *EwE* applications. One of these limitations is related to the fact that fewer ecosystem studies have been developed to represent non-exploited marine ecosystems. Thus, studies in non-fished ecosystem are needed to provide a reference point for how Mediterranean marine ecosystems are structured and how they function in the absence of fishing or when other human impacts are low. *EwE* applications are almost absent from the southern and the most eastern sites of the Mediterranean. Future research will benefit from the wider application of the *EwE* methodology in the Mediterranean basin with new case-studies and will make it possible to extend our comparisons in fruitful meta-analyses, as was carried out, for example, with existing worldwide models using a new measure of ecosystem effects of fishing (Tudela *et al.* 2005; Coll *et al.* 2008c; Libralato *et al.* 2008). The addition of more models to describe traits of the Mediterranean Sea will allow the reinforcement of such analyses and to set new

references for the basin itself, while accounting for its peculiarities.

Given that even 'relatively imprecise models, coupled with a thoughtful exploration of uncertainty, can advise and inform policy decisions' (Essington 2007), the assessment of uncertainty of model inputs and propagation of errors is of overwhelming importance and should be included in future ecosystem modelling exercises and applications as has been already carried out in few applications (e.g. Coll *et al.* 2008a; Ciavatta *et al.* 2009). Although the constrains because of data availability is a recognized issue, fitting models to time series of data for their validation should be considered as a priority in the future. Moreover, to move towards more realistic representation of marine ecosystems and given the general importance of spatial management (e.g. MPA), the application of spatio-temporal dynamics for capturing spatial ecosystem features and patterns should be pursued. The link of *EwE* with biogeochemical and hydrodynamic models will allow accounting for possible synergistic effects of impacts, including

climate change and nutrient inputs. First attempts to couple biogeochemical and *EwE* models have shown promising potential to link low and high trophic levels in an end-to-end description of ecosystems (Libralato and Solidoro 2009; Libralato *et al.* 2010a). The challenges and drawbacks of this linkage, however, have not yet been revealed in all their detail, and thus future progress, applications and insights are expected in this field.

We conclude that *EwE* models have been widely applied in the Mediterranean Sea to analyse relevant issues under the context of an EAM approach, were used to illustrate results of management options and can be useful to derive further knowledge at the ecosystem level. Despite this, modelling tools are not yet being used for real management of marine resources in the Mediterranean Sea. It is hoped that the growing interest and attention in developing ecosystem models, and the accumulation of ecosystem-based knowledge that has occurred over the past decades, will be translated into useful applications of models towards a real implementation of an ecosystem-based management of Mediterranean marine resources in the future.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Ecopath, Ecosim and Ecospace modelling tool – A brief summary.

**Appendix S2.** Ecosystem properties of the Mediterranean Sea (n = 39 models, excluding the Gulf of Tunis from Table 1).

**Appendix S3.** Identification of Keystone species.

**Appendix S4.** Ecosystem impacts of fishing (n = 39 models, excluding the Gulf of Tunis from Table 1).

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